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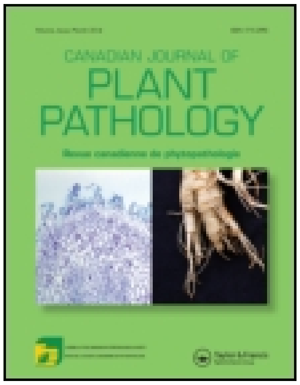


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# Direct and indirect impacts of climate change on forests: three case studies from British Columbia

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Symposium contribution/Contribution du colloque

# Direct and indirect impacts of climate change on forests: three case studies from British Columbia†

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**Abstract:** Climate is an important driver of forest dynamics. In this paper, we present three case studies from the forests of British Columbia to illustrate the direct and indirect effects of climatic variation and global warming on forest composition and function. (1) Tree mortality rates in old forests of western North America have doubled in recent decades. Regional warming and water deficits directly affected tree death rates or indirectly increased insect and pathogen activity and wind storms causing tree deaths. Concurrently, tree density and basal area declined significantly, indicating lagged growth responses of surviving trees or long-term decline of these forests. (2) Yellow-cedar decline along coastal British Columbia and Alaska shows that small changes in average climatic conditions, coupled with extreme weather events, can have large ecological effects. A small persistent increase in mean temperatures has reduced snow-cover depth and duration. Coupled with extreme cold events which damage unprotected tree roots, these climatic changes are considered the primary cause of widespread yellow-cedar mortality. (3) Interactions between climate and disturbance are complex in the mountain forests of the East Kootenay region. Understanding historic climate–fire interactions is key to anticipating future frequent and severe fires. Here, climate change effects may be exacerbated by the cumulative effects of human land use, fire exclusion and mountain pine beetle outbreaks. We conclude that understanding past climate variation and its effects on forests help us to anticipate the potential effects of global warming.

**Keywords:** climate variation, coastal forests, disturbance regimes, fire regimes, forest decline, mortality rates, mountain forests, mountain pine beetle, old forests, tree deaths, yellow-cedar

**Résumé:** Le climat est un important moteur de la dynamique des forêts. Dans cet article, nous présentons trois études de cas tirées des forêts de la Colombie-Britannique afin d'illustrer les effets directs et indirects de la variation et du réchauffement climatiques sur la composition ainsi que sur la fonction de la forêt. (1) Le taux de mortalité des arbres dans les forêts anciennes de l'ouest de l'Amérique du Nord a doublé au cours des dernières décennies. Le réchauffement régional et le déficit en eau contribuent directement au taux de mortalité des arbres ou, indirectement, par l'accroissement de l'activité des insectes et des agents pathogènes ainsi que par la violence des tempêtes de vent qui causent la mort des arbres. Simultanément, la densité des arbres et la surface terrière déclinent significativement, ce qui indique une réaction de croissance décalée des arbres qui survivent ou un dépérissement à long terme de ces forêts. (2) Le dépérissement du cyprès jaune le long des côtes de la Colombie-Britannique et de l'Alaska indique que de faibles modifications des conditions climatiques moyennes, ajoutées à des évènements météorologiques extrêmes, peuvent avoir de graves répercussions écologiques. Une petite augmentation constante de la température moyenne a réduit l'épaisseur et la durée du couvert neigeux. Ajoutés à des périodes de froid intense qui endommagent les racines non protégées des arbres, ces changements climatiques sont perçus comme étant la cause première de mort à grande échelle chez le cyprès jaune. (3) Dans les forêts de montagne de la région d'East Kootenay, les interactions entre le climat et les perturbations sont complexes. Afin

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d'anticiper à l'avenir les nombreux et graves incendies de forêt, il importe de comprendre les interactions historiques qui impliquent le climat et le feu. Ici, les conséquences des changements climatiques peuvent être aggravées par les effets cumulatifs de l'utilisation du territoire par l'homme, par la suppression des incendies de forêt et par les proliférations de dendroctone du pin ponderosa. Nous terminons en concluant que la compréhension des variations climatiques passées et de leurs effets sur les forêts nous aide à anticiper les conséquences possibles du réchauffement climatique.

**Mots clés:** cyprès jaune, dendroctone du pin ponderosa, dépérissement de la forêt, forêts anciennes, forêts côtières, forêts de montagne, mort des arbres, régimes d'incendies, régimes de perturbation, taux de mortalité, variation climatique

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## Introduction

Understanding climate-change impacts has important implications for conservation of biodiversity and sustainable management of forests. The current paradigm of ecosystem management is based on the fundamental premise that management to maintain historic forest composition, structure and function will sustain suitable habitat for the biota adapted to the ecosystem (Christensen *et al.*, 1996). In this context, understanding past climatic variability and its impacts on ecosystem processes is essential. It defines biologically-based boundaries for our current actions and provides an analogy for future change (Landres *et al.*, 1999). This knowledge becomes increasingly important if we are to anticipate the effects of future climates on potential trajectories of forest change, particularly when conditions are predicted to exceed the historic ranges of variation.

Climate is an important driver of forest dynamics. To predict vegetation response to global warming, we must understand vegetation–climate interactions and vegetation responses to known climatic variation and past change (Prentice, 1992). Direct effects of climate on vegetation include altered rates of tree mortality, growth and regeneration success, which interact and ultimately affect species distributions (Hansen *et al.*, 2001). Indirect effects are through climate-mediated disturbances such as fire, insects, pathogens and their interactions. These disturbances are essential components of forest dynamics and altered disturbance regimes may serve as a catalyst facilitating changes in species distributions and community composition. In this discussion paper, we present three case studies from the forests of British Columbia to illustrate the direct and indirect effects of climatic variation and global warming on forest composition and function.

## Background mortality rates in old forests

Tree death is a natural part of forest dynamics. In fact, it is an integral process creating many of the unique structures, like large snags, logs and canopy gaps, associated with old-growth forests (Wells *et al.*, 1998). Each year we expect a small number of trees to die, but long-term monitoring of old forests in the western United States and southwestern British Columbia shows that tree mortality has been increasing over time (van Mantgem *et al.*, 2009). In these forests, the background mortality rates, the rate at which trees die in the absence of stand-level disturbances, have increased significantly with doubling periods of 17 to 29 years. Furthermore, the increase in dying trees has been pervasive. Tree mortality rates have increased across a wide variety of forest types, elevation classes, tree sizes and among genera, including *Pinus*, *Abies* and *Tsuga*.

After testing and rejecting a number of possible mechanisms to explain the increasing tree mortality rates, such as air pollution, long-term effects of fire exclusion, and stand development, van Mantgem *et al.* (2009) showed that increasing regional temperature was correlated with tree deaths. During the study period from *c*. 1977 to 2007, average temperature in western North America rose by *c*. 1.0 °C (Diaz & Eischeid, 2007). Throughout the study area, including the coastal forests of southwestern British Columbia, water deficits in the summer are pronounced so that increased temperatures and/or decreased precipitation can lead to increased moisture stress (van Mantgem *et al.*, 2009). Although the reported 1.0 °C temperature increase was modest, it has been sufficient to significantly reduce winter snowpack (Mote *et al*., 2005; Knowles *et al.*, 2006), cause earlier snowmelt (Stewart *et al.*, 2005) and lengthen the summer droughts (Westerling *et al.*, 2006) in the region.

In longitudinal and retrospective studies that reconstruct forest disturbance and development, the specific causal agents contributing to tree death can be difficult to identify. The decline and death of individual trees can take years to decades and involve multiple causal agents, and decomposers can colonize trees rapidly after death (Franklin *et al.*, 1987; Manion, 1991; Manion & Lachance, 1992). Combined, it is difficult to discern predisposing, contributing and inciting causes of death when multiple agents are involved (Manion, 1991;

Manion & Lachance, 1992). Therefore, van Mantgem *et al.* (2009) classified dead trees as those dying from mechanical processes, such as stem breakage, uprooting, or crushing by large fallen trees, versus stress mortality likely related to water deficits. The rate of tree deaths due to mechanical processes is influenced by storm frequency and intensity, which also vary with climatic variation and change. Stress mortality can be directly related to climate as changes in the severity or length of summer drought are related to soil water deficits that can lead to higher death rates. Indirectly, warm temperatures can affect endemic insects and pathogens. Several studies have demonstrated that warm temperatures can facilitate bark beetle (Berg *et al.*, 2006; Hicke *et al.*, 2006) and defoliator (McCloskey *et al.*, 2009) outbreaks, while increasing host-tree susceptibility and subsequent mortality (Allen *et al.*, 2010). Warm temperatures may also trigger fungal pathogens; however, the interactions among climate, fungi and trees can be difficult to assess and are less well understood than insect disturbance regimes (Allen *et al.*, 2010).

An example of a climate-triggered insect outbreak is the western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst) outbreak that contributed to death of some western hemlocks (*Tsuga heterophylla* (Raf.) Sarg.) in permanent sample plots in coastal British Columbia between 1999 and 2002. Outbreaks of western hemlock looper during the 20th century have been linked to low precipitation and high temperatures leading to soil moisture drought during the growing season (McCloskey *et al.*, 2009). With predicted increases in summer drought in this region (Plummer *et al.*, 2006; Christensen *et al.*, 2007), it is tempting to predict that the frequency of outbreaks will increase in the future. However, the frequency of western hemlock looper outbreaks has not changed significantly over the past 200 years, despite a marked change in climate, and not all historical droughts have caused an outbreak of western hemlock looper (McCloskey, 2007). For instance, western hemlock looper populations do not necessarily respond to droughts that recur at short intervals because factors such as the density of parasites, predators and pathogens control the duration and ultimate collapse of looper populations (McCloskey *et al.*, 2009). This example illustrates the complex interactions among climate, biotic disturbance agents and tree survivorship and mortality.

In addition to doubled mortality rates, van Mantgem *et al.* (2009) reported that rates of tree establishment and growth had decreased in many old forests. As a result, density and cumulative basal area, representing the biomass of living trees, have declined. If these trends persist over the lifespan of the dominant species, the average age and size of trees in old forests will be reduced by half. Such changes in forest structure could have cascading effects on plant and animal habitat availability and biodiversity. However, lags in the growth responses of surviving trees and the initial unequivocal effects of death versus growth on the total biomass of living trees suggest that the observed decrease in biomass in forests may be temporary. For example, our findings from old-growth western redcedar (*Thuja plicata* Donn ex D. Don) – western hemlock forests of coastal British Columbia indicate a gain in radial growth rates and the biomass of surviving trees following the death of nearby canopy-dominant trees (Stan & Daniels, 2010*a*, 2010*b*). Nevertheless, when large-diameter, canopy-dominant trees die, a substantial amount of living biomass is abruptly removed from the forest. Although neighbouring trees of a range of species and sizes respond by increasing their radial-growth rates, the amount of living biomass gained on an annual basis is relatively small. Based on observed rates and durations of radial-growth releases (Stan & Daniels, 2010*a*, 2010*b*), it takes several decades for full recovery of the living biomass that is lost when large-diameter, canopy-dominant trees die. Therefore, the future balance of biomass in old forests depends on the relative rates of gains and losses and the uncertain effects of climate change on these processes.

Lastly, the trend of increased death rates indicates that many of the old forests assessed by van Mantgem *et al.* (2009) are stressed, despite their relatively remote locations and protection from human disturbances like commercial logging, and may be susceptible to abrupt change. In some cases, increasing tree deaths could indicate that forests are more vulnerable to sudden, extensive die-back when critical climatic thresholds are exceeded (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009; Allen *et al.*, 2010). Given projected increases in mean temperatures and occurrence of regional droughts (Christensen *et al.*, 2007), tree death rates and occurrence of forest declines will likely increase in future due to the direct and indirect climatic effects (Allen *et al.*, 2010).

**Yellow-cedar decline**

The widespread and ongoing mortality of yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) is the most severe forest species decline in North America (Auclair *et al.*, 1990; Hennon *et al.*, 2005; Allen *et al.*, 2010). Standing dead and dying yellow-cedar currently occupy >250 000 ha along the coasts of southeast Alaska and northwestern British Columbia (Lamb & Wurtz, 2009; Westfall & Ebata, 2009). Symptoms of affected trees include root nodules, wood staining and synchronous

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crown loss, all of which implicate root injury (Hennon *et al.*, 1992). Following extensive research of nematodes and fungi associated with yellow-cedar, biotic agents have been ruled out as the cause of yellow-cedar deaths (Hennon *et al.*, 1986, 1990*b*; Hennon, 1990; Hennon & Shaw, 1994, 1997). The current hypothesis is that regional climate change predisposes yellow-cedar to decline (Hennon *et al.*, 1992, 2006; Beier *et al.*, 2008).

During the 20th century, the climate of coastal British Columbia became warmer; mean annual temperatures increased 0.6 °C (British Columbia Ministry of Water, Land and Air Protection, 2002). Dendrochronological analyses indicate growth rates of yellow-cedar correlate positively with warmer temperatures: increased growth in healthy populations of yellow-cedar on Vancouver Island and along the coasts of British Columbia and Alaska are associated with warm and dry conditions in autumn and late winter (Laroque & Smith, 1999, 2005; Beier *et al.*, 2008; Stan *et al.*, 2009). In warm years without thaw–freeze events in the spring, yellow-cedar grows vigorously due to longer growing seasons and less cloud cover. Growth in this last century was greater than in the last several centuries (McKenzie *et al.*, 2004; Sink, 2006).

Examining low-frequency variation in growth rates corroborates the positive influences of warm temperatures on yellow-cedar growth. For example, the Pacific Decadal Oscillation (PDO) represents variation in the North Pacific monthly sea surface temperatures, which shift between warm and cool phases over *c*. 30 years (Mantua *et al.*, 1997; Mantua & Hare, 2002). The PDO affects marine productivity and regional climate, including seasonal weather in British Columbia (Moore & McKendry, 1996). Climates during a warm phase of the PDO are very similar to mean climates projected for 2050, so we can compare growth under warm and cold phases of the PDO to help understand possible responses of yellow-cedar trees to changes in mean climates due to global warming. Yellow-cedar on the north coast of British Columbia exhibit a positive response to PDO (Stan *et al.*, 2009), so this evidence leads us to expect increased growth as temperatures warm.

Other aspects of climate also have changed, which may contribute to the death of yellow-cedar trees. As the climate of coastal British Columbia warmed, there have been fewer days with temperatures below 0 °C (British Columbia Ministry of Water, Land & Air Protection, 2002). At more locations along the central and north coast, mean winter temperatures now average *c*. 0 °C, so that above-average temperatures result in more rain than snow, a reduced snowpack and an earlier snowmelt (Mote *et al.*, 2005; Beier *et al.*, 2008). Furthermore, the intensities and frequencies of extreme climatic events, such as late-winter thaws and freezes, have increased disproportionately relative to climatic means (Christensen *et al.*, 2007; Field *et al.*, 2007). Normally, snowpack insulates fine roots from extreme cold. When the snowpack is absent, freeze events are fatal to unprotected roots of yellow-cedar. Root death is followed by moisture stress, canopy loss and mortality of the tree (D'Amore & Hennon, 2006).

This climate-driven hypothesis explaining yellow-cedar decline is supported by a growing body of evidence. Forest declines driven by abiotic causes most commonly occur at the margins of a species' distribution on edaphically- and climatically-limited sites (Sinclair & Hudler, 1988). Similarly, yellow-cedar snags are concentrated at low elevations on the outer coast in the northern part of the species' distribution, on poorly drained soils near unproductive sloping bogs, on exposed warm-aspect slopes and in areas of low snow accumulation (Hennon *et al.*, 1990*a*, 1990*b*, 1990*c*, 2005; Hennon & Shaw, 1994; Wooton, 2010). Temporally, the sampled yellow-cedar in declining stands tend to be young (<500 years) relative to the species' potential lifespan (>1000 years), implying that mortality is affecting recently established trees that migrated to lower elevations during cooler climates between 1350 and 1850 (Hennon *et al.*, 1990*a*; D'Amore & Hennon, 2006). Based on historical photos and using the presence of snags and their decomposition rates, yellow-cedar decline is hypothesized to have begun in the 1870s, coincident with regional warming trends (Shaw *et al.*, 1985; Hennon *et al.*, 1990*c*). Low growth of yellow-cedar in Alaska since 1950 is correlated with low-snowpack and frequent freeze–thaw events (Beier *et al.*, 2008).

Morphological, phenological and physiological characteristics of yellow-cedar roots further support the climate-driven decline hypothesis. The fine roots of yellow-cedar grow in shallow soils to better access nutrients (D'Amore *et al.*, 2009) and dehardening is thermoregulated to track microbial activity in late winter (Schaberg *et al.*, 2005). In contrast, co-occurring tree species maintain fewer roots in shallow soils and their growth is regulated by photoperiod, so they are less vulnerable to spring freezes (Hennon & Shaw, 1994). These species-specific differences explain yellow-cedar's tolerance of marginal habitats and its unique vulnerability to root freezing and decline (D'Amore *et al.*, 2009).

Given projections of future climate change and regional warming in coastal British Columbia, the overall bioclimatic envelope of yellow-cedar is predicted to expand over the next 40 years; however, the effects will vary in different parts of its distribution (Hamann & Wang, 2006). For example, new seedlings are establishing at a greater rate in northeastern British Columbia (Carrarra

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*et al.*, 2003). Similarly, we might expect yellow-cedar to increase establishment at high elevations, where growth rates have increased with warm temperatures. In contrast, the populations growing at low elevations are susceptible to declining snowpacks and decreasing tree survivorship, resulting in a contraction of the species' range closer to the coast.

The future of yellow-cedar along the coast of British Columbia is uncertain, but the species is likely to continue to decline and decrease in range at low elevations. High rates of yellow-cedar mortality are already leading to ecologically relevant changes in stand structure, composition and productivity (Hennon *et al.*, 1990*a*, 1990*c*, 1992, 2002; Stan *et al.*, 2010). In the field, we have observed a variety of stand responses. At some sites regeneration of yellow-cedar is evident. However, declining and dead yellow-cedar may be replaced by lodgepole pine (*Pinus contorta* Douglas ex Louden) near bogs and western hemlock or mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) on many hillslopes, indicating a shift in the composition of tree species in many coastal ecosystems.

In summary, the decline of yellow-cedar highlights several aspects of our understanding of how forests in coastal BC respond to climatic change in a variety of ways. (1) Modest but persistent directional change in temperature may affect the relative fitness of tree species, forest composition and structure. If current conditions continue then western hemlock is likely to become increasingly dominant in the landscape as yellow-cedar die. (2) Small changes in mean climatic conditions can result in large, unexpected ecological change. When late-winter temperatures increase above freezing, reduced snowpack and ground insulation leave yellow-cedar roots susceptible to low soil temperatures during freeze events. A small change in late-winter temperatures in forests located near the rain–snow threshold is contributing to the death of yellow-cedar. (3) Extreme climate events can cause abrupt responses (Parmesan, 2006). Frequencies of extreme events such as freeze–thaws are increasing disproportionately to mean climates (Field *et al.*, 2007) and it is these extreme freeze events that are considered the primary cause of the widespread mortality of yellow-cedar trees.

## Climate-mediated disturbance regimes

Fire and insects are examples of climate-mediated disturbance agents that have significant impacts on the many forests in British Columbia (Wong *et al.*, 2003). Historically, in the mountain forests of the British Columbia interior, fire frequency generally decreased and fire severity increased with elevation (British Columbia Ministry of Forests & Ministry of Environment, 1995). High-frequency but low-severity fires maintained the grassland–forest ecotones in warm, dry valley bottoms. These fires also influenced the composition and structure of low-elevation forests. In the cool, mesic, subalpine forests growing at high elevations, fires burned less frequently but they were more commonly high-severity, stand-replacing fires. At intermediate elevations, fire regimes included a mix of fire frequencies and severities (Schoennagel *et al.*, 2004). As well, at any given location along this elevational and climatic gradient, fire frequency and severity vary over periods of years to decades to centuries in response to climatic variation and other drivers (Agee, 1998; Lertzman *et al.*, 1998).

Our research on fire regimes in the mountain forests of British Columbia aims to reconstruct fire history and quantify the climate conditions associated with historic fires. The information is needed to anticipate potential impacts of global warming on future fire regimes and the interactions between fire and other disturbance agents. We have used tree rings to reconstruct fire frequency of 30 montane (900 to 1550 metres above sea level) forests in the East Kootenay Region of British Columbia (Cochrane, 2007; Daniels *et al.*, 2007). All study stands included large-diameter western larch (*Larix occidentalis* Nutt.), Rocky Mountain Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), or ponderosa pine (*Pinus ponderosa* C. Lawson) trees and were in the Montane Spruce biogeoclimatic zone (Meidinger & Pojar, 1991). Each stand was structurally complex with an upper stratum of veteran trees that established prior to 1870, after which Europeans arrived and settled in the region.

Fire scar records from the 30 sites were based on 249 fire-scarred cross-sectional samples that yielded 568 fire scars between 1509 and 2003 (Cochrane, 2007; Daniels *et al.*, 2007). At the site level, median fire intervals ranged from 10 to 78 years, with two to 138 years separating successive fires within sites. Our reconstructions indicate historic fires formed a mixed-severity regime that included both frequent, low-severity fires and infrequent, high-severity fires. Although frequent, the impacts of these fires were relatively low. Many large trees survived, although some were damaged and formed fire scars. The greatest negative impacts likely were to seedlings, saplings and understorey trees. In essence, these low-severity fires created and maintained old-growth forests and unique wildlife habitats. High-severity fires that initiated a new generation of forest also burned in the East Kootenays, but they burned less frequently.

The fire regime changed abruptly during the second half of the 20th century (Cochrane, 2007; Daniels *et al.*, 2007). Over the 400 years between 1540 and 1940, fires

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burned and scarred trees somewhere in the sampled East Kootenay forests once every three years. Given this historical frequency, we expected about 20 fire years since the 1940s, but our fire scar records included only six fire years. The low incidence of fires since the 1940s is partly due to variations in climate, but largely explained by cessation of burning by First Nations and very effective fire suppression.

Climate variation is an important driver of the mixed-severity fire regime in the East Kootenay forests. Historic fires burned during pronounced droughts and decades of warm and dry climate caused by changes in the circulation patterns in the Pacific and Atlantic Oceans, which affect regional climate (Daniels *et al.*, 2007). Historically, fires burned under three conditions: (a) the Pacific Decadal Oscillation (PDO) was in a warm phase and the Atlantic Multidecadal Oscillation (AMO) was in a cool phase; (b) during El Niños when both the PDO and AMO were in the warm phase; and (c) during La Niñas when both the PDO and AMO were in the cool phase. Fires were least likely to burn when the PDO was in the cool phase and the AMO was in the warm phase. The latter conditions prevailed from 1946 to 1966 and were not conducive to fire. In contrast, conditions suitable for fires have dominated since 1981 since both the PDO and AMO have been in the warm phase, meaning fires are most likely to burn during El Niños. In fact, El Niño conditions have dominated global climate during the past 30 years. These climate conditions explain the severe drought and fires that burned in British Columbia in 2003, but climate does not explain the low occurrence of fire scars in recent decades.

In large part, the decrease in fire frequency and increase in intervals between fires are caused by human actions, independent of climatic variation and change. Fire frequency began to decrease in the early 20th century due to human land-use change. Agriculture, ranching and mineral exploration for mining changed the distribution of forests and fuels, decreasing the spread of fires. These processes indirectly excluded fires and reduced the occurrence of fire scars. In the past *c*. 70 years, low-to-moderate severity fires were essentially eliminated from many forests due to very effective fire suppression, leading to the 'fire-suppression paradox'. By trying to protect our forests from fire, many dry forests of the East Kootenays may have become more susceptible to severe fires. In absence of the low-to-moderate severity fires, tree densities are sustained and fuels gradually build up, increasing the chance of a severe stand-replacing fire that is difficult to control and may threaten human communities (Filmon, 2004).

This new knowledge of fire history and climate–fire interactions can help us anticipate the potential impacts of global warming on future fire regimes of the East Kootenay forests. Historically, fire was associated with years and decades of warm, dry climate. Given observed trends (British Columbia Ministry of Water, Land and Air Protection, 2002) and predictions of reduced snowpacks, longer growing seasons and warmer summer conditions in this region (Christensen *et al*., 2007), we anticipate increased fire frequency in future. As well, fire size and severity may increase with stand-replacing fires more common than stand-maintaining fires particularly in mid- and high-elevation forests (Westerling *et al.*, 2006). Fire severity will also be influenced by the cumulative effects of climate change, human land-use change and fire exclusion. Due to the reduction of low-to-moderate severity fires in many parts of the landscape during the 20th century, accumulated fuels add to the increased risk of severe fires in future.

Other climate-mediated disturbances interact with fire. For example, the ongoing mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak is particularly extensive and severe, affecting >130 000 km$^2$ of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) forests in British Columbia (Kurz *et al.*, 2008). Warm climate has contributed to this outbreak in multiple ways (Logan & Powell, 2001; Stahl *et al.*, 2006). Drought stresses the host lodgepole pines, making them vulnerable to the insects (Safranyik *et al.*, 1975). Temperature controls vital aspects of the life stages of mountain pine beetle and climate synchronizes the life cycles of beetles over large areas (Logan *et al.*, 2003). Historically, winter temperatures of −40 °C limited populations by freezing the beetles, as would temperatures of −25 °C to −29 °C in autumn or late spring when cold-hardening of beetle tissues is incomplete (Safranyik & Wilson, 2006). However, with an increase in mean winter temperatures during recent decades, the frequency of population-limiting cold temperatures has decreased (Stahl *et al.*, 2006) and mountain pine beetle range is expanding northward and eastward (Carroll *et al.*, 2004; Kurz *et al.*, 2008). Superimposed on these climate effects, recent research also implicates fire exclusion as factors contributing to the extensive, mature pine-dominated forests in British Columbia that are ideal habitat for mountain pine beetle (Axelson *et al.*, 2009*a*, 2009*b*). The high degree of tree mortality caused by mountain pine beetle outbreaks results in significant changes to forest structure, including more open tree canopies and increases in coarse-sized fuels as dead trees fall (Axelson *et al.*, 2009*a*, 2009*b*). Increased fuels in mountain pine beetle-affected forests, in combination with warm, dry summer climate, may contribute to aggressive fire behaviour and severe fire effects in future (L.D. Daniels, unpublished data).

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## Summary and conclusions

The case studies presented in this paper illustrate the direct and indirect impacts of climate on the dynamics of three forests in British Columbia. At the sub-continental scale, regional warming was identified as the most probable cause of the doubled mortality rates of trees in old forests of western North America, including southwestern British Columbia. Warm temperatures and climatic water deficits may have directly increased tree stress and rates of death. Potential indirect climatic effects included increased insect and pathogen activity and wind storms resulting in mechanical damage to trees. Concurrent with increased mortality, tree density and basal area declined significantly, indicating either lagged growth responses of surviving trees or long-term decline of many old forests.

The case study on yellow-cedar decline illustrates the direct effects of climate on a single, regionally significant tree species. Specifically, small changes in average climatic conditions, coupled with extreme weather events, can have large ecological effects. Increased temperatures along the north coast of British Columbia and southern coastal Alaska have resulted in decreased depth and duration of the snowpack in low-elevation forests. Reduced snowpack makes yellow-cedar roots susceptible during freeze–thaw events in autumn and late winter. Unable to recover from this damage, these extreme freeze events are considered the primary cause of the widespread mortality of yellow-cedar trees.

The third case study on climate-mediated disturbances in mountain forests illustrates the complex interactions among climate, multiple disturbance agents and human impacts on the environment. In this case study, understanding historic climate–fire interactions was key for anticipating future fire regimes under the predicted influences of global warming. Given the past influences of broad-scale climate patterns on drought and, subsequently, fire occurrence, we anticipate more frequent fires in the East Kootenay region as temperatures increase and the growing season lengthens. Fire severity may also increase due to the cumulative effects of fire exclusion and high levels of tree mortality due to mountain pine beetle. These processes contribute to increased fuel abundance, which increases the chances of a severe burn if a fire is ignited.

In conclusion, research on historic and contemporary forest dynamics illustrates the importance of climate on population dynamics and disturbance regimes. Climatic impacts on forests can be direct or indirect, with the specific mechanisms and processes varying among species and ecosystems. Understanding past climate variation and its effects on forests help us to anticipate the potential effects of global warming. However, factors other than climate, such as land use and other aspects of human environmental change, must be taken into account since they can have contrasting or cumulative effects on climate–forest interactions.

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