Research Report

Migrating Like a Herd of Cats: Climate Change and Emerging Forests in British Columbia

Fred L. Bunnell & Laurie L. Kremsater, University of British Columbia

Abstract

We combine climate tolerances of tree species with probable changes in insect, disease, fire, and other abiotic factors to describe probable changes in distribution of tree species in British Columbia. Predicting changes in forests confronts three major sources of uncertainty: predicting weather and climate, predicting tree species' responses, and predicting changes in factors modifying the trees' responses (e.g., pathogens, insects, and fire). Challenges in predicting weather exist because climate projection models differ and downscaling climate is difficult, particularly where weather stations are sparse. Challenges in predicting responses of individual tree species to climate are a result of species competing under a climate regime that we have not seen before and they may not have experienced before. This challenge is aggravated by the differential response of pathogens and insects, as well as by the effects of changes in fire frequency. We first examine the responses of individual species, then we consider implications for broad regional forests. Despite the uncertainty, some trends are more likely than others. We present estimates of the relative species composition of future forests in British Columbia.

KEYWORDS: climate change; insects; new regional forests; pathogens; moisture stress; tree migration

Introduction

onifers first appeared about 300 million years ago and have since experienced extremes of drought, heat, and cold, encoding this experience into their genomes that are among the largest and most complex of all organisms (Morse et al. 2009). Fossil evidence shows that for millions of years forests have moved across landscapes in response to changing climate. What appears as movement of a species is not a simple product of trees' ability to disperse or migrate. Changes in mortality rates play a major role, as do available substrates and barriers to movement. Though some tree species show great plasticity in their ability to cope with changes in temperature, precipitation, and CO_2 concentrations, this does not preclude them from being influenced by changing climate. Climate, particularly temperature and drought, influences trees' resistance to pathogens and insects.

Several researchers have projected climate envelopes to assess how tree species' ranges are likely to respond (e.g., Hamann and Wang 2006; McKenney et al. 2007;





Vol 13, No 2

Murdock and Flower 2009). Others have reported likely changes in insects and pathogens in response to climate change (e.g., Kliejunas et al. 2009; Woods et al. 2010).

Our objective is to combine basic autecology of tree species and their climate preferences with probable changes in insect, disease, fire, and other abiotic factors to suggest likely changes in the distribution of tree species in BC forests. We first examine responses of individual tree species, and then we consider what those responses imply for broad regional forests in British Columbia.

Bunnell & Kremsater

FORESTS IN

MIGRATING LIKE

A HERD OF CATS:

CLIMATE CHANGE AND EMERGING

BRITISH COLUMBIA

Current forests and methods

Over the past 10,000 years, forests of British Columbia have changed greatly, but slowly from human perspectives. For more than 50 years, we have used the Biogeoclimatic Ecological Classification (BEC) system (Pojar et al. 1987) to describe broad forest types with little major refinement. The BEC system recognizes 16 zones in the province, 12 of which are forested (Figure 1).

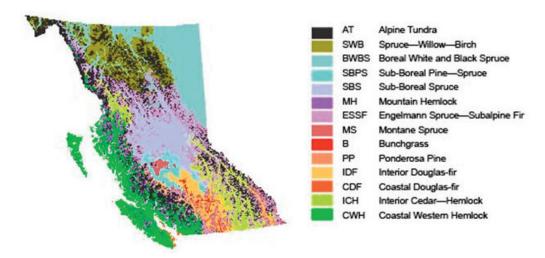


Figure 1: Biogeoclimatic zones of British Columbia; divisions within alpine tundra are not shown. Source: http://www.for.gov.bc.ca/hfd/library/documents/treebook/biogeo/biogeo.htm

Trees comprising the zones reflect the climate of each zone, but that climate is changing differently in various portions of the province, thus differently in various zones (Table 1).

Trees, for which zones are commonly named, will migrate or adapt in response to changing climate, and the long history of many tree species will help them cope with the changes. But the migration of individual species comprising a forest may be more like a herd of cats than a herd of buffalo. Species comprising a zone are unlikely to migrate at the same pace or even the same direction.

The potential redistribution of forested BEC zones in response to changing climate was projected by Hamann and Wang (2006). They compared current distributions of BEC zones and ranges of selected species with distributions described by climate envelopes, and generally obtained good agreement. They also projected those envelopes into the future to assess potential distributions of both BEC zones and tree species. A remaining challenge is to assess how much of those climatically suitable areas will be colonized.

History indicates that trees will migrate and adapt in response to changing climate. They also will encounter problems. Major challenges to migration are seed production, seed dispersal, and appropriate conditions for regeneration. Climate directly influences







Table 1: Changes in seasonal^a and annual air temperatures by the 2050s for regions of British Columbia for an ensemble of Global Circulation Models

Change in air temperature (°C)					
Region	Winter	Spring	Summer	Fall	
Columbia Basin	1.8	1.5	2.4	1.9	
Fraser Plateau	1.9	1.6	2.0	1.8	
North Coast	1.5	1.3	1.4	1.5	
Peace Basin	2.4	1.7	1.8	1.8	
Northwest	2.0	1.6	1.8	1.7	
Okanagan	2.0	1.8	2.6	2.0	
South Coast	1.5	1.3	1.7	1.6	
Change in Precipitation (%)					
Region	Winter	Spring	Summer	Fall	
Columbia Basin	7	9	-8	8	
Fraser Plateau	8	10	-4	11	
North Coast	6	7	-8	9	
Peace Basin	9	9	3	10	
Northwest	10	9	4	8	
Okanagan	5	12	-8	8	
South Coast	6	7	-13	9	

Source: Modified from Pike et al. 2010

how well and how frequently trees produce seed. Mode of seed dispersal (e.g., by wind or by bird) influences the distance seed is dispersed, while climate and other circumstances, including fire (also influenced by climate) and availability of soil, determine whether the environment seeds reach is favourable for regeneration. For example, trees adapted to subalpine climates cannot simply march up mountains as temperature increases, because formation of soil at high altitude is slow. If trees are "trapped" at lower elevations by unfavourable soil above them, or by the presence of established plants on what little soil is present, they may perish before having a chance to migrate upwards.

Tree species and populations of trees also have different genetic potential to respond to various climate variables, such as cold and moisture stress. Depending on their location and adaptability, in the near term they may not need to migrate. They will need to adapt to the changed climate in terms of growth and reproduction, and to how competing tree species and potential pathogens adapt and respond to the same climate changes.

The variety of relationships acting simultaneously (some noted above), in addition to the increasingly erratic extremes accompanying climate change (IPCC 2011), make global weirding a more appropriate term than global warming (Friedman 2008; Bunnell et al. 2011). Weirding encompasses all responses to global warming, and, in this case, different responses of individual tree species to fire frequency, insects, fungi, and other organisms that are, themselves, responding to climate variables.

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater





All the variables noted as affecting future distribution of trees are in some way a function of climate. The 23 GCMs (General Circulation Models or Global Climate Models) summarized by the Intergovernmental Panel on Climate Change, do not predict the same regional climates across the globe or within British Columbia (see Tebaldi & Knutti 2007; Annan and Hargreaves 2010; Mbogga et al. 2010; Werner 2011). The models generally agree on the direction of temperature change, although there are short-lived temporal and longer-lived regional exceptions, such as the China effect and the Asian brown cloud (Gustafsson et al. 2009; Kaufmann et al. 2011). There is less agreement on where and by how much precipitation will change. Values in Table 1 are averages across models, but nature will choose only one course and is under no obligation to follow the average of our best estimates. The result is that there is uncertainty in both the direction of some climate variables, and the magnitude and rate of change of all variables. The actual effect of those changes on the variety of variables influencing trees' response is still more uncertain.

Species distribution models combine maps of species' presence or abundance with maps of environmental variables to infer causal relations. The mathematics underlying these models have improved significantly, but that avails relatively little when there is great uncertainty of how climate variables, different pathogens, moisture stress, and other variables interact. Consequently, there is no rigorous or tidy approach to incorporating all the effects we currently expect to influence tree responses, let alone the as yet unanticipated effects. Our approach is to note current trends in factors affecting distribution and, where possible, their known response to climate variables for individual tree species. The aggregated impact on a species is then compared to other tree species that share the current distribution. Rather than consider BEC zones as units, we examine selected foundation tree species sensu Dayton (1972). This allows us to estimate broadly what the forest cover may become over large areas of the province. Though the approach is far less precise than modelling outcomes resulting from a specific tree species' or tree pathogen's response to climate variables (e.g., Hamann & Wang 2006; Murdock & Flower 2009), it is potentially more accurate (though still highly uncertain) because known effects are not omitted.

The trees that make the forests

In forested ecosystems, trees are the foundation species. They define forest structure, alter microclimates, and their mass and chemical composition contribute substantially to ecosystem processes, such as decomposition. We know from experience elsewhere that when there are only one or two foundation species in a forest; there is little functional redundancy (Ebenman & Jonsson 2005). The loss of such foundation species can lead to rapid, potentially irreversible changes in ecosystem structure and function (Ellison et al. 2005). Most BEC zones are dominated by two or three species that give a zone its character. As climate change continues, species mixtures may first become more equitable across more species, but will likely settle down to only a few species, some different from those currently present.

In this article, we consider responses of 16 tree species. Not all are foundation species at the scale of BEC zones, but are for smaller areas, such as the whitebark pine (*Pinus albicaulis*) in the subalpine. Responses of these species will have major effects, not simply on the structure of the forest, but also on the associated flora, fauna, and fungi. All tree species are likely to be impacted, so our consideration of only 16 undoubtedly overlooks some interactions among species that will result from climate change.

Below, we note differences between distributions of trees based solely on climate envelopes and those acknowledging climate's potential effects on tree pathogens or other

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater

> > 4



JOURNAL OF Ecosystems & Management

environmental factors. Using climate envelopes, Hamann and Wang (2006) obtained good fits between predicted and current distributions. Below, we cite their projections of net change in distribution based solely on climate. Their projections provide an opportunity to compare simple climate envelopes to a broader-based approach. Climate models predict the direction of change far better than the rate of change. Unless noted, the following comments attempt to address conditions to about 2055, comparable to projections by Hamann and Wang (2006).

MIGRATING LIKE
A HERD OF CATS:
CLIMATE CHANGE
AND EMERGING
FORESTS IN
BRITISH COLUMBIA

Bunnell & Kremsater

Lodgepole pine (Pinus contorta)

Lodgepole pine is the most common tree in BC. Its widespread nature results partly because it can tolerate water-logged and dry sandy soils that other species cannot. Even before the mountain pine beetle outbreak, this species contributed the largest portion of volume cut within the province. It is a significant component of several BEC zones (e.g., Subboreal Pine-Spruce, Montane Spruce, Sub-boreal Spruce). The climate envelope of the species, as projected by Hamann and Wang (2006), expanded by 15%; the actual range may not expand.

The largest mountain pine beetle (*Dendroctonus ponderosae*) outbreak in history was a product of three phenomena: large amounts of older, less healthy pine; winters too mild to kill overwintering beetle larva; and, temperatures warm enough to increase beetle growth and breeding rates (Carroll et al. 2004, 2006; Safranyik & Wilson 2006). These increased attacks on pine are being replicated by other insects (Heineman et al. 2010). Throughout the province there are scattered patches of surviving older lodgepole pine, but also more extensive tracts of young lodgepole pine that were not large enough to attract the beetle during its initial attack. Unfortunately, mild winters and warm days are likely here for a long time yet (Carroll et al. 2006; Dawson et al. 2008; Werner 2011), but there is some hope that the changing climate may cause asynchrony between beetle life stages and their environment that may eventually hinder their reproduction and spread. This uncertain future for lodgepole is troubling because the species inhabits sites that other trees cannot. Though predicted increases in fire frequency will encourage potentially dense stands of lodgepole, the beetles will remain, ready to attack once trees grow large enough (Li et al. 2005). Moreover, the mountain pine beetle is just one of many insects and diseases that attack lodgepole pine (Swift et al. 2002; McCulloch et al. 2009; Heineman et al. 2010). Some of these, like red-band needle blight (Dothistroma septosporum), are infecting more extensive areas than ever before in the province (Woods et al. 2005; McCulloch & Woods 2009), killing foliage and eventually whole trees. The increased severity and extent appear linked to rain during periods of warmer temperatures (Woods et al. 2005), which, given that periods of both more drought and summer rain appear likely, makes attack and greater damage more probable.

Ponderosa pine (Pinus ponderosa)

British Columbia's driest forests are ponderosa pine forests. On many upland sites, it is the only tree present that can provide cavity sites and other requisites that support biodiversity. Based on climate envelopes alone, the species range is expected to triple with the effects of climate change; significant range expansion appears less likely. Mountain pine beetle has achieved sufficient densities that ponderosa pines are now being devastated (Westfall & Ebata 2009). With much of the lodgepole pine dead, the bark beetle may not again achieve sufficient numbers to overwhelm ponderosa pine. It is equally possible that increasing drought, predicted by most models for the southern interior (e.g., Table 1;





Mbogga et al. 2010; Werner 2011), will sufficiently weaken trees' ability to contest insect attack, and consequently, ponderosa pine will continue to decrease.

Whitebark and limber pine (Pinus albicaulis and P. flexilis)

The whitebark and limber pines are not timber-producing species, nor do they occupy much area in BC. They inhabit subalpine areas in the Rocky Mountains, the east slope Cascades (whitebark pine), or only the Rockies (limber pine). They often are the only tree species surviving just below alpine tundra, attaining the highest elevations of any tree in the province (shrubby juniper excepted). As the major tree at the highest elevations, they provide shade and cool soil that allows the establishment of smaller plant species. Projected climate envelopes suggest gains in a suitable range of 3% for whitebark pine and 281% for limber pine; however, Hamann and Wang (2006) acknowledged that the latter projection was unrealistic.

Both species could become examples of the "rapture hypothesis," running out of suitable habitat above them, as the lower boundaries of subalpine and alpine areas rise with increased warming (e.g., Bunnell et al. 2011). There is likely little suitable soil higher on the slopes. While moving up is limited, moving northward is not easy, they cannot move down slope to ascend another mountain further north because other tree species are better adapted to the environments lower down. Sequestered where it is, in extreme southeastern British Columbia, limber pine faces the greatest challenge to surviving the effects of climate change. Whitebark pine has a better opportunity to migrate, but must depend on Clark's nutcracker (Nucifraga columbiana), grizzly bears (Ursus arctos), or other animals to move its seeds over or through the valleys. Both tree species suffer from pine beetle attack and white-pine blister rust (Cronartium ribicola), pathogens that are favoured by the changing climate. Surveys in British Columbia suggest that if the rust does not kill these species, the beetle will (Campbell & Antos 2000). Similarly, Mountain hemlock (Tsuga mertensiana) plays an analogous role in subalpine forests of the coast. Though it is not subject to bark beetle attack, it is equally unlikely to find well-developed soils at higher elevations, limiting its ability to adapt to a changing climate.

Subalpine fir (Abies lasiocarpa)

Subalpine fir is the second most widely distributed tree in the province, occupying coastal and interior sites from 49° to 60° N. It is a dominant tree in several BEC zones, including Engelmann Spruce-Subalpine Fir, Sub-boreal Spruce, Spruce-Willow-Birch, Interior Cedar-Hemlock, and Montane Spruce (see Figure 1). Based on climate envelopes, Subalpine fir is projected to experience a net loss of range of 12%, as it prefers cooler temperatures and extends its growing season less at higher temperatures than do lodgepole pine and interior spruce (Green 2005). The species will generally also decrease at lower elevations generally, and at higher elevations in the southern interior. Range expansion is likely to occur at higher elevations in the north. Unlike many tree species, climate change so far does not appear to have greatly encouraged pathogens whose activities can counter predictions based on climate alone (Woods et al. 2010).

Because pathogens of white spruce (following) are encouraged by the current climate change, subalpine fir is likely to comprise greater proportions of northern forests. From the perspective of commercial forestry, this is unfortunate because subalpine fir commands a lower price than does White spruce. In some situations, forest pests also will impact subalpine fir. Tomentosus root rot (*Inonotus tomentosus*) may flourish in warmer conditions, provided there is sufficient moisture (likely in the north); western balsam

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater



bark beetle (*Dryocoetes confusus*) seems to be expanding attacks on subalpine fir (Westfall & Ebata 2009), likely encouraged by warmer winters.

White spruce, Engelmann spruce and black spruce (Picea glauca, P. engelmannii, P. mariana)

White spruce, along with its hybrids with Engelmann and black spruce, is the third most widely distributed tree "species" in British Columbia, closely following subalpine fir, stretching from 49° to 60° N. It is a dominant tree in several BEC zones (Figure 1), including Boreal White and Black Spruce, Sub-boreal Spruce, Spruce-Willow-Birch, and Sub-boreal Pine-Spruce and occurs south through the Interior Cedar-Hemlock zone. As such, white spruce is a commercially important timber species. Engelmann spruce is characteristic of continental subalpine forests. In its pure form, it occurs mainly in the Rocky Mountains and does not extend as far north as does white spruce. It is a dominant tree in the Engelmann Spruce-Subalpine Fir zone, the most extensive BEC zone in the province. Black spruce is a smaller, usually non-commercial species, more restricted to northern regions and wetter sites than is white spruce. It is a major tree species in the Boreal White and Black Spruce zone, the second largest BEC zone in the province. Projected net changes based solely on climate envelopes are -23% for white spruce, +48% for Engelmann spruce, and -22% for black spruce.

White spruce appears likely to migrate northward, but unlikely to retain its abundance. The relationship between white spruce growth and temperature is not simple. An extension of growing season at high northern latitudes seems clear from satellite observations of vegetation extent and duration (Keeling et al. 1996; Myneri et al. 1997), but a review by Soja et al. (2006) shows an inverse relationship of white spruce growth with temperature. Temperature-induced drought appears to cause a decline in growth of white spruce (Barber et al. 2000); however, drought has not yet been documented in northern BC.

Spruce beetle (*Dendroctonus rufipennis*) is killing spruce in a fashion analogous to the mountain pine beetle in pine, and rates of attack increase as temperatures warm (Candau & Flemming 2008). To date, the most catastrophic impacts have been farther north, precisely in the direction spruce will have to move. By 2004, outbreaks of spruce beetles that had begun around 1990 had caused extensive mortality of spruce across about 1.4 million ha of forest in Alaska and 350,000 ha in the Yukon (Berg et al. 2006; Soja et al. 2006). A warming climate encourages a one-year life cycle for the spruce beetle, yielding larger populations and more intensive outbreaks (Logan et al. 2003). In BC, the beetle is predicted to increase in the north and decrease in the southern part of the province (Murdock & Flower 2009). White spruce is also becoming more susceptible to *Tomentosus* and other root rots, and likely the western spruce budworm (*Choristoneura occidentalis*). Root rots often are more aggressive when trees are stressed (Kliejunas et al. 2009; Klopfenstein et al. 2009), and the budworm kills trees more frequently in warmer, drier climates.

In the boreal of BC, it is unclear whether conditions will get drier or wetter (Werner 2011). If conditions get wetter, then white spruce may remain well adapted, but spruce bark beetles will still be encouraged and able to kill large proportions of older trees; however, with increased temperatures, conditions must be considerably wetter to maintain the same available soil moisture and avoid moisture stress. Conversely, if conditions get drier the area burned may increase. In this case, old spruce would decline and lodgepole pine would increase, but conditions would remain favourable to the pine beetle. The area burned in boreal regions of Canada already has increased substantially, but area burned

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater

> > 7



JOURNAL OF Ecosystems & Management

in BC has decreased with less frequent summer drought, with about a 0.5° C increase in temperature, but a 20-30% increase in precipitation (Mote et al. 2005; Meyn et al. 2009, 2010). See the next section for variability in projected fire regimes.

Engelmann spruce is more constrained than white spruce. It faces the same array of more favourable climate conditions for its enemies (insects, fungi, and fire), but is more restricted to montane and subalpine regions. Moving upwards, it confronts unfavourable soils, while moving northwards it must enter lower elevations where it will contend with better adapted tree species.

Black spruce appears to experience less bark beetle or root rot damage than other spruce species. Tomentosus, for example, is found on the mesic sites where white spruce is abundant, but not on the subhydric and hydric sites that host black spruce (Bernier & Lewis 1997). Most scenarios suggest that black spruce on cold, wet sites, or on northern aspects will not be greatly affected by climate change. Although climate change is increasing moisture stress for white spruce (Barber et al. 2000), we found no reports of moisture stress from wetter sites inhabited by black spruce. In the eastern Canadian boreal, Huang et al. (2010) suggested warming will increase growth of black spruce, paper birch (Betula papyrifera) and jack pine (Pinus banksiana) north of 49°, but decrease growth rates further south.

In British Columbia, black spruce is largely restricted to the northeastern corner of the province that is underlain by discontinuous permafrost, causing "drunken forests," where permafrost is melting and the trees are tipping. Thaw rates of permafrost have increased over the past 50 years across the North American and Russian boreal (Englefield 1994; Camill & Clark 1998; Romanovsky et al. 2002). Consequently, rising water tables are reducing moisture stress, but simultaneously undermining the stability of all tree species.

Douglas-fir (Pseudotsuga menziesii)

Douglas-fir is a dominant tree in four BEC zones: Interior Douglas-fir, Coastal Douglasfir, Coastal western hemlock, and the Ponderosa pine zones. Based on climate envelopes, a net increase of 71% is projected for Douglas-fir. To date, Douglas-fir bark beetle (Dendroctonus pseudotsugae) has not responded as rapidly to climate change as the mountain pine beetle, but outbreaks have increased over the past 8 years and have expanded north in BC (Westfall and Ebata 2009). Recent outbreaks in Oregon (Powers et al. 1999) were larger than any in the past 35 years. Similarly, in Washington outbreaks in 2009 were the largest ever recorded (Johnson et al. 2010).

Douglas-fir beetle outbreaks are often associated with drought and windthrow (Furniss & Carolin 1977; McMullen 1984; Powers et al. 1999) and are correlated with moisture stress and non-vigourous or small-crowned trees (Kano 2006). Increasing moisture stress in the Interior Douglas-fir and ponderosa pine zones will favour the beetle (Table 1). Growing evidence predicts increases in bark beetle as a result of climate change, given that high temperatures at time of gallery building increase female fecundity (Kano 2006), while warm, dry summers increase flights without damage by rain. It is not known if Douglas-fir tussock moth (Orqyia pseudotsuqata) will increase, but attacks are now extensive in some areas (Westfall and Ebata 2009).

Western spruce budworm has a long history of outbreaks in dry Douglas-fir dominated forests of BC (Campbell et al. 2006). Current budworm outbreaks in the province are notable for their expansion into higher elevations (MacLauchlan et al. 2006). The most recent outbreak period, 1995 to the present, has seen the budworm move north into Douglas-fir stands that had no prior records of infestation. As the climate becomes

MIGRATING LIKE A HERD OF CATS: **CLIMATE CHANGE** AND EMERGING **FORESTS IN BRITISH COLUMBIA**

> Bunnell & Kremsater



more conducive to budworm, the stand structure is also at a higher hazard/susceptibility than in the past.

With a warming climate, the budworm may expand its range to encompass the entire range of its primary host, Douglas-fir (Murdock & Flower 2009). In the interior of the province, we could lose most Douglas-fir from all but the higher elevations in the southern interior and in the wetter parts of the Interior Douglas-fir Zone. Most of the northward expansion of Douglas-fir will be into areas currently occupied by species such as white spruce or lodgepole pine. Although amounts of summer precipitation are expected to decline in the central interior (Fraser Plateau in Table 1), they begin from a higher level than in the southern interior, and moisture stress is not predicted to increase as much. The species appears secure in the Coastal Douglas-fir zone.

Western hemlock (Tsuga heterophylla)

Western hemlock is a dominant species in only two BEC zones: Coastal Western Hemlock and Interior Cedar-Hemlock. Based on climate envelopes, a net gain of 85% is projected for western hemlock as a consequence of warming. Like Douglas-fir, there is no strong evidence yet of the weirder effects of climate change; moreover, western hemlock has the advantage of expanding from at least three major loci, including the near maritime climate in the Kootenays (Figure 1). If weirder effects occur, they will most likely appear as a defoliating insect, the hemlock looper (*Lambdina fiscellaria lugubrosa*). Outbreaks of the looper are often preceded by summer moisture deficits. Future summers will clearly be warmer, but it is less clear how dry they will become where hemlock currently exists. Most climate change models predict warmer and drier summers for coastal BC (Table 1), the very conditions that historically have triggered outbreaks of the looper (McCloskey et al. 2009).

The combined effects of more frequent droughts, changes in forest cover, and expanded range of western hemlock due to climate change may result in increased frequency, size, and severity of looper outbreaks in the future. As a result of a warming climate, outbreaks of the looper have been forecast to occur more frequently and to be more widespread in coastal BC (McCloskey et al. 2009).

Western redcedar (Thuja plicata)

Western redcedar is dominant in the same two BEC zones as western hemlock, and can be abundant in the lower elevations of the Mountain Hemlock Zone. Based on climate envelopes, a net gain in suitable area of 89% is projected. That appears unlikely to be realized, even though, like western hemlock, it has three loci from which it could expand. Redcedar is a relative newcomer to the coast, where paleoecological records suggest it became a dominant species only about 4,000 years ago as the climate became cooler and wetter. The age structure of existing stands (Daniels 2003) indicates that the species experiences frequent, though irregular disturbances and favourable periods, and shows little constancy in its recruitment. On the coast, the warming and summer drying trends currently favour Douglas-fir and potentially Garry oak (*Quercus garryana*), but precipitation projections are particularly uncertain.

Currently, more redcedar trees on the coast appear to be moisture stressed, losing branchlets and developing dead tops. There are abundant old spike-topped cedars in the Interior Cedar-Hemlock zone as well, but it is unclear whether this is a result of too little moisture in the soil, breakage of fine roots by windstorms (both increase the difficulty of getting water up to the top branches), or other combinations of stresses and pathogens (Seebacher 2007).

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater

> > _



Yellow-cedar (Chamaecyparis nootkatensis)

Yellow-cedar is common in wetter parts of the Coastal Western Hemlock zone and in the Mountain Hemlock zone (Figure 1). It is a slow-growing tree, found more commonly in older stands. Based on climate envelopes, a net gain in suitable area of 17% is projected. That assumes lower elevations will become less favourable, while higher elevations become more favourable. Where it has been assessed in southeastern Alaska, yellow-cedar has declined over 200,000 ha, primarily at lower elevations; this decline extends 150 km south into British Columbia (Hennon et al. 2005). Preparation for growth and decreased frost resistance (de-hardening) is particularly temperature sensitive in yellow-cedar. Decline appears to be caused by reduced snowpack, early de-hardening, and freezing injury, all of which are induced by warming (Beier et al. 2008; Hennon et al. 2005). Yellow-cedar is often shallow-rooted in wetter soils, and reduced snowpack provides less insulation against soil freezing (Hennon et al. 2005, 2006). As with other species, it is unclear whether it can simply move upslope as temperatures increase, but, if it cannot, it is likely to decline.

Western larch (Larix occidentalis)

Western larch usually grows in mixed forests in valleys and lower slopes of mountains in the southern interior, but can be found in pure groups after severe wildfire. Low temperatures currently limit its distribution because it is sensitive to frost damage. Thus, western larch should respond well to warming, drying climates because it demands full sunlight, grows well on fire-blackened soil, its roots are deep and its bark thick, and it has a habit of shedding lower branches which makes it well-adapted to fire (BC Ministry of Forests and Range n.d., a). Climate envelopes alone suggest a three-fold expansion in distribution. Western larch usually are not attacked severely by root rots, but larch casebearer (Coloephora laricella), western spruce budworm, and larch needle blight (Hypodermella laricis) all affect the species. It is not clear how these will respond to the changing climate. An increase in range of larch (see projections by Rehfeldt & Jaquish 2010) would benefit the forest industry, as its wood is one of the strongest among conifers. Commercial planting of western larch continues to increase in BC with 6 to 7 million seedlings planted annually over the past five years (BC Ministry of Forests and Range n.d., b). That currently appears a wise decision.

Hardwoods

Hardwood trees are also confronting problems associated with climate change. Attributes of aspen (Populus tremuloides)—high genetic variability, light seed broadcast over large distances, the ability to re-sprout after disturbance, and tolerance of high temperatures and light—suggest it will be more successful in tolerating or migrating in response to climate change than its associates. It is, however, encountering problems with insects and disease in concert with temperature and moisture stresses. Aspen dieback has become conspicuous over parts of the southern boreal forest and aspen parkland in western Canada, largely due to drought and defoliation by tent caterpillars (Malacosoma disstria; Hogg et al. 2002, 2008). Climate change will exacerbate both (Johnston et al. 2010); indeed, forest tent caterpillar and aspen leaf miner (Phyllocnistis populiella) were recently at outbreak levels in Alaska (Juday et al. 2010).

Because of its pioneering ability and capacity to reproduce vegetatively, it is likely that where insects and/or fire have killed conifers, aspen will occupy the sites. Some climate projections suggest that, where soil conditions are suitable, trees will colonize a broad front of currently treeless tundra, often preceded by a transitional savannah phase like the aspen parkland of the Prairie region. Other projections indicate that portions of

MIGRATING LIKE A HERD OF CATS: **CLIMATE CHANGE** AND EMERGING FORESTS IN **BRITISH COLUMBIA**

> Bunnell & Kremsater



the taiga will become shrubland (Soja et al. 2006; IPCC 2007; Tchebakova et al. 2009). Confusion results from our uncertainty in projecting relative drying (e.g., Mbogga et al. 2010) and the consequences of melting permafrost. Across the boreal, permafrost is thawing earlier and freezing later in the year, increasing run off and drying out the soil in some places, while pooling water in others (e.g., Turetsky et al. 2007). Since balances between moisture and temperature govern available soil moisture, and these remain unclear, the impact of climate change on colonization of the tundra by trees is unknown.

Poplar subspecies (*Populus balsamifera* subsp.) share many of the fungal and insect pathogens of aspen, but have not shown similar decline syndromes. Currently, they are not predicted to respond greatly to a changing climate. Decline of paper birch is evident throughout much of southern BC, and is region-wide rather than localized (e.g., Vyse & Simard 2007). The decline results from several factors working in concert to prevent normal tree growth, reduce the tree's defence mechanisms, and cause top-kill and tree death. An insect–pathogen complex of bronze birch borer (*Agrilus anxius*), several birch leafminer species (e.g., *Fenusa pussila, Profenusa thomsoni*), and fungal pathogens (*Armillaria*, butt and trunk rots, leaf spot and cankers) is suspected (Woods et al. 2010). Not only does the changing climate damage birch vitality, but the damage also reduces its resistance to insects and fungi, while the changing climate favours them, leading to increased mortality. Climate envelopes alone suggest an approximate 40% increase in the range of birch, which currently seems unlikely.

New regional forests

The preceding review reveals that trees are more likely to migrate like a herd of cats than a herd of bison – tree species in the forest or "herd" will not move at the same pace or direction, unlike animals in a herd of bison. Such a scattered pattern has recently been quantified in forests of the eastern United States (Zhu et al. 2012). Climate change affects trees and the resulting forest in four different ways. First, it can significantly reduce trees' ability to grow and reproduce, most obviously through moisture stress. Second, it can fool the tree into doing something harmful to itself by providing untimely cues for physiological responses (e.g., hardening and de-hardening). Uncommonly warm periods, even if short, can cause trees to begin growth when attempted growth is damaging. This phenomenon appears to be killing low elevation yellow-cedar, by inciting roots to be active when frost appears, creating fine root mortality and subsequent crown death. Third, the same climate that is stressing trees can favour insect and fungal pathogens; the confluence of these events can be lethal. Fourth, a changing climate can alter the frequency and magnitude of forest fires.

Of these four potential climatic impacts on forests, data are most readily available for fire. Predictions of future fire regimes develop correlations between fire and weather variables, and then apply the correlations to day-by-day projections of weather by climate models. There are two barriers to interpretation: 1) the 23 GCMs encouraged by the IPCC are different and predict different weather; and 2) increasing variability or ruggedness in topography reduces predictability. Even in the less rugged boreal, predictions are highly variable. When predictions of fire occurrence in the boreal are converted to area burned, studies predict increases of 7% to about 2000% in area burned annually (Huggard & Kremsater 2011), with an even spread (on log-scale) across intervening values. The highest of these estimates are clearly unrealistic, equating to impossible stand-replacing fire cycles. There are fewer studies of more southern forests, and though estimates again vary among models, they suggest a large increase in area burned, of 78% by 2055 (Spracklen et al. 2009) and more than double by 2090 (Flannigan et al. 2005).

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater





Projections are highly variable and fire suppression is almost never considered. Most studies projecting fire in American forests take a much more complex view of forest disturbance than do Canadian studies, emphasizing the interaction of harvest, fire suppression, fuel build-up and treatment, and relationships of these with insects, fire, and climate change (e.g., Stephens et al. 2009; Parker et al. 2006; Youngblood et al. 2009).

Given that these are all projected impacts, all four major climatic influences on forests are uncertain. Similarly, permafrost melt across large areas is also a new phenomenon, making predictions of the consequences in boreal forests difficult and imprecise. The direction of change, however, is much clearer than the rate. IPCC models are each somewhat different and do not project the same amount of change in climate variables (e.g., Mbogga et al. 2010; Werner 2011); moreover, global and regional examples of positive feedback have been identified that are increasing the rate of warming (e.g., faster melt rates of sea ice, glaciers, permafrost, and snow fields). Ultimately, the models are not keeping pace with our understanding. Given the uncertainty, we can do little more than offer reasoned estimates of how regional forests will look in the future We have limited the timeframe for which effects are evaluated to one rotation or shorter (Table 2); estimates summarized in Table 2 are based on projection to about 2055.

Table 2: Probable trends in area occupied by major species comprising current forested Biogeoclimatic Zones in British Columbia under generally warmer, drier conditions. Zones are ordered by area, from largest to smallest.

BEC Zone	Major species	Winners and losers ¹	
Engelmann Spruce -Subalpine fir	Engelmann spruce, subalpine fir, lodgepole pine	subalpine fir ↑ alpine larch ↑ Engelmann spruce ↓ lodgepole pine ↓	
Boreal White and Black Spruce	white spruce, trembling aspen, lodgepole pine, black spruce, balsam poplar, birches	trembling aspen ↑ or ↓ black spruce↔white spruce ↓ lodgepole pine ↓ birches ↓	
Coastal Western Hemlock	western hemlock, western red- cedar, yellow-cedar, Douglas-fir, red alder	amabilis fir ↑ or ↓ grand fir ↑ Douglas fir ↑ western redcedar ↓ yellow-cedar ↓ hemlock ↑ or ↓	
Sub-boreal Spruce	hybrid white spruce, subalpine fir, lodgepole pine, aspen	aspen ↑ Douglas-fir ↑ lodgepole pine ↓ hybrid white spruce ↓ lodgepole pine ↑	
Spruce-Willow-Birch	white spruce, subalpine fir, aspen	aspen ↑ white spruce ↓ subalpine fir ↔	
Interior Cedar-Hemlock	western redcedar, western hemlock, white & Engelmann spruce, subalpine fir	grand fir ↑ western larch ↑ Douglas-fir ↑ subalpine fir ↓ western redcedar ↓ western hemlock ↑	
Interior Douglas-fir	Douglas-fir, lodgepole pine, ponderosa pine	Douglas-fir ↓ or ↑ ponderosa pine ↓ or ↑ lodgepole pine ↓	
Mountain Hemlock	mountain hemlock, amabilis fir, yellow-cedar	western hemlock ↑ Douglas fir ↑ subalpine fir ↔ yellow-cedar ↓ mountain hemlock ↔	
Montane Spruce	hybrid white spruce, subalpine fir, lodgepole pine	Douglas fir ↑ hybrid white spruce ↓ lodgepole pine ↓	
Sub-boreal Pine- Spruce	lodgepole pine, white spruce, aspen	Douglas-fir ↑ aspen ↑ or ↓lodgepole pine ↓ white spruce ↓	
Ponderosa Pine	ponderosa pine, Douglas-fir	bluebunch wheatgrass ↑ ponderosa pine ↓ Douglas-fir ↓	
Coastal Douglas-fir	Douglas-fir, grand fir, western redcedar	grand fir ↑ arbutus ↑ Garry oak ↑ Douglas- fir ↔ western redcedar ↓ western hemlock ↓	

 $^{^{1}}$ ↑ = probable increase; ψ = probable decrease; \leftrightarrow = little change; ↑ or ψ = large uncertainty in projecting the moisture balance (e.g., boreal white and black spruce) or variability within a zone (e.g., dry sites drying further in the Interior Douglas-fir zone will encourage ponderosa pine, but bark beetles are likely to remove them).

MIGRATING LIKE A HERD OF CATS: **CLIMATE CHANGE** AND EMERGING FORESTS IN **BRITISH COLUMBIA**

> Bunnell & Kremsater





Because it appears to be the most likely widespread outcome, the consequences of warming and drying are summarized in Table 2. It is possible that some areas will become warmer and wetter, particularly in the north.

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater

Coastal forests

Climate change will likely affect tree species in coastal forests in three ways: 1) increased moisture stress; 2) mistimed physiological responses; and 3) increased fire frequency or intensity. Most IPCC models predict higher temperature and lower precipitation along the coast during summer (see Table 1; Werner 2011). Among coastal species, western redcedar and western hemlock appear most susceptible to increased moisture stress. Burton and Cumming (1995) and Cumming and Burton (1996) suspect that mistimed physiological responses will cause catastrophic losses to some lowland species (notably Douglas-fir and western hemlock). With warming, the trees may not receive sufficient chilling to induce cold-hardiness and could suffer serious damage from recurrent frosts that come despite generally warmer temperatures. Other species may meet their chilling requirements in timely fashion to avoid winter freezing but remain susceptible to early de-hardening and frost damage if mild spells in midwinter or spring are followed by colder periods. Yellow-cedar (Hennon et al. 2005) and paper birch (Woods et al. 2010) are already experiencing this change and not faring well.

Variability in seasonal warming makes realized consequences uncertain. The risk of fires will increase, but the southern coast is so well populated that fire control will be intensified. If moisture stress does not increase greatly, the warmer temperatures will encourage expansion of Garry oak. Other than climate itself, the largest uncertainties are the response of pathogens to climate and mistimed physiological responses.

Over a rotation, we expect little change in tree species composition on the south coast, although grand fir (*Abies grandis*), arbutus (*Arbutus menziesii*), and Garry oak regeneration may increase. No incursions of tree species into the region appear imminent, but the composition will likely shift to a smaller proportion of western redcedar and yellow-cedar (particularly at lower elevations). The boundaries of the two lower BEC zones—Coastal Douglas-fir and Coastal Western Hemlock—should remain relatively stable, though the Douglas-fir zone will likely encroach into the Western Hemlock zone. All along the coast, higher elevation forests should benefit from longer growing seasons, stimulating higher productivity. Both western hemlock and Douglas-fir should migrate upwards, though these species cannot migrate far in a rotation. While new seedlings and saplings may become established, old trees, more resilient to stress, will likely remain relatively unscathed.

We expect no marked changes in species composition on the mid- and north coasts. The forest itself, however, is likely to become a wilder place as the increase in the frequency and intensity of storms creates more windthrow and landslides. It is possible that more yellow-cedar will cross the coastal mountains, as already has occurred in some places (e-flora BC), and move further inland.

Southern interior forests

Models generally project moisture declines in summer (see Table 1; Dawson et al. 2008; Werner 2011), with the anticipated consequence being severe episodes of summer drought causing higher mortality of seedlings and saplings. Because they have deep roots and substantial reserves of carbohydrates and nutrients, mature trees are less vulnerable to drought; however, severe or prolonged drought renders even mature trees less resistant to insects or disease. As temperature increases and summer droughts become more fre-





quent, mortality of trees of all age classes will increase. Increases in fire activity have already been documented in the adjacent United States. Westerling et al. (2006) reported a four-fold increase in large wildfire activity in the adjacent western United States. The southern interior of BC will likely follow a similar pattern that will challenge fire suppression and encourage more open areas.

The two larger tree species of the region, Douglas-fir and ponderosa pine, are fire-adapted and thick-barked. Ponderosa pine is better able to withstand drought than Douglas-fir, but warming and moisture stress will make both species more susceptible to insects and disease. In the driest areas, savannah-like forest will likely be replaced by grassland, with shrubland on higher slopes (e.g., Hamann & Wang 2006). On somewhat less dry areas, current mixtures of Douglas-fir and ponderosa pine are likely to become scattered ponderosa pine. In each case, the species composition will be changed, in some instances dramatically so, as trees become very scarce. Although resistant to frost and drought (Minore 1979) and able to grow in many environments, lodgepole pine has the bark beetle and a host of other insects and pathogens with which to contend. It is thus unlikely to remain as large a component of Interior Douglas-fir forests.

With a changing climate, losses from current distributions are imminent. The question is how far north will Douglas-fir and ponderosa pine migrate? Both trees have relatively large seeds that do not disperse well on their own, with those of the pine being about four times heavier and more dependent on dispersal by seed-caching rodents and birds. Moreover, bark beetle may reduce the pine's ability to produce seeds. We expect forests much like the current Interior Douglas-fir zone to persist for at least another rotation and to extend farther north, but with fewer accompanying lodgepole pine. Ponderosa pine will straggle along, probably not realizing its predicted increases in range because beetles will prevent trees from getting old enough to produce abundant seed. The Ponderosa Pine zone could eventually disappear as a recognizable BEC zone.

In the southeastern interior, the composition of tree species in the area currently designated as the Interior Cedar-Hemlock zone (Figure 1) will likely shift but not as dramatically as in drier regions. Western hemlock will probably expand at the expense of western redcedar, while western larch will expand on drier areas.

In summary, unless drought is less than current projections, we anticipate grassland and shrubland to expand at the expense of forest, and an increase in the proportion of Douglas-fir, with lodgepole pine diminished and ponderosa pine becoming increasingly rare and largely confined to upper slopes rather than low valley bottoms. This trend should be evident within a rotation. In the southeast, larch may become a foundation species, but this will likely happen more slowly.

Central interior forests

The major BEC zones in the central interior of British Columbia are the Sub-boreal Spruce, Sub-boreal Pine-Spruce and Montane Spruce zones. Currently, the major tree species in these zones are lodgepole pine and white spruce, as well as its hybrids. Both species appear to be in trouble; the pine because the warming climate encourages mountain pine beetle, the spruce for similar reasons but also because warming and drying make the area less hospitable. Both climate envelopes and empirical changes of temperature and precipitation from 1950 to 2003 (McKenney et al. 2009) suggest that expanding Douglas-fir could replace spruce on the better sites; conversely, there seems to be no candidate to replace lodgepole pine on the drier sites. Douglas-fir is likely to expand into higher elevations on areas presently dominated by lodgepole pine or their dead stems. On the least productive sites,

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater





JOURNAL OF Ecosystems & Management the void left by lodgepole pine is more likely to be filled by shrubby growth. Even during extensive bark beetle attacks, not all the lodgepole pine die, so it will likely still dominate portions of the central interior. On the other hand, the area of aspen is likely to increase, but could be thwarted by moisture stress (Mbogga et al. 2010). Thus, both white spruce and lodgepole will persist, but in many areas will likely have much diminished abundance. Areas of the central interior that now attain most of their commercial timber harvest from those species must hope that another species takes their place, with Douglas-fir being the most likely candidate.

Complexes of pathogens, insects, and abiotic factors in central BC will continue to be more important than most individual agents. For example, in young lodgepole pine stands, it is common to encounter western gall rust (*Endocronartium harkenssii*), stalactiform rust (*Cronartium coleosporioides*), comandra blister rusts (*Cronartium comandrae*), atropellis canker (*Atropellis piniphila*), terminal weevil (*Pissodes terminalis*), mountain pine beetle, and pine engraver beetle (*Ips spp.*) all coexisting in one stand (Heineman et al. 2010; Woods et al. 2010). Tree mortality is often not attributable to any one agent, but is the result of several acting together.

Much depends on the amount and timing of precipitation. If wetter periods accompany the warmer summers, then *Dothistroma septosporum* and other rusts and fungi will increase, as they already have in some areas of interior BC (Kleijunas et al. 2009; Woods et al. 2005). If drought increases in frequency and duration, then fires and beetles will increase. The tree species that win or lose will depend largely on the complex of insects and pathogens encouraged by the new climate and the tree's stress levels. Douglasfir currently appears least likely to be negatively impacted.

Boreal forests

The Boreal White and Black Spruce and Spruce-Willow-Birch zones comprise boreal forests. Primary tree species are white and black spruce with smaller inclusions of lodge-pole pine, aspen, poplar, and birch. Tension in interactions among tree physiology, permafrost, and fire, in addition to differential responses of pathogens to climate change, make the boreal forest difficult to project. GCMs agree that winter warming across the circumboreal will be in excess of 40% above the global mean in 2100 (Soja et al. 2006); however, Predictions for precipitation are very dependent on the scale of data and modelling approach (e.g., Mbogga et al. 2010). Across Canada drying is predicted, but in BC precipitation has increased (Mote et al. 2005). Most GCMs project an increase in winter precipitation for the region, with about half projecting a strong decrease in summer precipitation (Werner 2011). Consequences of melting permafrost are equally difficult to project.

Significant changes in temperature and precipitation have occurred. Still, greater increases in average growing season length and annual precipitation are projected up to 2080, particularly in the northeast (Pacific Climate Impacts Consortium 2010). Tree growth in the boreal could be encouraged by the increased CO_2 concentrations (CO_2 "fertilization" effect). Increasing temperatures also could encourage growth by stimulating increased decomposition of soil organic matter and therefore nutrient availability; however, any increase in precipitation appears unlikely to offset increases in evaporative demand during the growing season, so increasing water stress will likely reduce growth of both mature trees and planted seedlings (Hogg & Hurdle 1995; Johnston et al. 2009). Historical changes in the treeline reveal growth declines more commonly on warmer and drier sites, suggesting that moisture stress may accompany increased warming, even in the coldest parts of the boreal forest (Lloyd & Fastie 2002).

MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

Bunnell & Kremsater





Bunnell & Kremsater

Currently, climate change is increasing water stress and peak summer heat stress, causing increased mortality, vulnerability to disease and subsequent fire in boreal regions of North America and Eurasia (Soja et al. 2006; Lloyd & Bunn 2007), as well as decreased reproduction, all potentially leading to large-scale dieback of forests (Joos et al. 2001; Lucht et al. 2006). Lloyd and Bunn (2007) included high-elevation species, such as mountain hemlock, among the 10 "boreal" species they evaluated at 232 sites (none in British Columbia). Empirically, white and black spruce were among the most susceptible species, with the effects being most pronounced in more continental climates. We found no reports documenting moisture stress in British Columbia's forests. Conifers tend to be more limited by moisture supply than by demand, so changes may appear as reduced growth rather than mortality.

It takes only small changes in annual temperature and rainfall to markedly change fire frequencies (Soja et al. 2006). In many parts of Canada, the rate of burn in boreal forests has already increased (Stocks et al. 1998; Flannigan et al. 2005; Xiao & Zhuang 2007), and with that there has been a shift to more hardwood cover (Bergeron et al. 1998). Nitschke et al. (2010) projected an expected increase in aspen as a result of increases in fire frequencies in subboreal forests; on the other hand, using a broader suite of models, Mbogga et al. (2010) project a decline in aspen in boreal regions. Fire suppression and rates of harvest that create relatively fire-resistant young forest increase uncertainty about effects of fire in the boreal.

Cold temperatures have limited northward expansion of white spruce, black spruce, and balsam fir (*Abies balsamea*), but as temperatures become warmer, these trees may spread north. Paleoecological evidence suggests that trees could become established in the tundra within 150 years (MacDonald et al. 1993). In southwest Yukon, northward expansion of white spruce and willow (*Salix* spp) is a function of aspect and associated permafrost, and shows evidence of a threshold effect, beginning slowly, then proceeding more rapidly, with periods of heavy recruitment (Danby & Hik 2007). Periods of heightened recruitment and rapid advance have been observed at subarctic tree lines elsewhere (Payette & Filion 1985; Gervais & MacDonald 2000; Kullman 1979). Thus, the response of the tree line to future warming is unlikely to be gradual.

With a changing climate, current boreal forests may become more suitable for lodge-pole pine, but less suitable for some spruce. Topography will play a role; namely, white spruce stands on south-facing slopes are likely to suffer from increased moisture stress, whereas black spruce on colder, north-facing slopes may be largely unaffected. Aspen may suffer in parts of the boreal due to sudden aspen decline, but is also likely to be the first species to pioneer newly warmed tundra. If drying accompanies the expected rapid warming, this could lead to the transitional establishment of a boreal grassland ecosystem resembling the aspen parkland of the Prairies. In much of Canada, grasslands and temperate forests could expand northward into the present boreal; the outcome in BC depends largely on precipitation and dynamics of permafrost.

The rate at which permafrost melts is greatly influenced by its depth. Permafrost in British Columbia is particularly susceptible to melting (Canadian Cryospheric Information Network n.d.). The fate of the water after melting depends on the depth of the permafrost, the local topography, and soil type and depth. Depending on these conditions, water from melting permafrost can drain away, thereby increasing moisture stress, or pool on the surface (e.g., Turetsky et al. 2007). Conditions in northern British Columbia appear to favour lower availability of water. Ultimately any northward expansion of the boreal forest will be limited by poor soils, permafrost, and the time required to migrate,



Management

likely resulting in overall decreases in boreal forest. The rate of change is more difficult to estimate than the direction because warming appears to be accelerating in the north.

Subalpine forests

Common tree species in subalpine forests include Engelmann spruce, subalpine fir, white-bark pine, limber pine, and mountain hemlock. Subalpine forests are not regional but occur at higher elevations throughout the province. Subalpine vegetation is a gradient rather than neatly demarked. In the southern interior of British Columbia, the gradient typically extends from the Engelmann spruce-subalpine fir zone, up through whitebark pine, limber pine, and juniper, becoming ever more sparsely treed until it is so open that we call it alpine tundra. Species composition differs across regions, but collectively the subalpine forest may be the most threatened broad forest type.

Warmer temperatures are a major challenge to subalpine species, because they can only move northward. They are usually ill adapted to lower elevations, and in order to move north, they must do so at higher elevations that provide limited options. This apparent entrapment, ascending until there is nowhere else to go and subsequently vanishing, has been termed the "rapture hypothesis." Moving quickly northward is hindered by the fact that favourable soil development may require centuries.

Subalpine forests are likely less adapted to drought and fire than forests experiencing such disturbances more frequently. Both phenomena will increase in frequency and severity, so these forests also will become increasingly vulnerable to opportunistic pests. Joy and Maclaughlin (2001) reported that mortality of subalpine fir in permanent monitoring plots located throughout the southern interior of BC had increased since 1998. Western balsam bark beetle was the main mortality agent then, and continues to increase in some areas, but has also decreased in others (Buxton et al. 2010). In addition, the usually innocuous *Pissodes* weevil now acts like a primary bark beetle and has become a significant mortality agent.

Tree species comprising subalpine forests in different regions are likely to fare differently. The white spruce–Engelmann spruce complex may not be greatly affected by climate change over the next 40 years because the range of suitable climate is not projected to change greatly. Predictions suggest only minor expansion into higher elevation regions and minor losses of area, particularly in the south (Hamann & Wang 2006) where water deficits are projected to become limiting. Beyond the 2050s, however, losses of suitable habitat are predicted to become more extensive, with much of the southern interior becoming too dry. Interior subalpine forests are likely to see subalpine fir, Engelmann spruce, and white spruce gradually replaced by more typical lower elevation species, including interior Douglas-fir and western larch.

At higher elevations, both whitebark and limber pine are likely to become increasingly susceptible to bark beetle and may be replaced by common (*Juniperus communis*) and Rocky Mountain juniper (*J. scopulorum*). Juniper is likely to persist because they tolerate cold, dry sites and poor soils, and may be joined by subalpine fir and Engelmann spruce where soil development permits. On the coast, mountain hemlock will likely climb as high as favourable soil allows, while western hemlock and possibly Douglas-fir will follow, but remain lower.

Conclusions

Future forests will be a product of both migration and adaptation through natural selection. There is considerable uncertainty regarding all influences on future species' distributions.

MIGRATING LIKE
A HERD OF CATS:
CLIMATE CHANGE
AND EMERGING
FORESTS IN
BRITISH COLUMBIA

Bunnell & Kremsater

17



JOURNAL OF Ecosystems & Management

The uncertainty itself does not imply complete disaggregation of current species mixes—truly migrating like a herd of cats—but current data suggest winners and losers in all BEC zones and variable responses across the province (Table 2). Those shifts in species composition are most likely to appear first at the variant level of the BEC system. Some trends appear far more certain than others (e.g., severe challenges to whitebark and limber pine, low-elevation yellow-cedar, ponderosa pine), but none are certain. Since a changing climate implies unprecedented impacts, the opportunities for reducing uncertainty are greatly limited. Despite that limitation, the requirement for forward planning in forestry remains. We consider this article less a combination of reasoned predictions than a call for increasing flexibility in forest planning, greater attention to maintaining adaptability, and focused monitoring to reduce existing uncertainty. We expect our predictions to be wrong or simplistic in some instances due to extensive uncertainties, but hope they will stimulate thought, monitoring, and, in combination with the perspectives piece featured in this issue, nudge management in useful directions.

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Notes

- 1. There is, as of yet, no conclusive study linking climate change to increased root disease activity in BC. Studies elsewhere were among the first to suggest that climate change was responsible for altered forest pathogen behaviour (Brasier & Scott 1994; Brasier 1996).
- 2. http://www.socc.ca/cms/en/socc/permafrost/futurePermafrost.aspx

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MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater



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MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

> Bunnell & Kremsater



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Author information

Fred L. Bunnell, Faculty of Forestry, University of British Columbia. 2424 Main Mall, Vancouver, BC V6T 1Z4. Email: Fred.Bunnell@ubc.ca

Laurie L. Kremsater, Faculty of Forestry, University of British Columbia. 2424 Main Mall, Vancouver, BC V6T 1Z4. Email: lkrem@shaw.ca

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MIGRATING LIKE A HERD OF CATS: CLIMATE CHANGE AND EMERGING FORESTS IN BRITISH COLUMBIA

Bunnell & Kremsater







Test Your Knowledge

How well can you recall the main messages in the preceding article? Test your knowledge by answering the following questions.

MIGRATING LIKE
A HERD OF CATS:
CLIMATE CHANGE
AND EMERGING
FORESTS IN
BRITISH COLUMBIA

Bunnell & Kremsater

Migrating Like a Herd of Cats: Climate Change and Emerging Forests in British Columbia

- 1. Conifer genomes are large and complex largely because:
 - a) Conifer trees are so big.
 - b) They have been around a long time and adapted to very different climates.
 - c) Accident, they don't use most of it anyhow.
- 2. Documented effects of climate on tree species include:
 - a) Moisture and heat stress influencing growth, mortality and reproduction and changing fire regimes.
 - b) Reduced resilience to fungal and insect pathogens encouraged by moisture and heat stress.
 - c) Shifts in competitive balance with other tree and shrub species plus all of above.
- 3. Continued climate change could eliminate two currently recognized forest types; specifically:
 - a) Ponderosa pine and the highest subalpine forests (limber and whitebark pine).
 - b) Impossible; there will always be some trees forest types will only be re-mixed.
 - c) Boreal and coastal (look at the trouble vellow cedar is in).

Management