Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest

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Key words: 3-PG model, boreal region, climate change, decision tree analysis, jack pine, lodgepole pine, mountain pine beetle, tree physiology.

Pre-print of published version.
Reference:
Coops, N.C., Wulder, M.A. Waring, R.H. (2012). Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest. Forest Ecology and Management. Vol. 274, pp. 161-171.

DOI.
http://dx.doi.org/10.1016/j.foreco.2012.02.011

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ABSTRACT

The mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) outbreak in western North America is the largest recorded in history, impacting over 14 million ha of pine forests in British Columbia alone. Large regions in western North America have become more favourable to the MPB, which has extended its range into higher elevations and more northerly latitudes, previously considered climatically unsuitable. Various investigators, and recent forest health surveys in Alberta have suggested that the beetle's range could shift further east on both lodgepole (*Pinus contorta* Dougl.) and jack pine (*P. banksiana* Lamb.) into the boreal forest. A risk assessment of the threat of MPB to Canada's boreal forest identified effective monitoring and detection in areas vulnerable to infestation as the most critical information need.

Changing climate may also be independently impacting pine forests, for instance through moisture stress. Species' vulnerability to climate change is reflected in modeled increases or decreases in the probability of its presence across its range. We hypothesize that areas within the current ranges of lodgepole and jack pine that have historically been sub-optimal for beetle expansion may become increasingly vulnerable as a result of climate change. In our analysis, we first test the ability of physiologically-based models to predict the recorded distributions of lodgepole and jack pine for 12,456 ground plots across British Columbia, Alberta and Saskatchewan, using monthly climatic data derived for a calibration period between 1950 and 1975. Both the presence and absence of the two tree species recorded on survey plots were predicted, on average, with an accuracy of 85% for the calibration period. We then identified locations that appear to have become less suitable for these pine species in each subsequent year between 1976 and 2006 and found that the suitable range area for lodgepole and jack pine for >50% of years in the period decreased by 45% and 40% respectively. These results were compared with outputs from a climate-suitability model that identified areas of potential range expansion by MPB for two periods: 2001–2030 and 2010–2040. The area of vulnerable lodgepole pine forests that coincided with the area of potential beetle expansion was 40,000 km^2 in 2001–2030 and 45,000 km^2 in 2010–2040. The area of vulnerable jack pine was much less, ranging from 4000–8000 km^2 for the two periods. This analysis is unique in that it acknowledges the complexity of the beetle-host interaction by incorporating the potential impact of climate change on each of these elements into predictions of future host susceptibility to infestation. Such information is vital for assessing the ongoing risk of MPB range expansion and for designing future monitoring programs.

1. Introduction

The current outbreak of the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins, (Coleoptera, Curculionidae)) in western North America is ten-times larger than any previously recorded (Wulder et al., 2010). This outbreak started in the mid-1990's and has spread to almost 14 million ha of pine forests in British Columbia alone (Wulder et al., 2010). The potential distribution of MPB covers a significant portion of western North America from northern Mexico to

central British Columbia in Canada, and east from the Pacific Coast to the Black Hills of South Dakota in the United States (Safranyik et al., 2010). The beetle can successfully attack a number of pine species; in western Canada; it principally infests lodgepole pine (*Pinus contorta* Dougl.,) and to a lesser extent western white pine (*P. monticola* Douglas ex D. Don), ponderosa pine, (*P. ponderosa* C. Lawson) and whitebark pine (*P. albicaulis* Engelm.). The distribution of MPB is determined by the occurrence of suitable host species and climatic conditions with the most recent outbreak attributed to range expansion which is understood to be due principally to intensive fire suppression activities, which have caused the amount of mature lodgepole pine forest to triple in the past century (Fettig et al., 2007), and several years of favourable climatic conditions, which have increased the climatically suitable areas for brood development (Carroll et al., 2004).

The range of lodgepole pine continues north to Alaska and east into Alberta, suggesting that climatic conditions associated with these limits are, or were, beyond that suitable for the bark beetle (Safranyik, 1978). The beetle's range is clearly temperature limited (Bentz et al., 2010). In summer, the temperature must remain sufficiently warm to ensure a univoltine lifecycle and synchronous emergence (Carroll and Safranyik 2003; Carroll et al., 2003). In the winter, temperatures below -40 $^{\circ}$C affect brood survival (Safranyik, 1978), with the most impact at the season's extremes when the concentrations of glycerol in the insects is below maximum (Safranyik and Carroll, 2006). Host-tree vigor also affects the rate that insect populations expand across a region (Waring and Pitman, 1985; Logan et al., 1998; Whitehead et al., 2006).

It has been posited that mature lodgepole pine are under increased susceptibility to infestation by MPB when physiologically stressed (Waring and Pitman, 1985). Changes in climate have also been linked to vegetation stress (Case and Peterson, 2007; Chhin et al., 2008). Susceptibility to infestation by MPB is typically based upon, at the stand level, the amount and age of pine, stand density, and a location factor (Shore and Safranyik, 1992). Stands can be found susceptible, but not at risk of infestation if there are few beetles present. As such, susceptibility alone cannot be understood as a likelihood of infestation. Beetle pressure, that is the presence of beetles, can be combined with susceptibility to form a notion of risk to infestation. An additional consideration to likelihood of mortality due to infestation is tree vigor. Larsson et al. (1983) present that trees with lower vigor as related by growth increment had a higher likelihood of infestation. Among a variety of mechanisms suggested (e.g., Safranyik, 1978), it can be understood that the capacity of a given tree to use natural defenses to expel attacking insects will be lessened in low vigor situations. As such, we propose that climatically driven pine stress can be used as an informative aspect of infestation likelihood by MPB

Under a changing climate, large areas in western North America have become more favourable for the MPB, leading to range expansion toward higher elevations and more northerly latitudes (Carroll et al., 2004). This expansion has lead to speculation that the beetle's range could extend into the boreal forest region creating an ecological pathway eastward on jack pine (*Pinus banksiana*

Lamb.) (Logan and Bentz, 1999; Logan and Powell, 2001; Safranyik et al., 2010). Mountain pine beetles have been recorded in increasing numbers in Alberta (http://www.mpb.alberta.ca/) since early in this millennium (Carroll, 2003). Moreover, areas of hybrid lodgepole and jack pine are known to exist in Alberta and in the Northwest Territories (Farrar, 1995). These hybrids, as well as genetically pure strains of jack pine, have proven susceptible to attack (Safranyik et al., 2010; Cullingham et al., 2011), and provide access to the boreal forest.

Whether MPB will thrive on a new host under a changing climate is a major concern because jack pine is a dominant tree species in the boreal forests, and its range extends from the east side of the Rocky Mountains through to the Atlantic coast in Canada (Nealis and Peter, 2008). We believe that climatic conditions have already changed sufficiently in western Canada to open increasing areas of pine forests to beetle attack Safranyik et al., 2010). We hypothesize that areas within the current ranges of lodgepole and jack pine that have historically been sub-optimal for beetle expansion may become increasingly vulnerable as a result of climate change. In this paper, we acknowledge the complex beetle-host interaction by incorporating the potential impact of climate change on both the MPB and its hosts into predictions of future host susceptibility to infestation. To achieve this, we apply a physiologically-based modeling approach to assess how recent variation in climate may affect both the growth of trees and the impact on beetles. We initiate the analysis by predicting the recorded distributions of lodgepole and jack pine during a long, cool, wet period (1950-1975). With these predictions of range as a reference, we contrast where the two species may have become more vulnerable to beetle attack based on the modeled increase or decrease in the probability of the species being present across its range during the period between 1976 and 2006. We extend the analysis through the rest of the century using climatic projections made with the Canadian Global Circulation Model (McFarlane et al., 2005). We then combine these results with output from a climatic-suitability model that predicts the future suitability of forests to MPB infestation. From this, we are able to identify those areas with increased host vulnerability that coincides with future areas of host suitability. We posit that the approach presented is important both for long-term risk assessments and for the design of future monitoring programs.

2. Methods

2.1 Modelling Approach

Although the most common approach to modeling the distribution of species relies on empirical correlations with sets of bioclimatic indices (Austin, 1985; Iverson and Prasad, 1998; McKenzie et al., 2003; Thuiller et al., 2008), the reliability of these correlations in predicting future distributions is unknown (Williams et al., 2007). As an alternative, one might consider more mechanistic approaches that have proven their ability to predict growth of forest plantations for a wide range of climatic conditions, often exceeding those characteristic of a species' native range (Sands et al., 2000; Rodriguez et al., 2002; Almeida et al., 2004; Dye et al., 2004; Waring, 2000; Coops et al., 2005; Waring et al., 2008). Unfortunately, for many tree species we lack sufficient knowledge of their

physiology to parameterize such mechanistic models. As a compromise, we chose here to apply a hybrid approach developed by Coops et al. (2009) that uses a physiologically-based growth model parameterized for one widely distributed species to serve as a reference to estimate the distributional limits of other species. Rather than use climatic data directly to correlate with species' distributions, the hybrid approach first assesses the relative constraints of five climatic variables that potential limit monthly photosynthesis for a reference species, and thereafter predicts the distributions of other species in reference to how climatic conditions throughout their native ranges differentially constrain photosynthesis, water use and growth. Similar to other approaches, the initial tests of the hybrid model is its ability to predict a species' presence or absence on inventory plots distributed across the region.

2.2 Structure and parameterization of the 3-PG stand growth

All process-based growth models have broadly similar design in the selection of climatic variables that limit the processes of photosynthesis, water use, and allocation of carbon to growth and turnover (see reviews by Mäkelä et al., 2000; Constable and Friend, 2000; Landsberg, 2003; Nightingale et al., 2004). The models differ principally in the details describing each process, the time-step, and whether nutrient accumulation, turnover, and losses are explicitly included. We chose one of the more simplified model formulations, 3-PG, Physiological Principles Predicting Growth, (Landsberg and Waring, 1997) because, with a monthly time-step, it is appropriate for the kinds of data that can be generated from weather stations and that are available from projections made with global climate models.

The 3-PG model provides a reasonable compromise between highly complex, fine-temporal scale, process models with daily resolution, and those applied at annual time-steps. The model contains a number of simplifying assumptions that have emerged from studies conducted over a wide range of forests types including that autotrophic respiration is assumed to be ~50% of gross photosynthesis (Landsberg and Waring, 1997; Waring et al., 1998; Law et al., 2001).

The basic model design works as follows: each month, absorbed photosynthetically active radiation (APAR) is estimated from global solar radiation and modeled predictions of leaf area index (LAI). The product of APAR and light-conversion efficiency of photosynthesis represents the upper limit on gross photosynthesis. The utilized portion of APAR, however, is usually less than the potential, so we reduce APAR by an amount determined by a series of environmental modifiers ranging between 0 (system 'shutdown') and 1 (no constraint) which reflect the degree that gas exchange via canopy stomatal conductance is reduced (Landsberg and Waring, 1997).

The monthly environmental modifiers include: (a) averaged day-time atmospheric humidity deficits; (b) the frequency of subfreezing conditions, (c) soil water deficits, and (d) deviation from suboptimal temperature defined for a particular taxon. Drought limitations are imposed as a function of soil properties and a simple water balance that calculates when the available soil water is less

than transpiration estimated with the Penman-Monteith (Landsberg and Waring 1997) equation. Each month, the most limiting climatic variable on photosynthesis is selected, based on departure from conditions that are optimum. The fraction of production not allocated to roots is partitioned among foliage, stem and branches based on allometric relationships and knowledge of annual leaf turnover (Landsberg et al., 2003).

As in other studies in western North America, we selected the wide-ranging Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) as a reference species to characterize the importance of climatic constraints on photosynthesis and growth across forested environments (Swenson et al., 2005; Waring et al., 2005, Coops et al., 2007). The physiological parameters and allometric relations used in the model match those reported in Waring and McDowell (2002), with a few exceptions. To limit the analysis to climatic effects, we set the available soil water holding capacity at 200 mm for a sandy loam soil as a constant throughout the region. This value assures that if drought occurs, it will be recognized (Nightingale et al., 2007). We also assigned a constant soil fertility rank of 50% of maximum, which results in an even partitioning of growth above- and belowground. The quantum efficiency was set at 0.04 mol C mol photon^{-1}, equivalent to 2.2 g C MJ^{-1} absorbed PAR, about mid-way between reported minimum and maximum values in the literature (Landsberg et al., 2003).

To take into account seasonal adjustments in temperatures responses (Hember et al., 2010) and the genetic variation within the species, we broadened the range that photosynthesis could remain above 50% of maximum to lie between 0°C and 35°C by setting minimum, optimum, and maximum temperatures at -7°C, 18°C, and 40°C, respectively. The photosynthetic response at temperatures less than -2°C was truncated to zero, because below that threshold, stomata are closed (Running et al., 1975; Hadley, 2000). The extent that lodgepole and jack pine encounter environments that would impose restrictions on the performance of Douglas-fir is incorporated through the second component of the modeling approach using an automated decision-tree analysis described in more detail below.

2.3. Climatic data

Multi-year climate surfaces were generated at a spatial resolution of 1 km using Climate-WNA that downscale data generated from PRISM (Parameter-elevation Regressions on Independent Slopes Model, Daly et al., 2002). The downscaling is achieved through a combination of bilinear interpolation and elevation adjustment (see Wang et al., 2006), the latter of which was obtained from the Shuttle Radar Topography Mission (SRTM; Rabus et al., 2003). The number of days per month with subfreezing temperatures (less than -2°C) was estimated from empirical equations with mean monthly minimum temperature (Coops et al., 1998). Day-time atmospheric vapor pressure deficits (VPD) were estimated by assuming saturation at the average monthly minimum temperature is equivalent to water concentrations of water vapor present throughout the day (Kimball et al., 1997).

Monthly estimates of total incoming short-wave radiation were calculated following a modeling approach detailed by Coops et al. (2000), which first calculates the potential radiation at the top of the atmosphere then adjusts for slope, aspect, and elevation as well as the effects of water vapor and clouds on the proportion of diffuse versus direct solar-beam radiation (Garnier and Ohmura, 1968; Swift, 1976; Running et al., 1987). The approach predicts direct and diffuse components of monthly radiation with 93 - 99% accuracy on flat surfaces, and on sloping terrain accounted for >87% of the observed variation with a mean error less than 2 MJ m^{-2} day^{-1} (Coops et al., 2000). The spatial variations of annual minimum, maximum temperature and precipitation across the focus area east of the Rocky Mountains in British Columbia, Alberta and Saskatchewan, are shown in Figure 1(a) - (c) for the calibration period, 1950-1975 (Figure 1).

To extend the analysis into the future, we used a “business as usual greenhouse” gas emission scenario from the Canadian Climate Centre’s Modelling and Analysis (CCCma) third generation general circulation model (CGCM3), which includes improvements in the treatment of clouds, solar radiation, and land surface processes along with a simple ocean mixed-layer model with a thermodynamic sea ice component (McFarlane et al., 2005; Scinocca et al., 2008). Downscaling of the GCM was undertaken within CLIMATE-WNA (see Hamann and Wang, 2005). We compared simulations for three 30-year periods, the 2020`s (2011-2040), 2050`s (2041 – 2070) and the 2080`s (2071 – 2100) provided by the Canadian global climate model.

Insert Figure 1(a) – (c) about here:

2.4 Tree species occurrence data

Across British Columbia, Alberta, and Saskatchewan tree species presence / absence data were assembled from three different sources. Across the region, data from the National Forest Inventory (NFI) were acquired (Gillis et al., 2005) that list species recorded at plot locations centered on a 20 x 20 km national grid. Additional plot data for Alberta was provided from the Alberta Biodiversity Monitoring Institute and from the Ecological Site Information System (ESIS) (Government of Alberta, 2012). Data acquired on permanent sample plots in Saskatchewan were provided by the Ministry of Environment - Forest Service Branch. The presence / absence data, when combined from all sources, represented a total of 12,456 observations.

2.5. Decision-tree modeling of lodgepole and jack pine recorded distributions

Across the region, we first applied the 3-PG model to predict stand growth and LAI for Douglas-fir, using the mean climate derived from Climate-WNA from 1950 – 1975. Differences in LAI are important as they place limits on water use and gross photosynthesis (Landsberg and Waring, 1997). Model simulations were run for 50 years of stand development by which time maximum LAI and maximum canopy closure were reached. The 3-PG model was then stopped, and at all of the 12,456 ground plots, the extent that each of the climatically-related

variables (other than solar radiation) restricting photosynthesis was extracted for each month.

To assess the extent that the 3-PG environmental modifiers, expressed as fractions of maximum unity, might serve to predict presence or absence of the two tree species, a decision- tree analysis was applied (Coops et al., 2009a). The technique automatically separates the dependent variables (presence or absence of a tree species) into a series of choices that not only ranks the importance of each variable but also identifies thresholds that best separates one species from another. Decision Tree Regression (DTREG, Sherrod, 2008) software was used to develop a classification tree for each species using a 10-fold cross-validation technique where the total dataset is partitioned randomly into 10 equally sized groups, a model is produced on nine of the groups, and then tested against the reserved 10%. This process, also known as k-fold partitioning, is repeated 10 times with the results merged to produce a final classification tree with an overall accuracy accessed by averaging the independent results of the 10 simulations (Breiman et al., 1984). This type of k-fold partitioning provides the most realistic accuracy test of the model. It is not, however, a truly independent validation of the model because we merged all three available datasets. Once each model was developed a confusion matrix was developed which provides an indication of the positive and negative predictive power of the model.

In addition to the percent (%) correct predictions, to provide a visual comparison of model accuracy, we generated maps predicting each species' distribution and compared these with recorded presence on survey plots as well as with published range maps (Critchfield and Little, 1966; Little, 1971) Figure 2(a) – (b)).

Insert Figure 2(a) – (b) about here:

2.6 Predicting areas of tree vulnerability and MPB suitability

Nitschke and Innes (2008) propose that a species' resilience or vulnerability to climatic change is reflected in modeled increases or decreases in its probability of being present across its range. We utilize this definition to evaluate possible changes in vulnerability of the two tree species in reference to their modeled distributions in the calibrated period (1950-1975) in each subsequent year between 1976 and 2006. The resulting maps displayed the probability of annual shifts in the areas remaining "suitable" for the two species based on the calibration period. We defined those areas as "vulnerable" within a species' baseline range as having less than a 50% probability of the species' occurrence between 1976 and 2006.

To identify where climatic conditions might favour the expansion of MPB activity, we used the predictions presented in a paper by Sanfranyik et al. (2010) based on earlier work (Safranyik et al., 1975; Carroll et al., 2004). The Safranyik et al. (2010) model uses climatic variables including heat accumulation during the growing season, minimum winter temperature, and mean maximum August temperature to predict beetle annual survival. Three additional climate variables

address the site water balance, to the extent that deficits are assumed to affect tree vigor and the probability of beetle success in attack and brood survival.

3. Results

3.1 Seasonal constraints on photosynthesis

We first contrasted seasonal variation in the climatic modifiers derived at sites where the tree species were recorded present on field survey plots. In regard to temperature (Fig. 3a), the two species were similar in their responses, both showing no photosynthesis in the winter. In March and November, lodgepole is somewhat less constrained by suboptimal temperatures than jack pine. In summer, neither species exhibits growth constraints imposed by temperature. In regard to seasonal variation in atmospheric humidity deficits (VPD) the species show similar ranking (Fig. 3b). The environmental constraints imposed by frost (Fig. 3c) follow the general pattern exhibited to deviations from the calculated optimum temperature, (Fig 3b). Both species show only moderate exposure to soil water deficits (Fig. 3d). In September, photosynthesis can be reduced by up to 50%, but the mean reduction is only around 20%. Although these analyses suggest that jack pine tolerates slightly more drought than lodgepole pine in the summer months, the variability across the three Provinces is large, and similar for both species.

The decision-tree analyses automatically selected the variables in order of their discriminating power. In the case of lodgepole pine, summer frost and winter soil water deficits ranked ahead of winter VPD and summer temperatures. In the case of jack pine, the selected order of modifiers was: fall temperature, the frequency of summer frost, VPD in the fall and winter, and soil water deficits in the summer and fall.

Insert Figure 3(a) – (d) about here:

3.2 Decision-tree model predictions

The predicted distributions of lodgepole and jack pine for the calibration period (1950-1975) are shown in Figure 4(a) and (b). The modeled distributions are similar to Little's range maps (outlined in red), although not as broad in some portions and less uniform at the edges. Based on the survey data acquired on 12,456 ground plots, the models predicted presence and absence of the species with an averaged 85% accuracy for both species (Table 1).

Insert Table 1 about here:

Insert Figure 4 about here:

3.3 Predictions of vulnerable areas for the two tree species between 1976 and 2006

We applied the decision tree models to assess the number of years between 1976 and 2006 when climatic conditions during one or more years

departed sufficiently from the calibration period to predict the absence of a species within previously modeled range (Fig. 4(c)-(d)). Lodgepole pine remained well adapted to the climate variability throughout most of British Columbia, becoming more vulnerable in the central regions of British Columbia and on the eastern slopes of the Rocky Mountains. jack pine remained well adapted to variable climate in the northern component of its range, but became more sensitive throughout much of southern Alberta and Saskatchewan Fig. 4(e)-(f)) .

3.4 Predictions of mountain pine beetle future expansion of range

The Safranyik et al. (2010) model projections of beetle climatic suitability, derived with six climatic variables, is shown in Figure 5(a) – (b). With the 2001 - 2030 climatic projections, areas of very low potential infestation are located in the north, including Alaska and northern Alberta and Saskatchewan. Areas of extremely high infestation potential are predicted in interior British Columbia and the southern portion of Alberta with small isolated pockets in Saskatchewan. By 2010 – 2040, the potential area for the infestation increases, particularly in central Alberta and southern Saskatchewan. The area of moderate infestation potential also increases in the north with the sites having a low potential for infestation shifting much further north under the forecasted climate.

Insert Figure 5(a) – (b) about here:

Figure 6 compares the areas designated as vulnerable for the two tree species with the areas predicted by the Safranyik et al. (2010) MPB climatic index to have a risk greater than moderate for the 2001-2030 and 2010-2040 projected climatic conditions. For lodgepole pine, the areas of vulnerability and high MPB climatic suitability occupy interior British Columbia and extend along the western edge of lodgepole pine's distribution, which occurs in three distinct regions. The first area is situated in mid-Alberta, the second, further south, and the third, just a small pocket above the United States border. By 2010-2040 the area suitable for the beetle is projected to increase along with an increase in vulnerable forests. Again, interior British Columbia is highlighted as a high risk area, which extends to the eastern slopes of the Rocky Mountains. In the case of jack pine, the highest risks for MPB outbreaks are projected to initially occur in two small areas, one in northeastern British Columbia and the second in southern Saskatchewan. By 2010-2040 the two identified risk areas are likely to increase and with a third risk area developing in central Alberta.

Insert Figure 6(a)-(d) about here:

The areas of vulnerable forest that coincide with those favorable for beetle expansion are presented in Figure 7. 40,000 km^2 of lodgepole pine forest are projected to be susceptible to beetle attack during the period from 2001-2030, with an increase to 45,000 km^2 in 2010-2040 period. In the case of jack pine, the area of high risk (vulnerable forest and favorable beetle expansion) is much lower, ranging from 4000 - 8000 km^2 over the same two intervals.

Insert Figure 7 about here:

4. Discussion

The modeling approach, built on common physiological principles, and applied to a wide-ranging species, appears sufficiently robust to identify differences among tree species that prove adequate to predict the competitive range over which they are likely to occur. Model predictions correspondence to field surveys with an average accuracy of 85% (Table 1). The hybrid approach offers a number of advantages over those constructed from correlations with climatic indices. First, process-based models predict canopy leaf area indices, a biological property that significantly affects the site water and radiation balance, and can serve, together with growth estimates, as an index of host vigor (Waring and Pitman, 1985; Coops et al., 2009). Secondly, the specific limitations on photosynthesis, water use, and growth are interpretable each month. When changes occur across a species' natural range, the significance can be interpreted biologically in reference to the underlying processes. This permits us to take into account latitudinal (and physiographic) variation in incident radiation, and its contribution to photosynthesis and water vapour transfer, as a function of the modeled LAI and stomatal conductance at the time of canopy closure (assumed by age 50) (Coops and Waring 2011). As noted, canopy leaf area is an important parameter assimilating information regarding site and vegetation structure, with a capacity to also enable modeling and comparison of measures to predictions. Coops et al. (2009) use remotely sensed estimates of leaf area to inform on increased infestation likelihood for stands found with conditions below expectation. The approach of Coops et al. (2009) could be applied to the areas of interest identified in this research (i.e., the vulnerable areas that coincided with areas of future MPB range expansion) as one element of a long-term monitoring program. Leaf area could be monitored at these locations over time to inform on increased infestation likelihood.

The analysis conducted in this paper compared changes in the annual predicted distribution of each species and compared with a calibration period when conditions were cooler and wetter (Coops and Waring, 2011). We hypothesize that areas within the range of the species have historically been ecologically suitable (not necessarily optimal) are now becoming more vulnerable to disturbance, be it by insect attack, fire, or invasion of more competitive tree species (Waring et al., 2011). Other types of simulation models predict similar shifts in the distribution of conifer species in western Canada (e.g., Cummings and Burton, 1996). It is those areas where expected beetle-range expansion coincides with the areas of increasingly vulnerable lodgepole and jack pine forest that health surveillance activities are most warranted. The areas of interest identified in this research could function as an initial strata for the design of a monitoring program. These could then be used (in concert with other appropriate data sources) to direct the acquisition of other data sources (i.e., remotely sensed imagery from airborne- and satellite-based platforms, and ground surveys) (Wulder et al., 2008). More extensive monitoring was identified as one

of the information needs associated with a recent assessment of the risk of MPB expansion into the boreal forest (Nealis and Peter, 2008); however given the large areas of forest potentially at risk, any *a priori* knowledge that can aid in focusing monitoring efforts is desirable.

A key with this approach is the creation of a modeling framework for scenario based planning including both lodgepole and jack pine. Further, considering the link between plant stress and predisposition for insects or disease (Waring, 1987), knowledge of stress is useful information in support of forest management. While the focus herein has been on the linkage between infestation by MPB and stress, other forest insects, pathogens, or disturbances may have an impact upon these stressed stands or ecosystems.

ACKNOWLEDGMENTS

We are grateful for the support received from the Government of Canada through the Mountain Pine Beetle Program (http://mpb.cfs.nrcan.gc.ca/), administered by Natural Resources Canada, Canadian Forest Service (CFS). In addition, Waring's participation was supported by the National Aeronautics and Space Administration (NASA Grant NNX11A029G) as part of the Biodiversity and Ecological Forecasting program and Coops' received financial support from a Canadian NSERC Discovery grant. Field plot data was generously provided by Mr. Dave Morgan (Alberta), Phil Loseth (Saskatchewan), and Paul Boudewyn (CFS). Field data compilation was undertaken by Collin Ankerson. Dr. Vince Nealis and Joanne White (CFS) are thanked for valuable insights and suggestions made on a draft version of this manuscript. We would also like to note our appreciation to Dr. Jacques Régnière (CFS) for generosity in sharing data and thoughts.

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LIST OF TABLES AND FIGURES:

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Figure 1(A)-(C): Predicted climate surfaces of annual minimum and maximum temperature, and precipitation across the study areas as derived from ClimateWNA for the calibration period (1950-1975).

Figure 2 Plot locations (n =12,456) *where the presence (closed circles) or absencef(open circles) were recorded for (A) lodgepole and (B) jack pine.*

Figure 3(A)-(D): Monthly mean variation in the four climatic modifiers for the two selected tree species for the calibration period (1950-1975).

Figure 4: Derived decision-tree models to predict (A) lodgepole and (B) jack pine recorded distributions for the (1950 – 1975) baseline (calibration) period climate. Little's (1971) range maps are outlined in red. Favorable (red and yellow colours) and unfavorable conditions (green and blue) for the two species are distinguished based on a variable number of years for which conditions departed or did not depart from the calibration period between 1976 and 2006 (C) and (D) and areas defined as vulnerable (red) within a species' baseline range that have less than a 50% probability of suitability for the species from 1976-2006 ((E)-(F)).

Figure 4: Predictions of the climatically suitable range for mountain pine beetle based on a model developed by Safranyik et al. (2010), which estimates the likelihood of a univoltine life cycle, over-winter survival, optimal emergence/dispersal conditions, and influence of variability in spring precipitation. Codes correspond to: 0: very low, 1: low, 2: moderate, 3: high and 4 extremely favourable for beetle range expansion. MPB suitability predictions are for (a) 2001 – 2030 and (b) 2010–2040 based on projected climatic conditions for a business as usual scenario of continually increasing levels of greenhouse gases (Canadian global climate model).

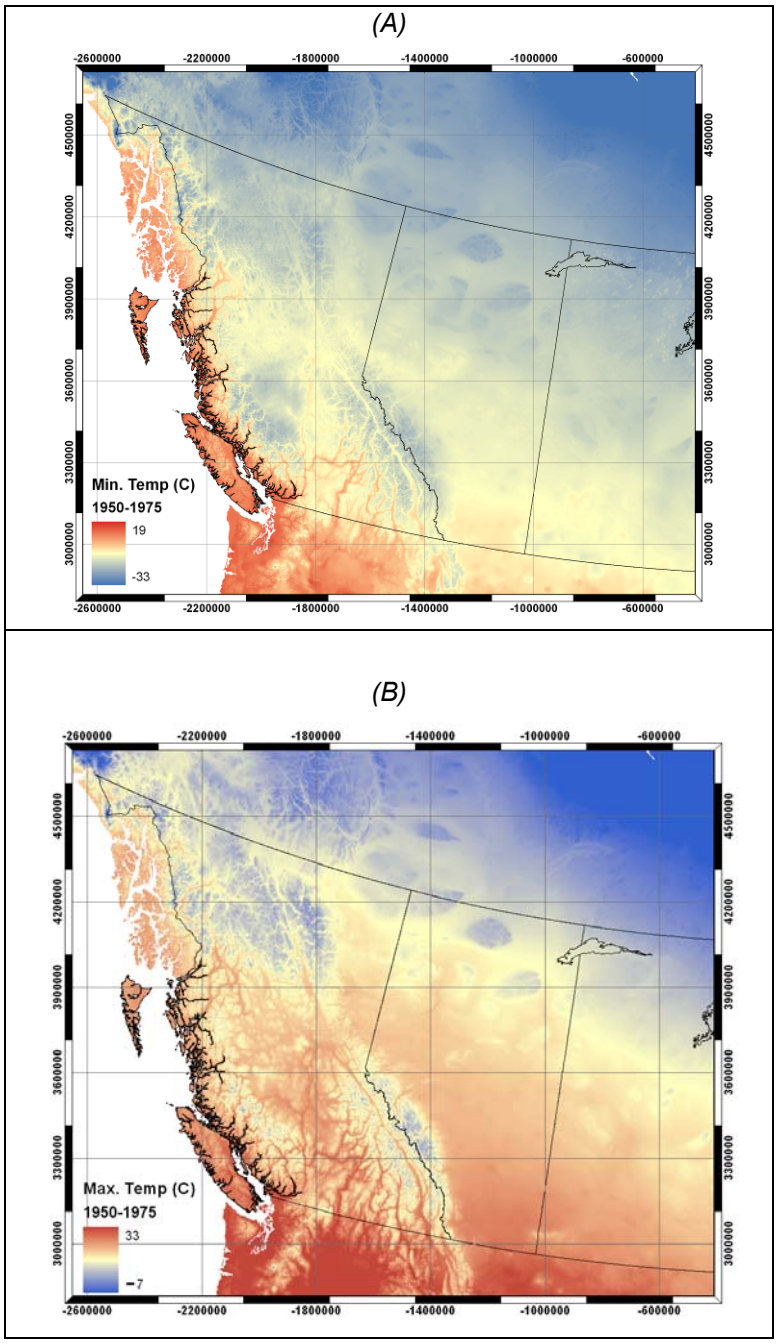
Figure 6: Tree species' ranges (green) overlaid with the vulnerable areas (orange) as well as where climatic conditions are moderate or higher for MPB (red) for (A) lodgepole pine and (B) jack pine using 2001 – 2030 climate and (C-D) 2010-2040 climate.

Figure 7: (a) Areas in km^2 where climatic conditions for mountain pine beetle expansion are ≥ moderate and coincide with where the tree hosts are deemed vulnerable for 2001 – 2030 climate (tan) and 2010-2040 climate (red) and (b) area statistics.

Table 1:

Species	Common name	Code	% P	%A	Accuracy Presence	Accuracy Absence	Overall Accuracy
Pinus contorta	lodgepole pine	LPP	0.22	0.78	85.6	84.8	85.2
Pinus banksiana	jack pine	JP	0.09	0.91	85.0	85.0	85.0

Figure 1(a)-(c):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-1000000
-600000
4500000
4200000
3900000
3600000
3300000
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Min. Temp (C)
1950-1975
19
-33
(B)
Max. Temp (C)
1950-1975
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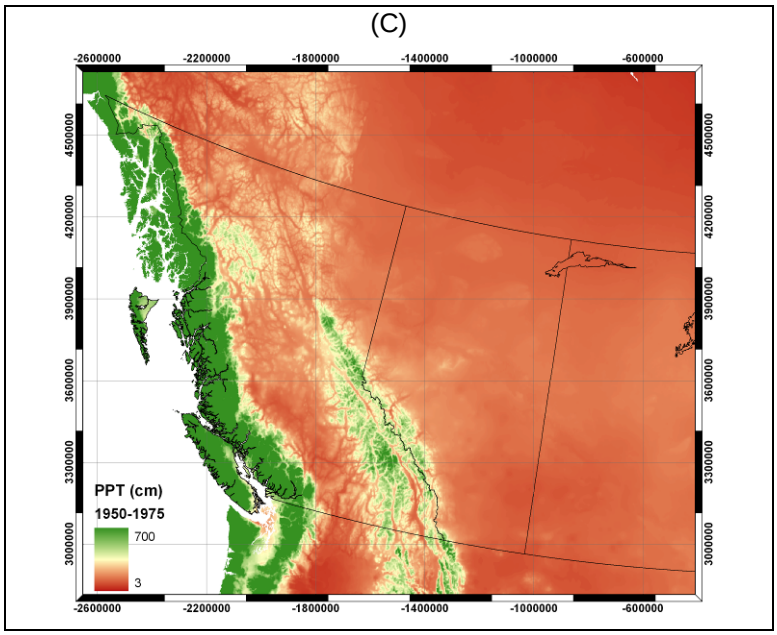
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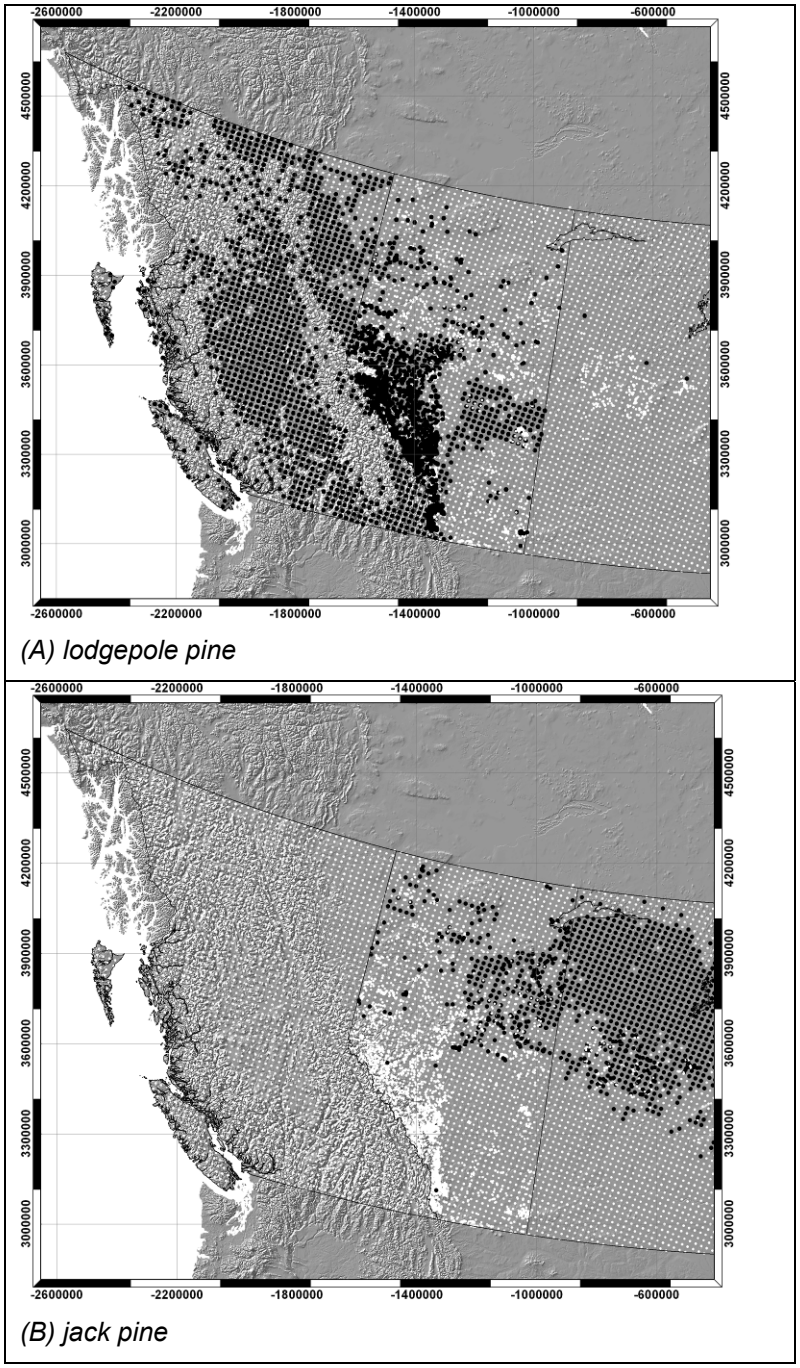
-1800000
-1400000
-1000000
-600000
4500000
4200000
3900000
3600000
3300000
3000000
PPT (cm)
1950-1975
700
3

2
3

Figure 2 (A)-(B):

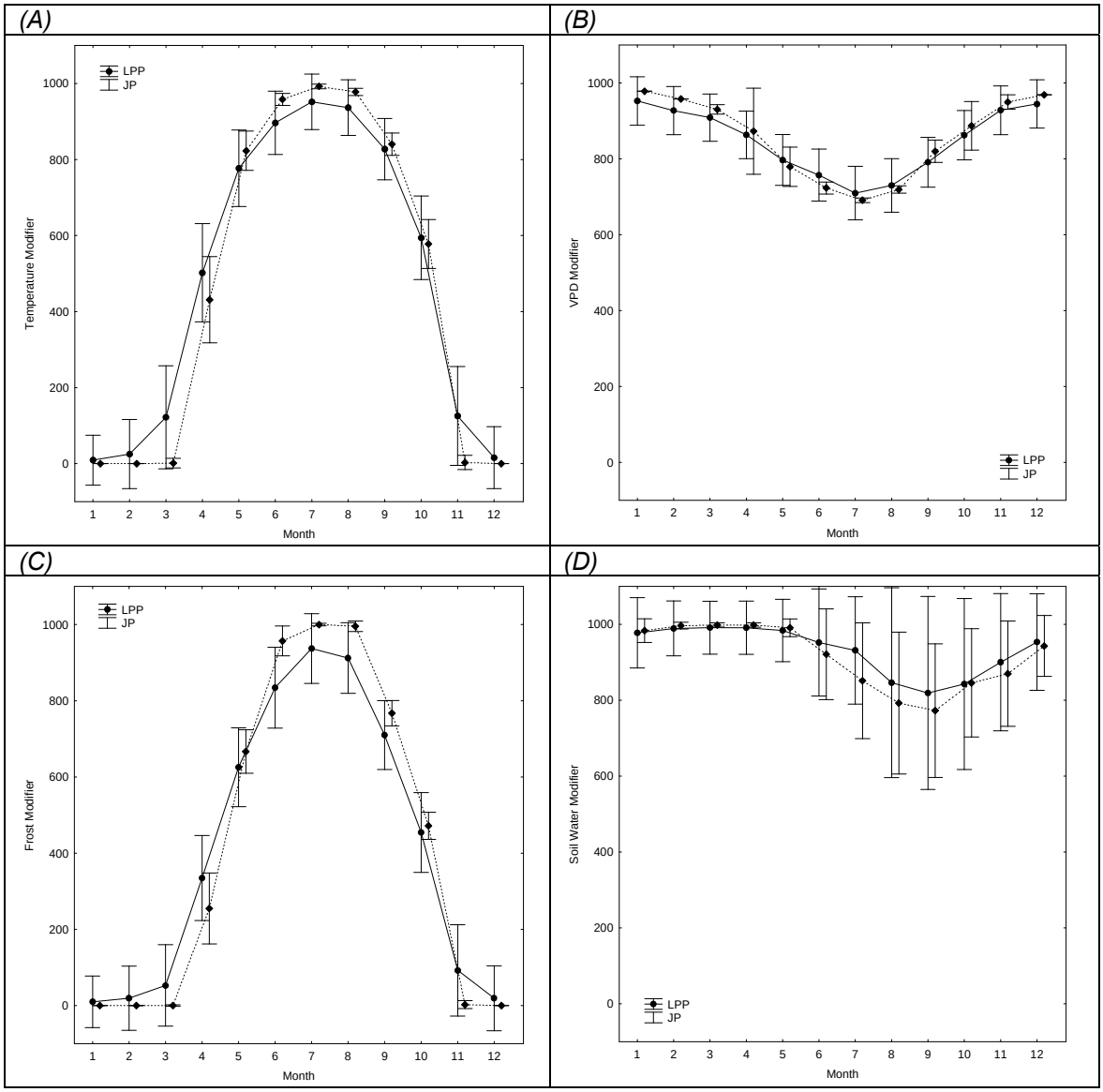


(A) lodgepole pine

(B) jack pine

1 Figure 3:

2


(A)
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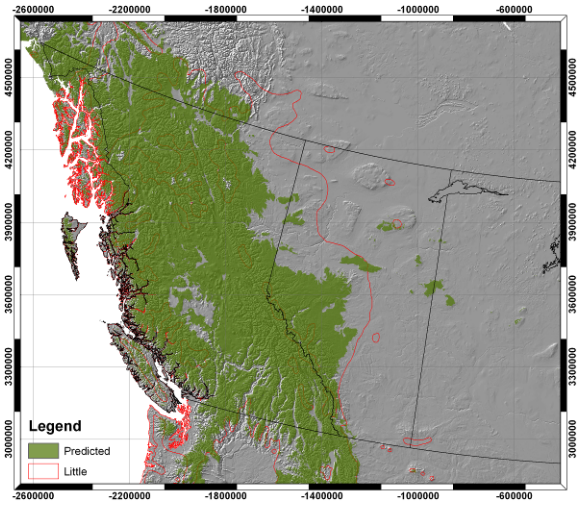
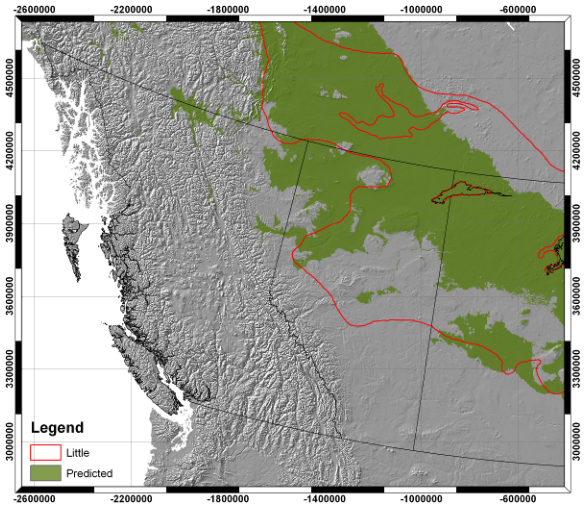
1 *Figure 4:*

(A)



(B)



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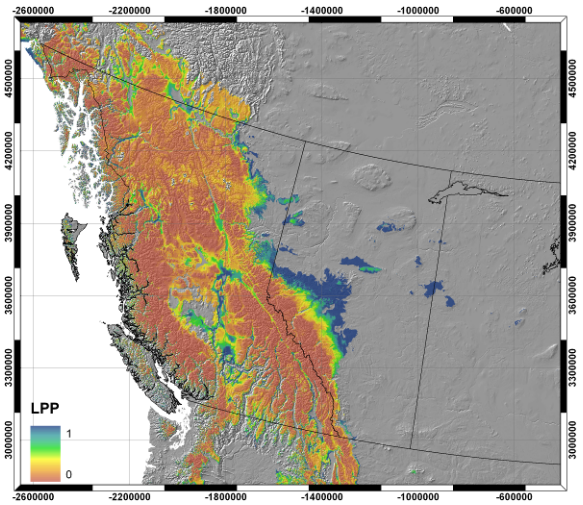

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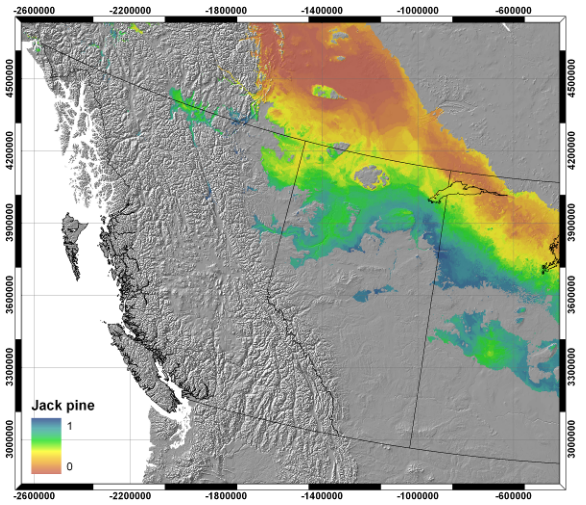

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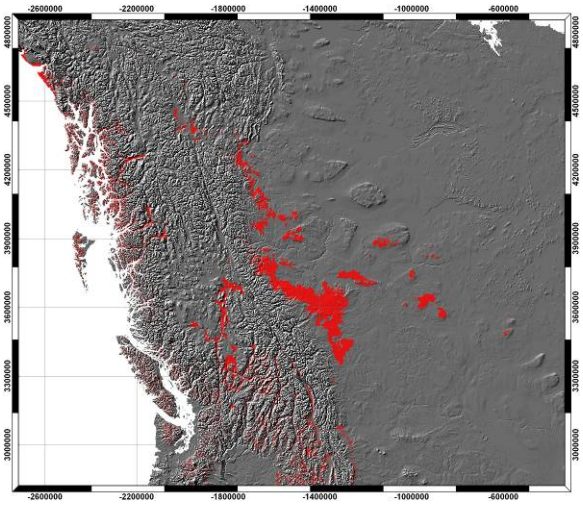

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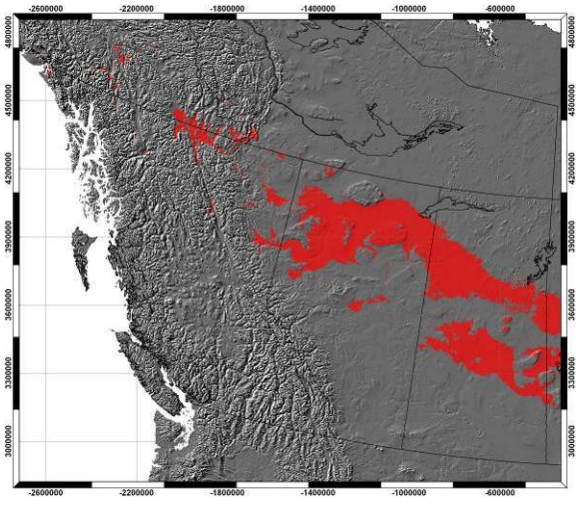

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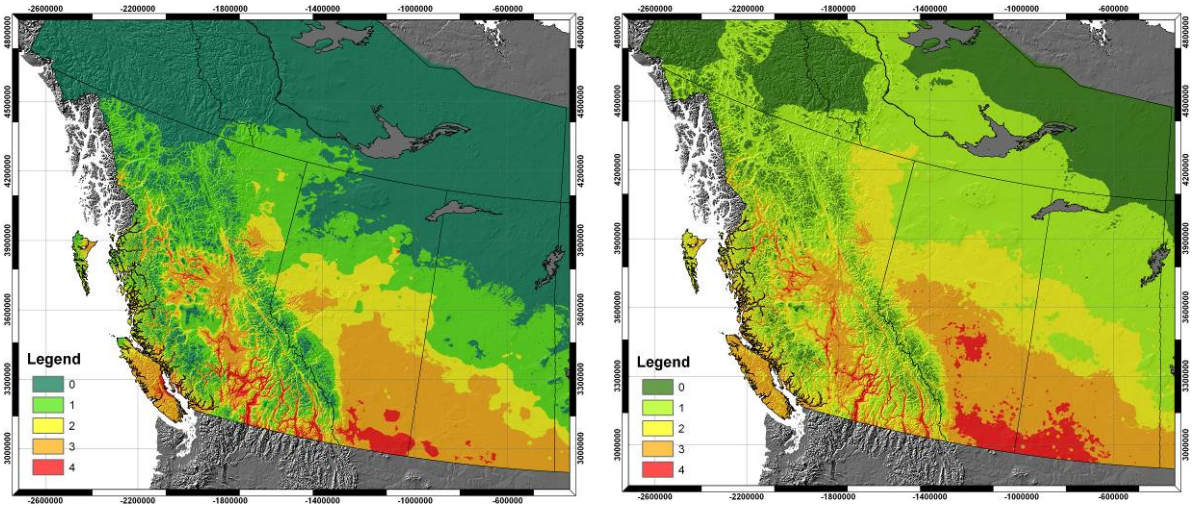
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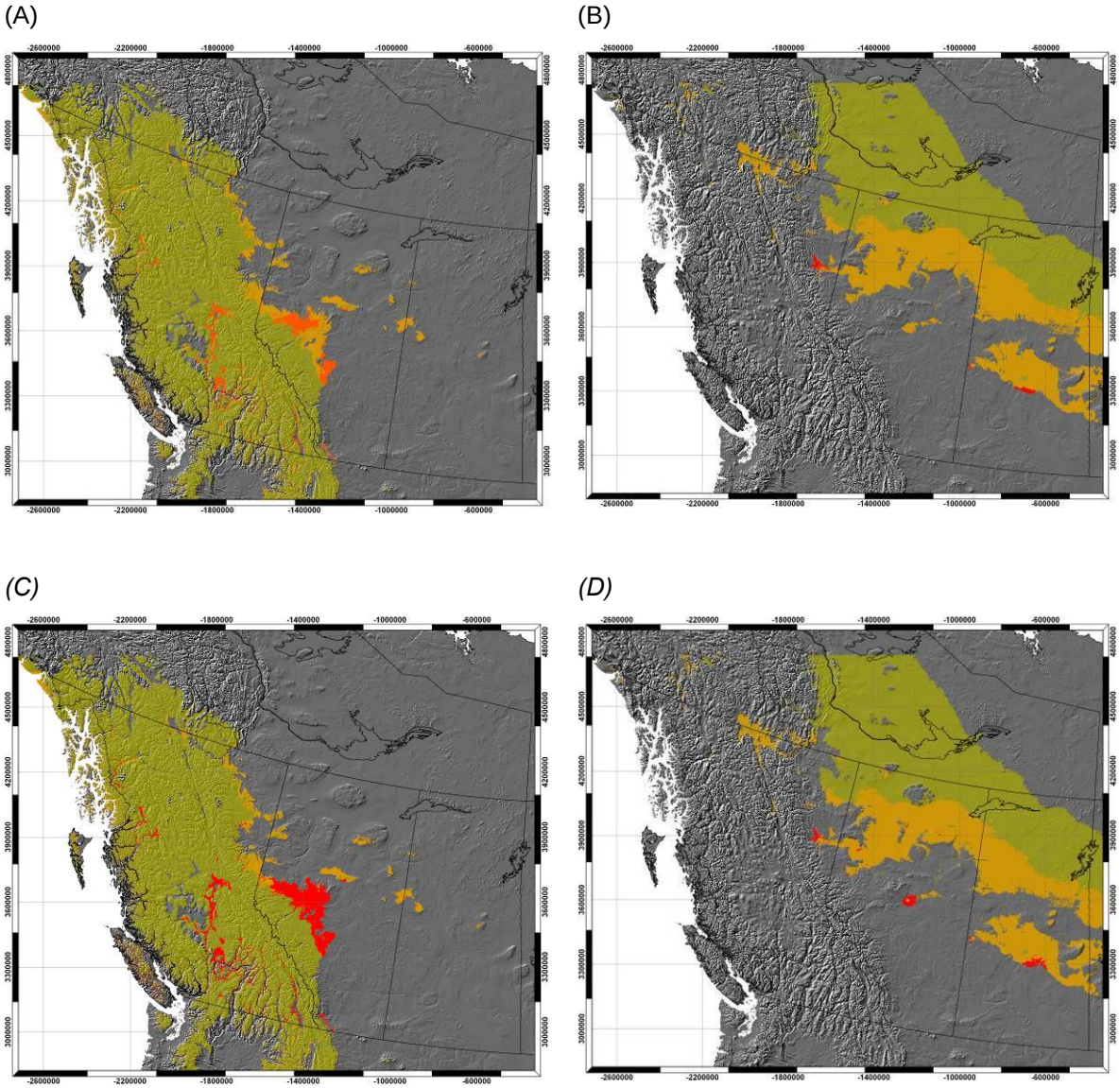
(A) (B)

Figure 6:



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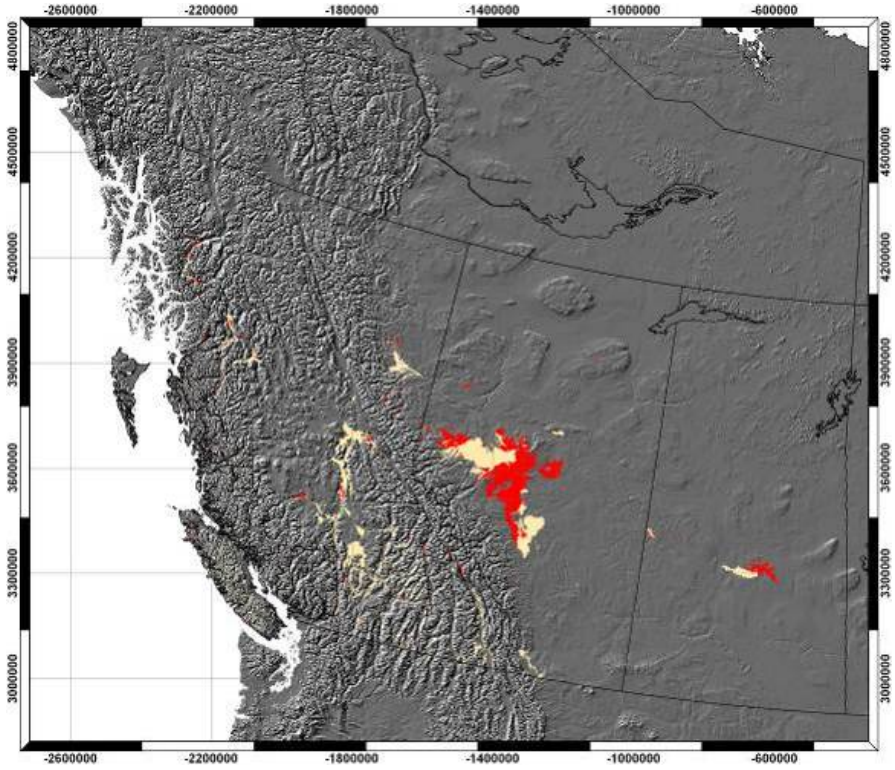
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