

CLIMATE CHANGE EFFECTS ON ERUPTIVE FOREST
INSECTS: A REVIEW AND SYNTHESIS OF EMPIRICAL
EVIDENCE

FRST 498

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ABSTRACT

Global climate change is affecting ecosystems through warming temperatures, changing precipitation, and increasing climatic variability. One of the major impacts is the alteration of forest disturbance regimes, including forest insect outbreaks that cause landscape-scale tree mortality and significantly affect the composition, function, and socioeconomic value of forests. Many studies have been conducted and models created to predict how future climate change may affect forest insects, but it may also be useful to determine how insects have already responded in order to detect where knowledge may be lacking and which species may be of most concern in future forest management. For this thesis, research papers providing empirical evidence to show a definitive climate change effect on an eruptive forest insect were identified and reviewed. The selected papers were then synthesized into a predictive framework for the likely responses of specific forest insect groups or species to changes in temperature or precipitation. Bark beetles and defoliators were the two functional groups for which evidence was found. All evidence pointed to bark beetle species responding positively to warming temperatures and decreasing precipitation through range expansion and increases in outbreak extent and severity. Evidence was less straightforward for defoliators, as some species, but not all, showed a negative response to warmer temperatures due to increasing asynchrony between insect emergence and host tree budburst on which they depend for food and survival.

KEYWORDS

Bark beetles, climate change, defoliators, forest insect disturbance, forest management

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INTRODUCTION

Over the past century and a half, the world has experienced climate change through a significant warming trend and an increase in climatic variability (IPCC 2007, Peterson and Baringer 2009). Record high temperatures have been occurring since the 1970s (IPCC 2007), especially at the higher latitudes in the northern hemisphere, such as the Arctic and boreal regions (IPCC 2007, Soja *et al.* 2007). Climate change has also been connected to rising seas levels (Church and White 2006, IPCC 2007), rapidly melting glaciers and ice caps (IPCC 2007, Kwok and Rothrock 2009), and more frequent extreme weather events (IPCC 2007). There has been an increase in heavy precipitation events, the frequency of heat waves and hot days and nights, and intense tropical cyclone activity in some regions. It is expected that in the 21st century there will be an increase in the mean annual global temperature of between 1.8°C to 4.0°C (IPCC 2007). Temperatures and temperature and precipitation extremes will continue to rise in the future, especially in Northern Eurasia, Alaska, and Canada (Soja *et al.* 2007, Safranyik *et al.* 2010). Summer warming in Northern Eurasia is predicted to be greater by almost half of the global mean, and boreal regions of Europe and Canada will also experience summer warming estimated to exceed the global mean (Soja *et al.* 2007). Most evidence points to human-induced reasons for climate change, as human activities have caused increased emissions of greenhouse gases into the atmosphere from factory waste, vehicles, deforestation, agriculture and other sources, and concentrations of these greenhouse gases have significantly increased globally since the late 1700s (Hegerl *et al.* 1996, Santer *et al.* 1996, Santer *et al.* 2003, IPCC 2007).

Climate change is a concern for forest management because shifts in temperature, precipitation, and atmospheric greenhouse gas concentrations are likely to have significant effects on trees and forest ecosystems (Bentz *et al.* 2010). By the end of the century, climate profiles that are completely different from current coniferous vegetation are predicted to affect much of the landscape. Furthermore, natural forest disturbances are predicted to be greatly impacted by climate change. Natural forest disturbances include pathogens, such as fungal root rot, rusts, dwarf mistletoe, and white pine blister (Ayres and Lombardero 2000); insect disturbances, like spruce budworm (*Choristoneura fumiferana* [Clemens]) and spruce beetle (*Dendroctonus rufipennis* Kirby) infestations that have had great impacts in boreal forests; overabundances of browsing herbivores, such as deer, moose, elk, and hares; and abiotic disturbances, such as fire,

drought, windstorms, ice storms, and landslides (Dale *et al.* 2001). Climate change impacts forests by creating changes in local, regional, and global temperature and precipitation that affect the occurrence, frequency, duration, extent, and intensity of disturbances (IPCC 2007, Dale *et al.* 2001). In other words, forest disturbance regimes may be completely altered. For example, there have been recent increases in fires, droughts, insect and pathogen outbreaks, introduced species, and extreme weather events, all of which can be linked to climate change (IPCC 2007, Dale *et al.* 2001, Wotton *et al.* 2010, Soja *et al.* 2007). The effects of these changes often have great impacts on forest ecosystems, and even alter them in unexpected and often undesirable ways (Dale *et al.* 2001). The social and economic effects that arise from these changes make it crucial to carefully manage forests with future climate change impacts in mind (Ayres and Lombardero 2000, Dale *et al.* 2001), especially as losses of valuable forests to large-scale disturbances can equal millions of dollars lost (Dale *et al.* 2001).

The most costly of forest disturbances are insects and pathogens, to which over \$2 billion and 20.4 million hectares of trees are lost in the U.S. every year (Dale *et al.* 2001). Insect herbivores, those that eat plant tissues, are a natural and important part of forests, but can significantly affect forest composition, ecosystem function, and socioeconomic value in ways that humans consider negative (Ayres and Lombardero 2000). Every major forest type has experienced strong impacts by insect disturbances; for example, bark beetles in the family Curculionidae (sub family: *Scolytinae*) have created some of the largest natural disturbances in pine forests (Ayres and Lombardero 2000). Loss of trees to forest insect disturbances not only creates economic losses, but also can result in negative impacts on other animal, plant, or insect species that live in forests (Ayres and Lombardero 2000, Conner *et al.* 1998), such as by removing important habitat like mature trees that cavity nesting birds rely on, or fragmenting forest stands by killing large groups of trees, thereby reducing the ability of certain animal populations to disperse (Ayres and Lombardero 2000). Landscape-scale tree mortality from insect herbivores also releases large amounts of carbon to the atmosphere, which can exacerbate climate change (Kurz *et al.* 2008).

Climate change appears to have been strongly and directly affecting insect herbivores, and warming conditions will likely increase insect outbreaks in the future (Ayres and Lombardero 2000, Soja *et al.* 2007, Bentz *et al.* 2010). The rate of development and reproductive potential of many insects will likely be increased by summer temperatures in temperate and boreal forests

(Ayres and Lombardero 2000, Soja *et al.* 2007), while warmer winter temperatures may reduce winter mortality of insects that are susceptible to cold weather, such as the southern pine beetle that experiences nearly 100% mortality when air temperatures fall below -16°C (Ayres and Lombardero 2000). Climate change may also indirectly affect insect herbivores; for example, excessive heat or drought create stress on trees and lower their defences, making them less resistant to insect attacks (Ayres 1993, Croise and Lieutier 1993). It has only been recently, however, that a connection has been established between insect infestations and changes in temperature in regions such as Alaska, where correlations have been shown between insect outbreaks, tree ring evidence and recorded air temperature (Soja *et al.* 2007). While experts generally agree that there has been increased forest mortality as a result of insect outbreaks responding to climate change, there is still a lack in complete documentation for some insect disturbance responses to warming temperatures (Soja *et al.* 2007). This makes it more difficult to predict how insects will respond with further climate change in the future, which is essential for effective management of forests that will inevitably face such disturbances.

OBJECTIVE

Many models have been created to attempt to project how insect herbivores might respond to future climate change (e.g., Robinet *et al.* 2007, Jonsson *et al.* 2009, Safranyik *et al.* 2010). A combination of climate models and quantitative models based on a mechanistic understanding of biological responses to temperature can give results to provide insight into ecosystem responses to climate change (Bentz *et al.* 2010, Seidl *et al.* 2011). While models may be useful for creating predictions that can be utilized by forest managers to help mitigate future disturbances, many uncertainties arise when using them, including uncertainties associated with climate model data choices (Jonsson *et al.* 2009, IPCC 2007), and the ability of the model to make good predictions more than a year or two in advance. For example, a model that was created to predict mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, when tested against past outbreaks, showed an 80% predictive capacity for one year, but its capacity to make a 2-year and 3-year forecast was reduced to 69% and 30% respectively (Aukema *et al.* 2008). It may be beneficial, therefore, to use current evidence of insect herbivore responses to establish a real and practical indication of how warming temperatures and changing climatic variability have affected insect disturbances. If patterns are found in their recent responses, then perhaps they may be applied to predictions of future insect disturbances.

The objective of this paper is to conduct a literature review that presents empirical evidence in scientific literature of climate change impacts on forest disturbances caused by outbreaking insect herbivores, as well as to synthesize the evidence into a possible framework for predicting the general trend of disturbances by certain insect groups or species in the future.

METHODS

To create a predictive framework, peer-reviewed scientific papers were selected based on their claimed strength of empirical evidence for climate change impacts on forest insect populations.

A general search was conducted first for papers that were focused on potentially eruptive insect species found in forest ecosystems and reliant on trees for food and reproduction, such as bark beetles, that have displayed some relatively recent change in life history characteristics, range, or outbreak dynamics. The search was constrained to select for evidence of definite change in approximately the last century, and to exclude studies that focused on making predictions for the future state, such as through the use of models. Next, the results were narrowed further by selecting for only those that linked the change in a forest insect to some impact of climate change. Studies providing evidence that an insect species population had responded positively or negatively to climate change effects, such as increased temperatures or variations in precipitation, were chosen as good candidate papers for the final selection. For a paper to be selected for the synthesis, it had to be accepted as definitively showing a climate change effect on an eruptive forest insect, which it only did if it met the following criteria: (1) empirical evidence was provided for a change in the insect outbreak frequency, intensity and/or range; (2) there was explicit evidence given that an effect of climate change had occurred at the same time, such as measurable increases or decreases in temperature, precipitation, or extreme weather events; (3) a strong link was made between the climate change effect and the response of the insect. Papers were excluded if they showed evidence for the response of a forest insect to a certain climatic variable, such as temperature or precipitation, but did not state or provide adequate support for the connection to recent climate change altering both the climatic variable and the insect response in a certain region.

Data on the forest insect species that responded to climate change impacts were extracted from the final selection of papers, including which functional group the species belonged to (e.g., bark

beetles), the host tree species and geographic location of the species in each study, the study methods used, the climate change effects on insect herbivory response (i.e., positive or negative), the mechanism of the effects, and how the responses were linked to climate change. To synthesize the data into a useful predictive framework, reoccurring patterns were looked for in the data. Within each functional group of insects, similarities in herbivory responses to climate change effects were noted; for example, the species that responded positively and the ones that showed a negative response were identified. The mechanisms of the climate change effects on the responses, such as range expansion or altered outbreak dynamics, were also compared, along with the specific effects that the responses were linked to (e.g., warmer winters and/or summers, or reduced precipitation). Different functional groups were then compared and contrasted for the climate change effects on the responses of forest insect species. Based on the analysis of similarities and differences in the responses within and between insect functional groups, a possible framework was created to attempt to predict how similar insect species within each group may respond to climate change in the future.

RESULTS AND DISCUSSION

In total, twelve papers were found to provide adequate evidence for climate change impacts on six outbreak forest insect species (Table 1). All studies linked changes in temperature and/or precipitation to positive or negative changes in the species' range expansion or frequency and intensity of outbreaks. Only two major functional groups of insects were addressed in the studies – bark beetles and defoliators. Bark beetles were found to respond positively to warmer summers and winters, increased average temperatures, and/or decreased precipitation. One species, the mountain pine beetle, expanded its range as a result of warming temperatures outside the limits of its range that allowed it to successfully attack hosts and reproduce in regions that were historically unsuitable for it. Another bark beetle, the spruce beetle, erupted in areas that previously had no records of outbreaks, as well as increased spatio-temporal synchrony of outbreaks. This was mainly due to increased temperatures and shorter extreme cold periods causing changes in the population dynamics. On the other hand, while defoliators were shown to generally respond positively for similar reasons as bark beetles, some studies produced conflicting results that indicated that the effects of climate change may have partially or wholly negative impacts on certain defoliators, such as the winter moth (*Operophtera brumata* Bkh.)

Table 1: Summary of studies that give empirical evidence for climate change effects on eruptive forest insects

Insect characteristics			Study					
Insect functional group	Insect species	Host species	Location	Methods	Climate change effects on herbivory	Mechanism of the effect	Link to climate change	Reference
Bark Beetles	Mountain pine beetle	Pines; primarily lodgepole pine	British Columbia	Climatic suitability model	Positive	Range expansion: • increased climatic suitability	• Warmer winters and summers	Carroll <i>et al.</i> (2004)
		Whitebark pine	Idaho, USA	Process-based model	Positive	Altitudinal range expansion: • increased climatic suitability	• Warmer average temperature than historically	Logan and Powell (2001)
	Spruce beetle	Spruce	• Alaska • Yukon	Field measurements (dendrochronology), simulation modelling	Positive	Outbreaks in new areas of range: • altered population dynamics • increased rates of reproduction	• Warmer summers (for 5-6 year periods) • Shorter and fewer extreme cold periods in winter	Berg <i>et al.</i> (2006)
		Spruce	Alaska	Field measurements (dendrochronology)	Positive	Increased spatio-temporal synchrony of outbreaks: • altered population dynamics • earlier emergence and dispersal	• Decreased winter precipitation • Warmer winter and summer temperatures	Sherriff <i>et al.</i> (2011)
Defoliators	Winter moth	Birch	Norway	Quantile regression modelling; spatial mapping	Positive	Expansion of core outbreak area: • increased climatic suitability	• Warmer mean annual and minimum winter temperatures	Jepsen <i>et al.</i> (2008)

Insect characteristics			Study					
Insect functional group	Insect species	Host species	Location	Methods	Climate change effects on herbivory	Mechanism of the effect	Link to climate change	Reference
		Oak	Netherlands	Modelling of egg hatch timing; field measurements of oak budburst	Negative	Asynchrony of larvae emergence and host budburst: <ul style="list-style-type: none"> • disrupted relationship • maladaptive behaviour 	<ul style="list-style-type: none"> • Increased mean daily warmth with no change in number of frost days from 1 Dec – 1 Mar 	Visser and Holleman (2001)
	Pine processionary moth	Pine	Spain	Field measurements	Positive	Increased defoliation: <ul style="list-style-type: none"> • increased larval survival in winter 	<ul style="list-style-type: none"> • Warmer winter temperatures 	Hodar and Zamora (2004)
		Pine (<i>Pinus sylvestris</i> and <i>Pinus nigra</i>)	<ul style="list-style-type: none"> • France • Italy 	Field measurements	Positive	Range expansion: <ul style="list-style-type: none"> • increased climatic suitability 	<ul style="list-style-type: none"> • Warmer average winter temperatures 	Battisti <i>et al.</i> (2005)
		Pine (<i>Pinus nigra</i>)	Italy	Field measurements, lab experiment	Positive	Altitudinal range expansion: <ul style="list-style-type: none"> • increased climatic suitability 	<ul style="list-style-type: none"> • Warmer average winter temperatures, temperature variability 	Hoch <i>et al.</i> (2009)
	Larch budmoth	Subalpine larch	Switzerland	Field measurements (dendrochronology)	Negative	Outbreak absence: <ul style="list-style-type: none"> • altered population dynamics • increased egg and larval mortality • asynchrony of emergence with host budburst 	<ul style="list-style-type: none"> • Extreme regional warmth outside of historical climatic envelope • Warmer winters 	Esper <i>et al.</i> (2007)

Insect characteristics			Study					
Insect functional group	Insect species	Host species	Location	Methods	Climate change effects on herbivory	Mechanism of the effect	Link to climate change	Reference
		Subalpine larch	Switzerland	Lab experiment	Negative	Outbreak absence: <ul style="list-style-type: none"> • altered population dynamics • increased egg and larval mortality • asynchrony of emergence with host budburst 	<ul style="list-style-type: none"> • Warmer spring temperatures than average for 3 consecutive years 	Baltensweiler (1993)
	Birch budmoth	Birch (<i>Betula pubescens</i> L.)	Norway	Calculations of monthly air temperature averages, statistical analysis: ANOVA, Tukey's HSD	Positive	New outbreak: <ul style="list-style-type: none"> • altered population dynamics • increased larval survival 	<ul style="list-style-type: none"> • Warmer winter temperatures and shorter extreme cold periods 	Tenow <i>et al.</i> (1999)

and larch budmoth (*Zeiraphera diniana* Gn.). It was shown that asynchrony between larvae emergence and host budburst may be occurring because of the insect and trees responding differently to warmer winter and spring temperatures, which leads the larvae that depend on new foliage for food to starve or attempt to disperse in search of a new host. These findings and the strengths and weaknesses of the evidence that each study provided is discussed in the following review of the literature, after which is an attempt to synthesize the results into a framework for predicting forest insect response to climate change.

BARK BEETLES

The range and outbreak area of the mountain pine beetle has expanded from central BC in the 1990's to more northern and eastern localities and higher elevations post-2000, including into regions of the province of Alberta (Bentz *et al.* 2010, Safranyik *et al.* 2010). Several observations and models in the past have attempted to predict the large-scale outbreaks of mountain pine beetle in naïve areas in relation to climate change effects (e.g., Aukema *et al.* 2008, Bentz *et al.* 2010, Safranyik *et al.* 2010); however, Logan and Powell (2001) and Carroll *et al.* (2004) were the first studies to provide direct evidence for the changes that have occurred due to climate change. They demonstrated that the mountain pine beetle has been able to move into and maintain self-sustaining populations at higher latitudes and elevations that previously did not have the right climatic conditions for it to survive or successfully outbreak. Carroll *et al.* (2004) used a model of climatic suitability that incorporated the direct and indirect effects of temperature and precipitation on habitat suitability to mountain pine beetle. They used that model, along with Environment Canada weather data, to produce maps of the distribution of the climatically suitable habitats in the past. Then they compared the distribution of infestations through time to the distribution of climatically suitable habitats in the past to show that mountain pine beetle populations had moved at an increasing rate over time into the areas that were historically unsuitable. There has been an apparent shift in climatically suitable habitats over the past three decades, which beetle populations have followed: prior to 1968, there were no infestations in areas with historically very low to low climatic suitability, but the increasing number of infestations at an increasing rate in those higher latitude/elevation areas points to a sufficient change in the climatic conditions that has allowed mountain pine beetles to now establish and persist. Similarly, Logan and Powell (2001) showed that the beetle has been able to

persist in pine stands at higher elevations than it could historically due to a change in climatic suitability. A process-based model was used to demonstrate that a previous outbreak during the 1930's in high elevation whitebark pines in the White Cloud Mountains of central Idaho was caused by beetles that were able to maintain a self-sustaining population as a result of the higher than normal temperatures.

The evidence presented by Carroll *et al.* (2004) and Logan and Powell (2001) for mountain pine beetle range expansion in response to climate change is strongly supported by the facts that only climate could have limited the boundaries of their range in the past (Carroll *et al.* 2004, Safranyik and Carroll 2006, Safranyik *et al.* 2010), and temperature has the biggest effect on the ability of mountain pine beetles to successfully establish, persist, and reach outbreaking populations (Safranyik and Carroll 2006, Raffa *et al.* 2008, Bentz *et al.* 2010). Lodgepole pine, ponderosa pine, and western white pine, the beetle's preferred hosts (Safranyik and Carroll 2006), grow throughout BC, and therefore could not have contributed to restricting the mountain pine beetle range within central BC in the early 1900s. Furthermore, the mountain pine beetle has been shown to successfully attack and reproduce in other species of pine, including whitebark pine that grows at high elevations in BC (Logan and Powell 2001), and jack pine, a species that is abundant in Alberta and other provinces outside BC (Safranyik *et al.* 2010). Thus, the beetle has plenty of acceptable hosts not only in BC, but throughout the country, and yet its occurrence had never been recorded in those areas at higher latitudes and elevations or east of the Rocky Mountains until the habitats warmed due to climate change in the recent time period (Logan and Powell 2001, Carroll *et al.* 2004, Safranyik *et al.* 2010).

In terms of climatic suitability of an environment, temperature plays a crucial role in the survival of the mountain pine beetle (Safranyik and Carroll 2006, Raffa *et al.* 2008). The overwintering larvae may not survive extremely cold temperatures, and the lethal temperature of -40°C will cause 100% mortality (Safranyik and Carroll 2006). Regions at higher latitudes and altitudes in BC were often free of beetle infestation because the lethal temperature was frequently met in winter, but climate change has led to warmer winters in which the beetle is better able to survive and emerge synchronously the following spring (Logan and Powell 2001, Carroll *et al.* 2004, Aukema *et al.* 2008). Increased temperatures also increase the developmental time of the mountain pine beetle so that it may complete its lifecycle in one year rather than two (Logan and

Powell 2001). Logan and Powell (2001) demonstrated that a semivoltine population can shift into a synchronous univoltine population with only about a 2°C increase in the average annual temperature. This shift allows the population to increase in size at a faster rate and attack larger, healthier trees with better success (Logan and Powell 2001, Safranyik and Carroll 2006), both of which allow for exceeding the threshold from endemic to epidemic, self-amplifying populations (Raffa *et al.* 2008, Boone *et al.* 2011). Finally, temperature indirectly influences the success of attacks on the host by affecting the resistance of trees (Raffa *et al.* 2008, Bentz *et al.* 2010). Trees under attack by bark beetles will generally defend with a combination of constitutive and inducible resins; however, high temperatures (as well as drought conditions) can stress and weaken trees to the point where they lack the resources to produce resin defences. Warmer temperatures may also aid blue-stain fungus carried by the mountain pine beetle in germinating and growing more quickly within the tree, where it desiccates the phloem and xylem, disrupting transpiration and bringing resin production by the tree to a halt (Safranyik and Carroll 2006). Climate change has led to warmer summer and winter temperatures at higher latitudes and elevations, directly aiding the survival of mountain pine beetle and indirectly increasing its ability to attack its hosts in previously uninfested habitats, and has resulted in the range expansion of the beetle.

The spruce beetle is the second bark beetle species which has evidence for responding to climate change. Berg *et al.* (2006) demonstrated that, because of increasing climatic suitability, new outbreaks have occurred in areas that previously did not experience them. Historically, periodic outbreak occurred in maritime regions of Alaska when forests matured and disturbances such as windthrow or fire favoured beetle reproduction (Berg *et al.* 2006); however, more recent outbreaks have occurred in interior regions where they were previously rare, without any clearly identifiable disturbance, and possibly outside the normal historical range of outbreak sizes. Berg *et al.* (2006) found that there were large, outbreaks of spruce beetle in the 1990s within Kluane National Park, Yukon, an interior region without previous records of outbreaks, that were likely initiated and sustained by 5-6 year periods of abnormally warm summer temperatures. Recent winters in the interior, although not significantly warmer, have also experienced shorter and fewer periods of extreme cold which has increased the survivability of the overwintering larvae. Sherriff *et al.* (2011) provided further evidence for an increase in spatio-temporal synchrony of outbreaks within the historic geographic range in Alaska due to warmer winters and summers,

and a decrease in winter precipitation, which has led to stressed trees that cannot defend well against attacks. It is suggested that outbreaks are increasingly having similar timings across not only Alaska, but in the Southern Rocky Mountains and Central BC as well, likely as a result of climate change creating similar patterns of synchrony in environmental variables such as temperature across many regions (Sherriff *et al.* 2011).

The results shown in the two studies can be explained in part by the way in which the life histories of the spruce beetle are tightly controlled by summer temperatures (Berg *et al.* 2006, Raffa *et al.* 2008, Sherriff *et al.* 2011). Warmer summer temperatures brought on by climate change increases the rate at which the beetle develops, allowing for earlier adult emergence, dispersal, attack, and breeding (Werner and Holsten 1985, Berg *et al.* 2006, Sherriff *et al.* 2011). This results in eggs being laid earlier and provides larvae with a longer growing season. Warmer air temperatures also increase the temperature of the tree phloem, which can lead larvae to develop in only one year instead of two, changing it to a univoltine life-cycle that promotes larger population sizes and outbreaks. Finally, larval development and subsequent adult emergence may be synchronized by higher temperatures, which allows for more successful mass attacks on trees. Historically, spruce beetles were limited to outbreaking in maritime regions because of the climate, but as the interior climate has warmed, summer and winter temperatures have risen, and the beetle has been able to successfully erupt in areas previously too cool (Berg *et al.* 2006, Sherriff *et al.* 2011).

The four papers that link climate change to increases in bark beetle range expansion and outbreaks correspond with other studies that have looked at the effect of temperature and other climatic variables on bark beetles. The methods also use empirical evidence to support their results, strengthening their conclusions. Carroll *et al.* (2004) and Logan and Powell (2001) took actual records of historical mountain pine beetle range and analyzed it with climate data records. Berg *et al.* (2006) and Sherriff *et al.* (2011) used dendrochronology techniques to determine spruce beetle outbreak occurrences and annual climate reconstruction records. They took spruce cores and analyzed the tree rings for growth releases that indicated spruce beetle outbreaks had occurred. This technique has been used in the past to analyze spruce beetle outbreaks (Veblen *et al.* 1991), and it is useful as a detection tool because aside from occasional fires, the only other large-scale disturbance in the northern region where the studies occurred is tree mortality by

spruce beetle outbreaks (Berg *et al.* 2006, Sherriff *et al.* 2011); therefore, identification of years where outbreaks created gaps and allowed neighbouring trees to be released should be fairly accurate. It should be noted, however, that the bark beetle studies were all located in North America, a continent that has been colonized for a much shorter time period than Europe, and historical records for climate data and forest insect disturbances only go back for a relatively short period compared to those that can be found in Europe (Quinlan *et al.* 1987, Mbogga *et al.* 2009). It is therefore more difficult to differentiate normal variability in insect disturbances in relation to climate. Dendrochronology has allowed these studies to examine disturbance regimes in the last 200 to 400 years, yet the lack of first-hand records during those years makes the interpretation of apparent disturbances somewhat less confident.

DEFOLIATORS

Evidence for climate change effects on forest insect disturbances was provided for four defoliating forest insect species, compared to only two bark beetles (Table 1); however, there was less consensus between the studies on how defoliating species were responding to a warming climate. The species that was most strongly linked to a positive response with climate change was the pine processionary moth (*Thaumetopoea pityocampa* [Denis & Schiffermuller]). Three studies provided evidence that the pine processionary moth has expanded its outbreak area range in latitude and/or elevation due to warmer than average winter temperatures in southern Europe (Hoch *et al.* 2009, Battisti *et al.* 2005, Hodar and Zamora 2004). This species has minimum winter threshold temperatures that must be met in order for the larvae to feed (Battisti *et al.* 2005), which has historically limited its range to warmer, more southern regions where winter temperatures rise above the threshold often enough for the moth to successfully develop and complete its lifecycle. Winter temperatures have been increasing outside of the moth's previous range, such as at more northerly latitudes and higher altitudes around central France and northern Italy (Hodar and Zamora 2004, Battisti *et al.* 2005, Robinet *et al.* 2007, Hoch *et al.* 2009), which has allowed the insect to expand further into those regions. Hodar and Zamora (2004) directly linked climate experienced by the pine processionary moth and the defoliation incidence in the following winter, showing an increased intensity of defoliation as the temperature in the previous winter increased. Battisti *et al.* (2005) provided substantial evidence that the pine processionary moth range has shifted in latitude in central France and in elevation in northern Italy, and that the expansion has accelerated in the past 10 years in response to warmer

temperatures at the limits of their range. Hoch *et al.* (2009) supported this with further results showing a range expansion in elevation in Italy. Even at the very limits of its range, the moth is able to cope with highly variable temperatures because of its moderate freeze tolerance (Hoch *et al.* 2009), the ability of the pupae to remain in the soil for up to 7 years (Battisti *et al.* 2005), and its tolerance for long periods of starvation in the larval stage. The moth is able to rapidly move into regions near the boundaries of its range that have begun to warm, even if there are still periods of variable, cold weather. The combination of warmer winters and the widespread, often homogeneous structured ranges of its host trees make it likely that this species will continue to move further north in Europe and into higher elevations.

Contradictory to the pine processionary moth, the response of larch budmoth, another defoliating species, to climate change was negative according to two studies (Table 1). Analysis of tree ring density profiles using dendrochronology techniques revealed that the larch budmoth in the subalpine larch forests of the European Alps has maintained highly regular outbreaks that have recurred every 8 to 9 years for over a millennium (Weber 1997, Esper *et al.* 2007). The extensive periodicity provides strong evidence for the predictability of outbreaks, and therefore the absence of any significant outbreaks since the 1980s, an unprecedented length in regards to the last 1173 years (Esper *et al.* 2007), indicates that the population dynamics of the larch budmoth has been disrupted. Esper *et al.* (2007) linked the absence of outbreaks since the late 20th Century to the period of extreme regional warmth outside of the climatic envelope of the past 1200 years, suggesting that a temperature variation threshold has recently been passed. Baltensweiler (1993), who examined the reasons for the collapse of the 1990 outbreak, agreed that consecutively warmer winters and springs affected the ability of the moth to outbreak. Both studies suggested that the increased winter and spring temperatures affected the overwintering eggs by inducing early development and egg hatch, leading to increased mortality of eggs when colder weather hit again or increased 1st instar larvae starvation and mortality when they hatched before budburst in their host.

Hatching in synchrony with the host's budburst and new flush of the leaves is crucial for the survival of the vast majority of Lepidopteran defoliating insects (Feeny 1970, Bale *et al.* 2002). The 1st instar larvae generally require the very soft leaves that first emerge from buds to be able to tear into them with their tiny mandibles (Feeny 1970). Furthermore, leaves very quickly lose

much of their nutritional quality as they age (Feeny 1970, Schultz *et al.* 1982), so that larvae that can eat older foliage will develop more slowly, gain less mass, and have a higher chance of dying from lack of necessary amounts of nutrients (Feeny 1970, Schweitzer 1979, Larsson and Ohmart 1988, Dongen 1997, Bylund 1999). There is only a very small window after budburst before foliage becomes less edible and nutrient-poor (Feeny 1970), and therefore the species that rely on it must hatch before that opportunity is lost. It is also important that the larvae do not emerge much earlier than budburst, otherwise they will have nothing to feed on and are likely to starve before the new leaves come out (Visser and Holleman 2001). Climate change, however, may be disrupting the synchrony by speeding up the development rate of eggs so that they have an increased probability of hatching before budburst (Bale *et al.* 2002, Visser and Holleman 2001). This is due to the insect responding more quickly than the trees to increased temperatures as a cue for development (Bylund 1999). Early egg hatch will result in increasing mortality rates and outbreak collapses among various species (Bylund 1999, Visser and Holleman 2001).

Asynchrony due to climate change is likely a significant factor in the absence of outbreaks by the larch budmoth, as the species must hatch simultaneously with the flushing of the larch in the spring or otherwise experience high rates of mortality (Baltensweiler 1993). The pine processionary moth, however, is one of the exceptions to the need for synchrony. Rather than overwintering as eggs and hatching with the new spring flush, pine processionary moth larvae emerge in the late summer or early fall and remain active throughout the winter (Battisti *et al.* 2005, Aimi *et al.* 2008). They live gregariously in silk nests and feed whenever the temperature thresholds are met. By the time spring comes around, the larvae will have finished feeding and entered the soil to pupate, so that they are not dependent on new foliage for their development. This difference between the pine processionary moth and defoliators like the larch budmoth is likely an important factor in the difference between their responses to climate change, since a mistiming between egg hatching and budburst is not an issue for species that actively feed in the winter (Bale *et al.* 2002).

The winter moth is another example of a defoliating species that requires synchrony of egg hatching and budburst (Feeny 1970, Watt and McFarlane 1991, Dongen *et al.* 1997, Visser and Holleman 2001). The evidence for the response of this moth to climate change was less clear-cut than the other species, as one study provided results for a positive response, while the other

suggested that it is more likely to be negative (Table 1). Jepsen *et al.* (2008) demonstrated a strong northward and eastward core outbreak area expansion of the winter moth in Norway by comparing historical outbreak records dating back to 1862 and the recent change in the boundaries of the moth's range to the warming that has occurred at its range's limits. The winter moth was historically restricted in its range by cold winter temperatures because it suffers substantial egg mortality at temperatures below -35°C , but the recent increase in mean annual and minimum winter temperatures has allowed the moth to expand its core outbreak area further north and east. It is clear from this study that there has been an expansion of range by the winter moth over the last few decades and that this expansion is linked to climate change because the moth, which is polyphagous mainly on birch and oak, has not been limited by its host range (Bylund 1999, Jepsen *et al.* 2008, Visser and Holleman 2001); however, what Jepsen *et al.* (2008) failed to take into account was that the fitness of the caterpillar is reliant on emerging from the egg in synchrony with budburst, and that warming temperatures within the historic range of the moth may be negatively affecting that synchrony (Bylund 1999, Visser and Holleman 2001).

Visser and Holleman (2001) used measurements of oak budburst and egg hatch timing within the moth's historic range in the Netherlands to show that climate change is likely having a negative effect on winter moth herbivory. Like the larch budmoth, the winter moth has strongly selected for close synchrony between hatching and budburst because of the risk of starvation if it hatches too early, or having to settle for less digestible leaves and a longer larval period that would increase its exposure to predators and parasites if it hatches too late (Feeny 1970, Bylund 1999, Visser and Holleman 2001). Because bud burst has no direct effect on hatching, the eggs must use an environmental cue to time hatching synchrony with budburst, and most likely uses temperature as its cue (Visser and Holleman 2001). According to Visser and Holleman (2001), the timing difference between the date of egg hatching and the date of bud burst has become more and more negative over the past 25 years. As a result, there has been an increase in mistiming of egg hatching recently, which leads to both higher mortality and dispersal of small larvae, likely causing severe effects on population dynamics (Bylund 1999, Visser and Holleman 2001). The study was able to link the mistiming to climate change by correlating the increasing ratio of warmer winter and early spring temperatures to the number of frost days with the stronger negative egg hatch timing difference. The conclusion was that extreme temperature

patterns brought on by climate change is likely increasing the asynchrony of winter moth hatching and oak bud burst, and therefore we should expect to see fewer outbreaks and less defoliation overall by this species as the temperatures continue to warm. Visser and Holleman (2001)'s and Jepsen *et al.* (2008)'s studies taken together indicate that it may be less clear how the winter moth may respond in the future with climate change, except that it may continue to expand its range at the northeast limits while possibly retracting its historical range where asynchrony between egg hatching and budburst is experienced.

Birch budmoth (*Argyresthia retinella* Zell.) may also be outbreaking more frequently, according to one study by Tenow *et al.* (1999). The outbreak that that was studied started in the late 1980s in birch forests in Norway and went into the mid-1990s before crashing. Although it is unlikely that birch budmoth attacks are a new phenomenon in the region (Tenow 1996), the only other birch budmoth outbreak in recorded history that the area likely experienced was in the 1940s, and Tenow *et al.* (1999) claimed that both outbreaks took place during much higher than average temperatures. According to the authors, it is likely that increased temperatures may promote outbreaks for this species, especially since the restriction of its outbreak area to maritime climate indicates that the population is limited by cold temperatures at the boundaries (Tenow *et al.* 1999), similar to the other defoliator species mentioned previously. Tenow *et al.* (1999) suggested that increased winter temperatures caused by climate change may increase the survival of overwintering eggs and could be a releasing factor of outbreaks, initially making outbreaks more frequent and severe and possibly shifting area. Unfortunately, this study only examined a single recent outbreak period and only had one other unconfirmed historical outbreak to compare it to, which reduces the confidence with which the 1990s outbreak can be attributed to climate change effects. Furthermore, it was not clear whether the birch budmoth in Norway, which displays similar characteristics to the winter moth, such as similar egg diapause and cold hardiness (Elverum *et al.* 2003), may be affected by budburst timing. Elverum *et al.* (2003) reported larvae appearing in birch buds 9 days before the leaves began to unfold, so synchrony may or may not be as important for this species as with other defoliators. How the fitness of the larvae will be affected by positive or negative differences between hatching and budburst as temperatures continue to increase is not yet known.

PREDICTIVE FRAMEWORK

The evidence in Table 1 suggests the following framework (Figure 1) for predicting the responses of bark beetles and insect defoliators to climate change:

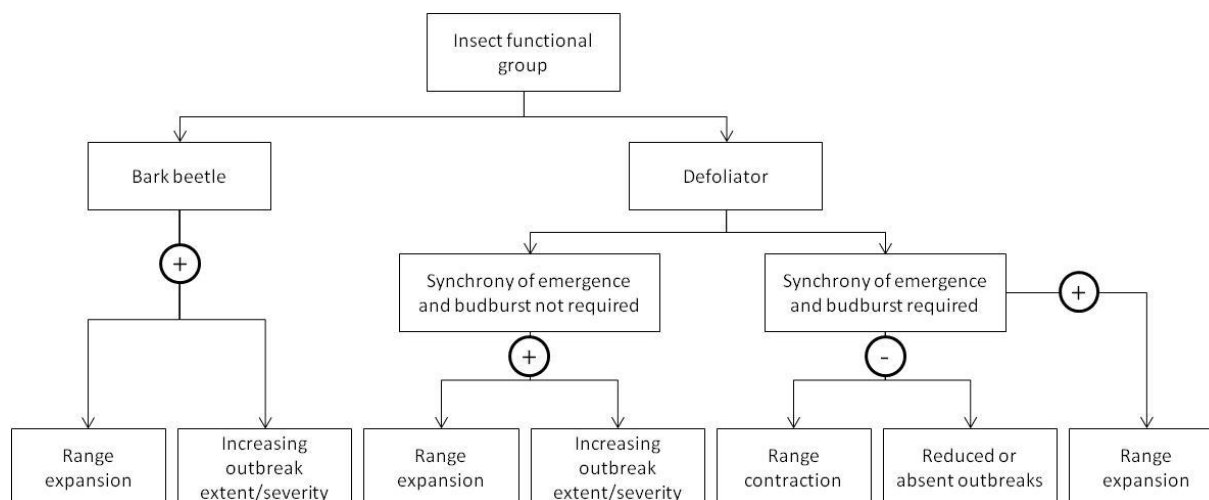


Figure 1: Flowchart summary of probably forest insect responses to climate change given the results in Table 1. The + and – symbols refer to positive and negative response to climate change effects respectively.

The four studies that examined bark beetles provided strong evidence for positive responses to climate change (Table 1), and it is likely that other bark beetles with similar biology and current climate restrictions in their range will respond positively as well (Figure 1). Various other bark beetle species have been observed to increase in frequency and intensity of outbreaks during periods of exceptionally warm and dry weather, especially other *Dendroctonus* species, such as the southern pine beetle (*Dendroctonus frontalis*) (Gan 2004) and Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Schmitz and Gibson 1996). Landscape-scale mortality by these types of insects is expected in Canada and the United States if they respond the same way to climate change as the mountain pine beetle and spruce beetle have (Bentz *et al.* 2010). *Ips* species, such as *Ips confusus* and *Ips typographus*, have also been known to have severe outbreaks during higher temperatures or drought-like conditions, even though under normal conditions they are generally not as destructive or aggressive as the *Dendroctonus* species (Wermelinger 2004, Breshears *et al.* 2005, Jonsson *et al.* 2009, Santos and Whitham 2010). *Ips* species are generally considered to be secondary bark beetles because they normally do not seek out or kill live, healthy trees, but infest those that are stressed, weakened, damaged or downed

(Bentz *et al.* 2010, Santos and Whitham 2010). While secondary bark beetles are not generally a concern as forest pests, they do have the ability to outbreak and cause high amounts of tree mortality under certain climatic conditions (Wermelinger 2004, Jonsson *et al.* 2009, Santos and Whitham 2010).

Two examples of *Ips* species that have become major pests with outbreaks that may be linked to climate change are pinyon ips (*Ips confusus*) and the European spruce bark beetle (*I. typographus* [L.]) (Wermelinger 2004, Jonsson *et al.* 2009, Santos and Whitham 2010). *I. confusus* is a major bark beetle in southwestern U.S.A, and in 1996 a large-scale infestation occurred that caused an estimated 70% mortality of local stands of pinyon pine trees (Santos and Whitham 2010). This outbreak was associated with a major drought event that happened at the same time. A second drought occurred in 2002, the most severe on record, and instigated another devastating pinyon ips outbreak. The droughts likely increased the stress on trees and weakened them against bark beetle attack, thereby allowing pinyon ips to infest more quickly and efficiently than before, leading to faster increases in the populations (Bentz *et al.* 2010, Santos and Whitham 2010). Although, unlike mountain pine beetle and spruce beetle, pinyon ips have not yet been shown to generate enough positive feedback in their outbreaks to become self-amplifying and continue to outbreak after the drought is over (Raffa *et al.* 2008), climate change may increase the frequency and severity of droughts (IPCC 2007), and cause an increase in pinyon ips outbreak events. The European spruce bark beetle is another *Ips* species that has caused a lot of destruction in mature spruce forests in central and northern Europe (Wermelinger 2004, Jonsson *et al.* 2009). Spruce tree mortality caused by the periodic large-scale outbreaks has been in the millions, and the damage has increased considerably in the last 15 years (Jonsson *et al.* 2009). Increased storm felling events and favourable climatic conditions have been suggested as the reasons for the increased outbreaks, and it is likely that they will continue to expand their outbreak area as temperatures continue to rise. These examples indicate that the evidence presented in Table 1 for mountain pine beetle and spruce beetle responses to climate change may be applied to many potential pest bark beetles, including both primary *Dendroctonus* and secondary *Ips* species, and species ranging within either North America or Europe.

There appears to be less certainty in regards to using the current evidence to predict the response of defoliators to climate change (Table 1, Figure 1); however, examining the life histories of the

species in question may help to make some tentative predictions (Bale *et al.* 2002). The pine processionary moth example suggests that species that have active overwintering stages in their life cycle will be more apt to benefit in their survival from warmer winters (Bale *et al.* 2002, Battisti *et al.* 2005, Battisti 2008), as that would reduce the periods of cold temperatures that prevent feeding (Battisti *et al.* 2005). This type of life history also does not depend on hatching and feeding in synchrony with budburst, and therefore will not be affected in that sense (Bale *et al.* 2002). Therefore, increased defoliation and range expansion into more northern latitudes and higher elevations is expected of species similar to the pine processionary moth. There are not, however, as many species that overwinter with active stages as there are those that wait until the spring to feed (Feeny 1970, Battisti *et al.* 2005, Battisti 2008). Two possible examples given by Battisti *et al.* (2005) of active winter feeding butterfly species that may expand in range are the North African *Colotis evagore*, which is likely to establish further in southern Spain once it is less limited by the winter temperature, and *Eucheria socialis*, a montane pierid that is like the pine processionary moth in that it has gregarious larvae that only feed when temperatures are above 0°C in the winter. The pine processionary moth appears to be somewhat of an exception among forest defoliators in that climate change effects will almost certainly be positive for it and it will likely continue to expand its range as long as temperatures are rising and at least one of its many hosts is available.

Warmer winters may also be better for frost-sensitive species that do not actively feed in the winter by reducing mortality caused by extremely cold periods on the overwintering stage (Bale *et al.* 2002). Furthermore, warmer summers may speed up development of the growth phase (Bale *et al.* 2002, Netherer and Schopf 2010). This leads to less time spent in egg, larval and pupal stages, which are the periods that are normally most exposed to predators and parasites (Netherer and Schopf 2010). Increased temperatures can also allow many insects to fly and immigrate earlier by advancing the time of year at which the threshold temperature for flight is first met (Bale *et al.* 2002, Netherer and Schopf 2010). Therefore, most defoliators will likely benefit from the direct effects of climate change to some extent and period of time, but their exact responses will vary from species to species (Bale *et al.* 2002), and the possible negative effects on species that rely on synchrony with budburst of their host or require certain low temperatures to be reached in order to complete diapause may make their responses more difficult to predict. Climate change was shown to cause mistiming between egg hatching and

budburst in the winter moth, resulting in higher mortality and dispersal of the larvae, and making it much less likely for outbreaks to occur (Bylund 1999, Visser and Holleman 2001). Other species that rely on synchrony will most likely be adversely affected by increasing temperatures. Alternatively, they may experience increased synchrony at the northern and higher edges of their current range boundaries as climatic conditions become more suitable (Jepsen *et al.* 2008), reducing mortality of larvae and increasing the population size so that increased defoliation and range expansion could occur. It is difficult to predict, based on current evidence, whether climate change will cause the range of these species to contract due to increased asynchrony, expand if they are able to adapt and become synchronous again, or merely shift as the southern range boundary contracts and the northern expands.

Another characteristic of many defoliating insects that makes responses more uncertain, and was not addressed in the studies in Table 1, is diapause. Diapause is very common among temperate species which experience reduced metabolic rates as inactive egg, pupa, larva or adult stages to increase cold hardiness (Bale *et al.* 2002, Netherer and Schopf 2010). It is an important process that promotes seasonal synchrony and helps to buffer the effects of varying temperatures so that some species may not be so restricted in their geographical range. Diapause is obligatory in many univoltine species and requires specific low temperature thresholds before the insect becomes active again when the growing season begins. Because completion of winter diapause requires lower temperatures than those that favour growth, warming winters may exceed the threshold at the southern range edges, creating a shift north in the distribution of a particular insect species (Bale *et al.* 2002). On the other hand, diapause may help to counteract the asynchrony effect of climate change. Higher temperatures have been promoting earlier larval emergence for many species, but because photoperiod, not temperature, controls diapause completion, diapause may prevent early emergence and help maintain synchrony with budburst. Some previous studies have shown this to possibly occur in the winter moth, in which higher temperatures prolong its autumn diapause so that even though development happens more quickly under warmer springs, the life cycle as a whole is not shortened (Bale *et al.* 2002, Buse and Good 1996). The added variable of diapause means that there will be even less consensus between species responses.

IMPLICATIONS FOR FOREST MANAGEMENT

The current studies that provide empirical evidence for climate change effects on eruptive forest insects suggest that bark beetles are likely to be more strongly impacted than insect defoliators because of the lack of need for emerging in synchrony with budburst of their hosts and their rapid response to stress in their host trees. Bark beetles that have the potential to outbreak are very likely to show range expansion and increased frequency and intensity of outbreaks as conditions become more suitable with climate change. Future forest management research should focus strongly on determining which bark beetle species are likely to be of most concern to forestry goals and how landscape-level tree mortality might be mitigated. Further studies should also be conducted on lesser known bark beetle species that are found farther south, such as those indigenous to the southwestern U.S. and Mexico, because of their potential to move northward as temperatures increase (Gan 2004, Bentz *et al.* 2010). Similar to the northern species, such as the mountain pine beetle, southern beetles – for example the roundheaded pine beetle (*Dendroctonus adjunctus*) that colonizes pines in southern Utah and Colorado down into Guatemala – are currently limited to their range by climate and not by the availability of their hosts. This indicates that as climate becomes more suitable at the northern limits of their range, these beetles may move up into currently uninfested hosts or adapt to novel hosts; however, unlike the spruce beetle and mountain pine beetle that have been studied extensively in the north, there is as of yet very little information on the temperature-dependent physiological aspects of the southern beetles' life histories (Bentz *et al.* 2010). While managers should expect increases in range expansion, and possibly new species from the south to shift up into new habitats, it is important to gather more information and evidence on other species aside from the two in Table 1, including more concrete links between climate change and bark beetle species that are secondary pests or from lesser known southern populations.

Defoliators may be more negatively affected by climate change compared to bark beetles; however, the impacts and responses will likely vary more from species to species. Species that feed during the winter, do not require newly flushed foliage to survive, and are currently limited by cold temperatures at their range limits are likely to benefit from climate change by being able to expand their range. Other species, such as those that depend on close synchrony of emergence and budburst, but are also limited in their range by climate, may experience both positive and

negative effects from climate change, and predicting the final outcomes of their responses is not feasible without further, longer term studies. The evidence is currently lacking for making general assumptions about forest insect defoliators, and so proper management for future responses to climate change requires more studies on the different types of life histories of the species and which will be most affected by changes in temperature and precipitation.

Other considerations that should be a focus in future studies are other variables that may increase the strength of insect pest responses to climate change. The rate of growth of population size may be impacted by increasing temperatures and climatic variability that could help insects escape the pressure of their natural enemies (Stireman *et al.* 2005). For example, an extensive data analysis conducted by Stireman *et al.* (2005) found that the frequency of parasitism in caterpillars declines with increasing climatic variability. Increased temperatures and drought-conditions also often lead to outbreaks of mountain pine beetle where the population size grows to the point where natural enemies have no affect on it and cannot control it (Safranyik and Carroll 2006). By escaping the pressure of natural enemies, bark beetles and defoliators may respond to climate change even more rapidly than expected (Stireman *et al.* 2005). Another concern is the connectivity of host trees that may encourage the spread of insect pests (Safranyik *et al.* 2010). In Europe, forests have been managed in a way that has created extensively homogeneous landscapes of pine, the pine processionary moth's preferred host (Felton *et al.* 2010). With few non-hosts in the way, it is easy for the moth to locate suitable trees by dispersing even a short distance, even if it locates hosts randomly (Dulaurent *et al.* 2012). In Canada as well, homogeneous forests of lodgepole pine throughout BC have aided the mountain pine beetle in quickly locating hosts and expanding its range (Safranyik *et al.* 2010). Similar forests of Jack pine across the prairie provinces will also likely increase the rate at which the beetles are able to spread eastward. While current evidence as shown in Table 1 provides an idea of whether insect pests will respond positively or negatively to climate change, more information is required to extend predictions to response strength as climatic conditions change in the future.

Finally, it is important to realize that this analysis of the literature is applicable only to the short term because it assumes that the forests as we know them will largely be intact and in the same place in the future. The effects of climate change on forest insect responses have been considered only in the context of the current forest structure, species composition, and range; however,

forest communities and tree species will be impacted by climate change, as shown by climate-based species distribution models and ecosystem-based climate envelope modeling (Hamann and Wang 2006, Aitken *et al.* 2008). As warming occurs, potential habitat is predicted to open up for tree species that are limited by cold temperatures at their northern range limits, while other species, such as some of BC's most important conifer species, will lose a lot of their suitable habitat in their historical range (Hamann 2006). The robust capacity of tree species to shift range has already been demonstrated by fossil pollen records and genetic data that indicate the occurrence of past glacial and postglacial migrations (Davis and Shaw 2001, Hamrick 2004, Aitken *et al.* 2008). Current evidence also suggests that recent climate change is already affecting forests; for example, research by Breshears *et al.* (2005) showed that drought was the main cause of regional-scale vegetation die-off occurring across southwestern North American woodlands in the early 2000s, and that the warming and vegetation die-off was more extensive than a previous recorded drought in the 1950s. They suggest that future drought conditions due to warming temperatures from global climate change will likely lead to severe and extensive death of woody plants in the overstory. When range shifts and die-offs of tree species are taken into account, it is impossible to predict the responses of eruptive forest insects given the current evidence of climate change effects. There are too many uncertainties regarding whether specific insect species will shift with their host species, expand or contract their range, adapt to novel host species that come into their historic range, or respond in other unexpected ways. Therefore, further research could be conducted to try to predict what will happen in the longer term with forest insects when climate change begins to render areas unsuitable for the tree species that used to grow there.

CONCLUSION

Climate change has been occurring for over 100 years and already there has been evidence that forest insect pests have been responding to the changes in temperature, precipitation, and climatic variability. Most of the focus has been on bark beetles and insect defoliators that have been known to outbreak in North American and European temperate and boreal regions. All selected studies showed that bark beetles have responded positively to climate change, and the majority of bark beetles that are of concern to management of forests will likely respond in similar ways. It was less simple, however, to generalize the responses of defoliators as increased

temperatures benefited some species, while negatively affecting others. While models can help us to predict future responses of insects, it could be useful to conduct more studies similar to those in Table 1 that focus on gathering current evidence on how climate change as affected various insect groups and species up to now. It may aid in determining the processes that are driving temperature-based responses in insects, and provide a concrete foundation upon which models could be built and predictions made.

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