EFFECTS OF CLIMATE CHANGE AND FOREST GOVERNANCE ON LARGE-SCALE INSECT OUTBREAKS: A SOCIO-ECOLOGICAL SYSTEMS CASE STUDY OF THE MOUNTAIN PINE BEETLE IN NORTH AMERICA

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DISSERTATION ABSTRACT

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The mountain pine beetle (MPB) has devastated trees on more than 1.3 million square kilometers of land in North America, converting these forests from a carbon sink to a carbon source. The beetle population has reached an unprecedented level over the 20th century, quickly expanding its outbreak range to regions historically too cold for it to survive. The range expansion has been widely attributed to climate change, yet the relative contributions of climate change and forest governance to MPB infestations have been largely overlooked. This dissertation studies large-scale MPB outbreaks with a perspective grounded in socio-ecological systems (SES) to illustrate the complex adaptive systems of MPB.

By primarily utilizing predictive models to reveal nonlinear and emergent patterns of MPB eruptions, the dissertation investigates cross-scale biotic and abiotic interactions in the MPB SES to explain both global and local controls on beetle outbreaks. In so doing, the case study makes four interdisciplinary contributions. First, it initially examines the continental-scale MPB range expansion that shows extraordinary patterns emerged from ecological processes at local and regional scales. Second, it provides a SES model of large-scale forest disturbances to advance the understanding of anthropogenic impacts on ecosystems. Third, it applies the concept of SES resilience to further clarify the relationship between regime shift and resilience. Fourth, it creates transferable data and methods for future landscape ecological research.

The dissertation uses climate space to visualize how the MPB climate niche has changed with its spatial expansion, species distribution modeling to demonstrate how bioclimate has contributed to outbreak probability, and geographically weighted regression to localize the significance of climatic and non-climatic factors in driving MPB outbreaks. The results show that the MPB has expanded to a colder climate space compared with its previous range. The landscape-level MPB eruptions exhibit a strong response to climatic warming. Non-climatic controls are common, especially as long-term fire exclusion causing positive feedback to MPB outbreaks. The complexity of MPB SES presents an archetypical 'tipping-point' model triggered by human impacts, in which a shift in the disturbance regime reveals that anthropogenically-amplified MPB outbreaks are transforming forest ecosystems.

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To our home planet, the Earth, the source of my life and passion

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CHAPTER I INTRODUCTION

1. Research problem and gaps

Human impacts are evident in transforming earth systems, and the need to understand impacts and search for appropriate responses is increasingly urgent. Theoretical and methodological scientific approaches, including socio-ecological systems (SES) research methods, are evolving to address global environmental challenges. The dissertation focuses on a critical threat to the forests of North America and explores the complex adaptive dynamics that result from the interplay of natural and human factors that contribute to the unprecedented mountain pine beetle (*Dendroctonus ponderosae*, MPB) outbreaks. Millions of acres of trees have been killed annually by this native insect, and there is well-founded concern that the extent of its damage may become far greater. This is a significant socio-ecological problem heatedly discussed across different disciplines.

The recent MPB outbreak range expansion to northern British Columbia and Alberta has largely been attributed to climate change (Bentz et al., 2016; A. Carroll et al., 2003; Safranyik et al., 2010; Sambaraju et al., 2012). Some researchers also discussed how fire suppression has potentially affected the MPB outbreak dynamics in British Columbia and Alberta (Ono, 2004; Taylor and Carroll, 2003). However, several questions remain unanswered in the understanding of large-scale MPB outbreaks, and this dissertation addresses the following research questions: 1) *How has the MPB climate niche changed during its geographical expansion?* (Chapter I) 2) *What is the relative contribution of climatic versus non-climatic factors in driving the MPB outbreak range expansion?* (Chapter III and IV) 3) *What is the relationship between fire suppression and MPB outbreaks in the American West?* (Chapter IV).

Most of the research on the beetle-climate relationship has been concentrated on regions such as provinces in western Canada, or states in the western United States, and does not incorporate the beetle-climate research for the complete MPB outbreak range. Meanwhile, the effects of fire suppression on MPB outbreaks have not been evaluated in the American West. To fill the research gaps, this dissertation will investigate the relative impacts of climate change and fire exclusion on MPB outbreaks, by answering the research questions using spatial analysis and modeling (SAM). The study will also apply the concepts employed in SES research, including resilience (and regime shifts) and complexity, which have not been widely discussed in the MPB literature.

2. Significance and broader impacts

Mountain pine beetle outbreaks have triggered massive tree mortality in the North American coniferous forests. They have turned these forests into a large net carbon source (Kurz et al., 2008), and have caused a substantial reduction of net ecosystem productivity (Ghimire et al., 2015) and had negative effects on ecosystem services (Dhar et al., 2016b). Substantial resources are being poured into the existing long-term and large-scale fire control practices by the US federal agencies, yet this has not reduced fire extent and severity, while creating concerns over their negative consequences, which are coincident with climate change and ex-urban development (Calkin et al., 2015). Fire exclusion and other forest health management policies (Gandhi et al., 2019) have directly and indirectly affected ecosystem services, including the consequences of MPB outbreaks. This dissertation will make a significant contribution to our understanding of effects of climate change and fire suppression on large-scale forest disturbances. The results of this study have the potential to benefit natural resource managers, conservation and restoration groups, and fire management agencies, and inform further land-use management projects. Improving our understanding of SES from the MPB case will advance more discussions of forest ecosystem resilience and continental disturbance regime shifts. The MPB complexity discussed in this research could be particularly useful for future investigation of forest socio-ecological systems in SES research networks. The study also has interdisciplinary applications and makes contributions to the related broad disciplines such as landscape ecology and biogeography. In addition, the data and modeling methods created from this dissertation are transferable to other research.

3. Geographical context

The geographical extent of the dissertation research work is North America, where the species distribution of the MPB ranges from the Pacific Coast east to the Black Hills of South Dakota, and from central British Columbia and western Alberta to northern Baja

California, Mexico (Gibson et al., 2009), following its major host pine species, which include lodgepole pine (*Pinus contorta*), ponderosa pine (*P. ponderosa*), limber pine (*P. flexilis* James), whitebark pine (*P. albicaulis* Engelmann), sugar pine (*P. lambertiana* Dougl.) and western white pine (*P. monticola*). The current MPB range is limited in western North America primarily by climate, due to physiological restrictions for MPB from colder temperatures, although the range of its novel host species, jack pine (*P. banksiana* Lamb), extends from Alberta to Nova Scotia. There are new concerns regarding the potential of changing climate promoting the expansion of MPB into the vast boreal forest (Cullingham et al. 2011; Rosenberger et al. 2017b).

The availability of host trees is another determinant for the geographic range of MPB, which is influenced by long-term climate change and forest governance. Specifically, active fire suppression in the US and Canada during the last century has increased the area of dense forests with a greater number of large and old pine trees that are more susceptible to MPB attack (Taylor and Carroll, 2003). Although since the 1960s there has been increasing recognition of the ecological role of fires, due to positive feedback from a century of active fire suppression, fire suppression regimes have remained largely the same (Calkin et al., 2015). In the United States, several factors have contributed to the preference for fire control, including residential development near forested areas, i.e. Wildland Urban Interfaces, the Forest Fires Emergency Act, and unlimited emergency funds (Berry, 2007). Thus, climate change and fire suppression are expected to have compound effects on the large-scale MPB outbreaks in North America and exploring their relative contributions will inform further management policies.

4. Research methods

The dissertation utilizes multiple SAM methods to answer the research questions, combining data visualization and regression analysis. The research methods are designed for the large-scale research problem of MPB outbreaks. The delineation of spatial extent is determined by the research questions, the current outbreak range of MPB and the political boundary of fire exclusion policies, while the grain size of 10km was selected as the appropriate observational unit given the targeted spatial extent and the ecological phenomena being modeled. Secondary data sourced from aerial mapping, climate and land use models are used to compute bioclimatic, spatial autocorrelation, and fire suppression variables. Variable selection is processed by steps. Climate space (multidimensional climatic conditions; Chapter II) visualizes the data distribution and screens the variables that cannot differentiate the climates occurring within and beyond MPB outbreaks. Species distribution modeling (prediction of outbreak probability using environmental variables; Chapter III) further filters the variables that do not contribute significantly to the prediction. More steps in SAM such as geographically weighted regression (GWR, modeling of the local relationships; Chapter IV) are included to determine the relative importance of bioclimatic and fire suppression variables

The statistical methods used in this dissertation favors 'goodness of fit' over 'parsimony' because predictive models are preferred over explanatory models to study emergence of complex systems (Schoon and van der Leeuw, 2015). Decisions for model optimization and selection are made according to data quantity and quality, model assumptions, and existing understanding of ecological relationships. Multiple methods are also used to address uncertainty, including different methods for robustness (e.g., bootstrapping, cross-validation) and goodness of fit (e.g., adjusted R squared, Akaike information criterion, and confusion matrix metrics), and spatial analysis techniques to account for spatial autocorrelation. The interpretation of results also considers the limitation of current research. Specifically, Chapter II explores data using multiple univariate and bivariate plots to identify constraint variables of range expansion, and quantile regression and a bootstrap test to examine the dynamics of climate space. Chapter III applies logistic regression with lasso regularization to predict MPB outbreak probability, and Chapter IV applies multiple linear regression to predict MPB-affected acres and GWR to identify locally-significant predictors. The dissertation methodological flow is presented in Figure I-1, which depicts the steps in each chapter and methodological connections among chapters.

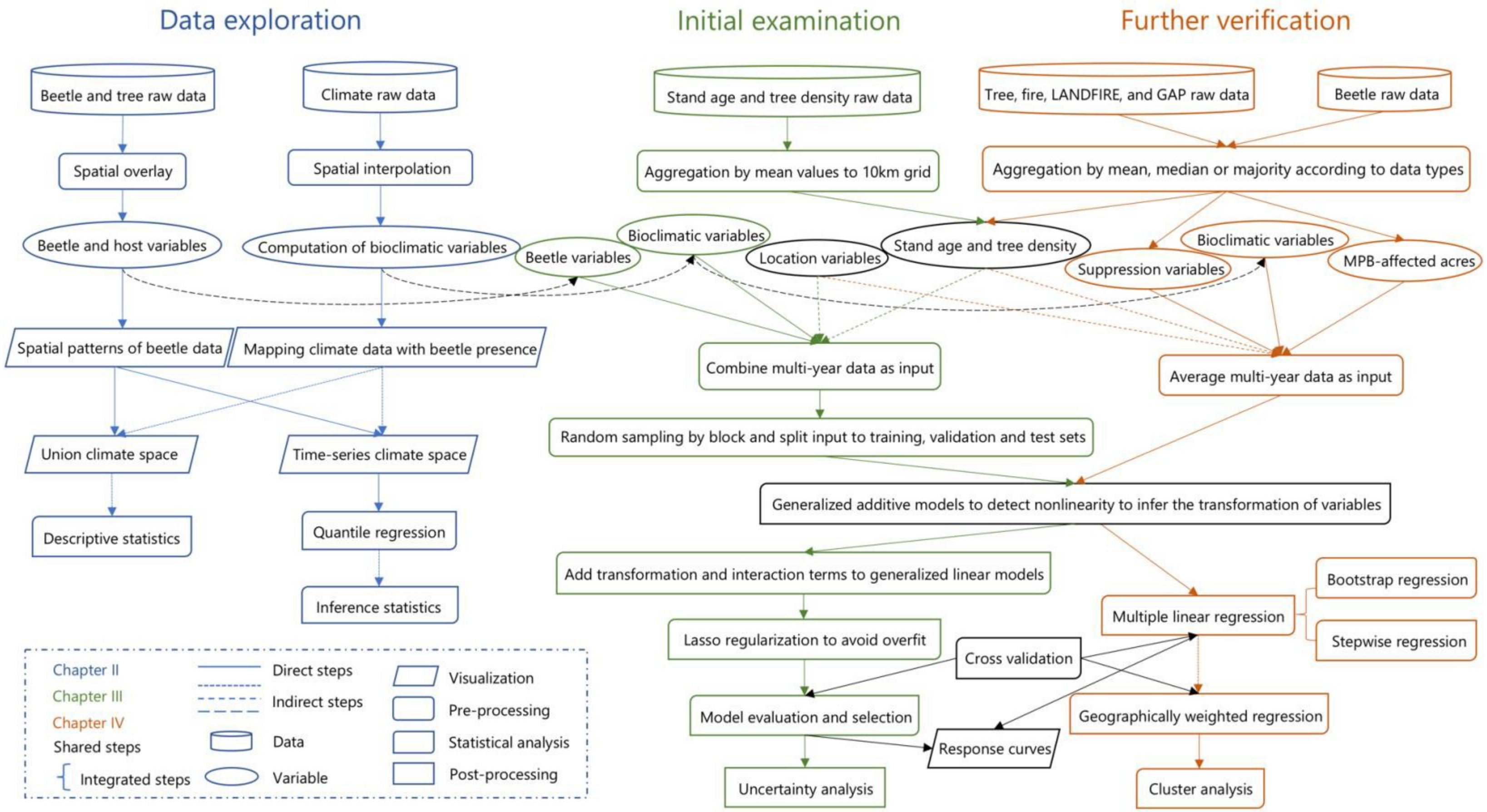


Figure I-1. Dissertation workflow. Arrows direct the steps from data to model interpretation. Chapter II is a data exploratory process while Chapter III and IV are both modeling processes shared with common data or methods in black color. Chapter IV is a development from Chapter III by examining one of non-climatic factors discussed in Chapter III.

5. Literature review

The dissertation examines the recent mountain pine beetle outbreaks using the theoretical framework of SES. The review of literature is divided into four sections: two theoretical, a topical, and a methodological sections. The objective of this review is to explain the relevant concepts and methods applied in the dissertation. The two theoretical sections review the framework of socio-ecological systems covering important concepts in SES research including complexity, vulnerability, resilience and sustainability, and addresses their linkages, with a focus on resilience. The topical section reviews the effects of climate change and fire exclusion on forest disturbances (fires and insects in particular), and then focuses on the ecology of the MPB with a discussion of its biotic and abiotic relationships. The methodological section describes my use of spatial analysis and modeling to analyze the data. Finally, I summarize the chapter and address its links with the subsequent data analysis chapters.

5.1. Key concepts in the socio-ecological systems framework

5.1.1. Socio-ecological systems

Due to growing and widespread human influences in the environment, natural ecosystems are now viewed and studied as socio-ecological systems (SES) (S. L. Collins et al., 2011). The term social-ecological systems (Ostrom 2007) has evolved in tandem with several closely related terms including human-environment systems (Turner et al., 2003a), social-environmental systems (Eakin and Luers, 2006), and coupled human and natural systems (Liu et al., 2007), reflecting a rise of integrative human-environmental science. In SES research, natural scientists see people as a part of ecosystems and social scientists see the natural environment as a component of social systems (Westley et al., 2002). As such, the distinction between social and natural systems is artificial and arbitrary, and these SES-related terms are basically interchangeable while some of them may emphasize different foci. With the increasing use of the SES perspectives, many researchers have proposed different ways of understanding SES, from complexity (Liu et al., 2007) to multiple frameworks (S. L. Collins et al., 2011; Ostrom, 2009; Pickett et al., 2005; Turner et al., 2003a) and their comparisons (Binder et al., 2013; Pulver et al., 2018).

SES researchers from different backgrounds look at SES with different perspectives and there is neither a specific definition of SES nor a universal conceptual framework.

5.1.2. Complexity and biocomplexity

Socio-ecological systems are increasingly understood as complex adaptive systems (Levin et al., 2013). Complexity generally explains “how large-scale complex, organized, and adaptive behavior can emerge from (relatively) simple interactions among myriad individuals” (Schoon and van der Leeuw, 2015). The concept of biocomplexity is an application of complexity and systems theory from physics and mathematics to environmental studies through interdisciplinary research. It was defined as “properties emerging from the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans”, emphasizing emergent properties (Michener et al., 2001) or “the degree to which the interactions in ecological systems comprising biological, social, and physical components incorporate spatially-explicit structure, organizational connectivity, and historical contingency”, emphasizing interconnected relationships (Pickett et al., 2005).
Briefly, spatial heterogeneity, organizational connectivity, and temporal contingencies were summarized as the three dimensions of biocomplexity (Cadenasso et al., 2006).

Biocomplexity can be defined in three distinct but related ways: 1) the structure of systems, 2) emergent, non-linear or self-organized outcomes, 3) a highly connected explanation or model (Cadenasso et al., 2006). The four frontiers of ecological research-community coalescence, ecological memory, emergent properties, and ecological topology -are also useful for providing pathways for understanding biocomplexity (Thompson et al., 2001). The complexity of SES, which exhibits nonlinear dynamics with thresholds, reciprocal feedback loops, time lags, resilience, heterogeneity, and surprises, can be traced from spatial, temporal and organizational dimensions (Liu et al., 2007). These complexity characteristics are highly overlapped. Overall, complexity or biocomplexity deals with the explanation of complex behaviors resulting from simple or complicated systems by connecting the interacting system components across space, time and organizational units. The complexity concept is applied to understand large-scale beetle emergence in this dissertation.

5.1.3. Vulnerability and resilience

Vulnerability and resilience, although originating from different research traditions, are linked in the processes of response to changes (Gallopín, 2006). Vulnerability and resilience are two connected concepts that can be used to measure the capacity of SES (a system, subsystem, or system component) to adapt to changes induced by external forces (e.g., environmental hazards, social changes, and perturbations), which involve components of complexity, or incorporate understanding of complexity and uncertainty. Vulnerability has divergent definitions in different research traditions, among them are "the state of susceptibility to harm from exposure to stresses associated with environmental and social change and from the absence of capacity to adapt" and "the degree to which a system is susceptible to, or unable to cope with, adverse effects of climate change" from the IPCC (Adger, 2006). For most useful decision-making in reducing vulnerability to change, the SES vulnerability framework emphasizes linking interacting subsystems and components and recognizing their variations in hazard exposure and coping capacity, to identify the most vulnerable sections and their connectors (Turner et al., 2003a). This framework treats vulnerability as both exposure to hazards and system sensitivity and resilience. The concepts of vulnerability and resilience are applied to understand the adaptations of different components to changes in MPB SES in this dissertation.

5.1.4. Sustainability

Sustainability, a term that seeks the balance between environment and development, is often linked to 'biodiversity' in biology or 'equity' in sociology, and related to 'futurity' in which sustainable development is defined as "development which meets the needs of the present, without compromising the ability of future generations to meet their own needs" (Basiago, 1995). Sustainability science is "an emerging field of research dealing with the interactions between natural and social systems, and with how those interactions affect the challenge of sustainability" (Kates, 2011). Three pivots of sustainability science were identified as SES, environmental services and tradeoffs among environmental services (e.g., water quality, phenology, or flood control) and between those services and human outcomes (e.g., poverty, hunger, or housing), which tend to gradually align vulnerability and resilience (Turner, 2010). Different SES studies use a mix of complexity, vulnerability, resilience and sustainability perspectives, and are inherently interdisciplinary and collaborative (Alberti et al., 2011).

5.1.5. Frameworks and linkages

Based on a systems approach, frameworks as conceptual maps, which depict components (e.g., social, ecological and technological components), connections (e.g., emergent properties, nonlinearity, path dependence, and feedback loops), scale (i.e., multiple spatial and temporal scales), and context (i.e., the socioeconomic, political, and ecological setting of an SES), are commonly applied to address the interdisciplinary challenge in complex adaptive SES (Pulver et al., 2018). SES perspectives stand for an ontological shift in understanding human-nature relationships, and study humans as an integral part of the biophysical world with a focus on the interactive interactions and feedbacks between the social and ecological subsystems using non-reductionist approaches (Schoon and van der Leeuw, 2015). Aiming for sustainability by studying human-nature interactions, SES research examines human-nature feedbacks (positive or negative feedbacks, tight or loose feedbacks) as its central components (Hull et al., 2015) and the complex adaptive system behaviors of SES as ‘more is different’ (Schoon and van der Leeuw, 2015).

The simplified complexity includes nonlinearity (a system does not respond to gradual change in a smooth way), emergence (behavior of a system that cannot be inferred from the behavior of its components) and self-organization (some form of aggregated or global order emerges from uncoordinated local interactions). The observation of SES behaviors often draws upon cross-scale socio-ecological interactions based on multiple-scale SES research. The outcomes of the complex system behaviors challenge the system capacity in terms of resilience and vulnerability, which is also scale-dependent. Scale mismatch, a mismatch between the scale of management and the scale of the ecological processes or natural resources being managed (Cumming et al., 2006), often occurs as a SES outcome.

Sustainable management thus needs the understanding and resolution of scale mismatch. Therefore, the key concepts, including complexity, uncertainty, resilience, vulnerability, sustainability, and scale, are intertwined within the SES framework.

5.2. Resilience and regime shifts

5.2.1. Concept of resilience

The concept of resilience has evolved with the understanding of ecosystems in ecology from views of system behaviors. In the 1970s, the theory that ecosystems often moved between alternative stable states was proposed to challenge the notion that ecosystems moved toward equilibrium (Hoiling, 1973; Schoon and van der Leeuw, 2015). Resilience is widely used in understanding disturbance and disturbance regime. Disturbance is “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett, 1985). A disturbance regime is characterized by the pattern and dynamics of disturbance events in a given ecosystem. When a system changes alternative stable states after disturbance, a regime shift occurs, which refers to a large, abrupt, persistent reorganization of the state of an ecosystem that can be triggered by a loss of resilience (Gunderson, 2000), the occurrence of stochastic events (Folke et al., 2004; Scheffer et al., 2001), and synergistic feedbacks (Brook et al., 2013; Mü Ller et al., 2014). With the recognition of complex adaptive SES, resilience is not limited to the capacity to absorb or adapt to change; it includes the ability to transform with change (Reyers et al., 2018).

Specifically, the widely-used definition of resilience has changed from “the magnitude of disturbance that a system can experience before it shifts into a different state with different controls on structure and function” (Folke et al., 2004; Holling, 1973), to “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity and feedbacks” (Walker et al., 2004). The first distinguished ecological resilience from engineering resilience (i.e., the speed of return to the equilibrium), which later was considered inapplicable when a system fails to retain essential functions permanently or temporarily (Walker et al., 2004).

The second is now the dominant perspective for SES, suggesting that resilience is not only about being persistent or robust to disturbance, but also about the opportunities that disturbance opens up in terms of recombination of evolved structures and processes, renewal of the system, and emergence of new trajectories (Folke, 2006).

The change of resilience concept, however, has created a different relationship between resilience and regime shift, since regime shift can be a process of reorganization. Social-ecological resilience focuses on the self-organizing capacity for learning and adaptation in SES, in which the role of human actions has become central in understanding the capacity of ecosystems to generate natural resources and ecosystem services (Folke, 2006). It is also a dynamic concept concerned with navigating complexity, uncertainty and change across levels and scales (Folke, 2016). The application of resilience thinking has influenced the understanding of vulnerability (Berkes, 2007) and sustainability (Folke, 2016) through SES research. Meanwhile, more discussion of the measurements of resilience (Carpenter et al., 2001; Walker et al., 2004) and resilience in social contexts (Adger, 2000; Cote and Nightingale, 2012; Cretney, 2014; MacKinnon and Derickson, 2013) has proceeded during the past two decades.

5.2.2. Measurement of resilience

To measure ecological resilience, Walker *et al.* (2004) suggest that four aspects of resilience are the magnitude of system change before losing its recovery ability (latitude), the flexibility of changing a system (resistance), the distance between the current system state and a system limit or threshold (precariousness), and the level of impacts on the resilience of a system from cross-scale interactions (panarchy). Adaptivity or adaptive capacity was introduced to describe the processes that modify ecological resilience, which is measured as the ability to either control the trajectory of the system (change precariousness), change the topology of the system resilience (latitude and resistance), or change the processes in response to dynamics at other scales (panarchy response) (Gunderson, 2000; Walker et al., 2004). Furthermore, transformability is the capacity of a system to renew itself under untenable conditions (Walker et al., 2004), or its capacity to cross thresholds into new development trajectories (Folke et al., 2010). Resilience, adaptivity and transformability are three related attributes of SES that govern the system's dynamics (Folke et al., 2010; Walker et al., 2004). As such, resilience in SES can be measured as 1) the amount of disturbance, shock or surprises that the system can absorb to remain in the domain of attraction, which is related to slowly changing variables that control the boundaries of the domain of attraction; 2) the degree to which the system is capable of self-organization, which is related to the extent to which reorganization is endogenous rather than forced by external drivers; 3) the degree to which the system can build capacity for learning and adaptation, which is related to the existence of mechanisms for the evolution of novelty or learning (Carpenter et al., 2001; Folke et al., 2002).

Adger (2000) defined social resilience as the ability of resource-dependent communities to withstand external stresses and shocks to their social infrastructure, and proposed institutional change, economic structure, and demographic change as proxy indicators to measure it. Cote and Nightingale (2012) further suggested critically examining the political, historical and cultural meaning of social resilience to help address the questions of resilience for whom and why. MacKinnon and Derickson (2013) also brought attention to the neglected organizational and spatial inequality of power relations in social resilience and provided an alternative concept of 'resourcefulness' for community groups to foster. Cretney (2014) reviewed the critiques of social resilience (e.g., lack of consideration for power, agency and inequality) and pointed out that social resilience is evolving and further research needs remain in regard to activists and community groups. Brown (2014) concluded that the resilience concept is malleable and contested, and can be co-opted by different interests under social contexts, while its related discussion is continuing. Finally, socio-ecological resilience has adapted to be more "resilient" when human impacts have become more and more significant in ecosystems, and when the concept of ecological resilience migrated from natural science to social science through SES research.

5.2.3. Concept of regime shift

From ‘resilience’ to ‘regime shift’, the classic ball-in-cup analogy of alternative stable states proposed by Holling (1973) has been developed gradually and shown in different conceptual models. Beisner *et al.* (2003) presented two ways of changing alternative states from community and ecosystem perspectives respectively. For example, gradual changes in ecosystems can trigger catastrophic shifts by reducing the size of the attraction basin with gradually changing conditions (e.g., nutrient loading, exploitation, or temperature rise) which may tip the system into one of several contrasting states as a result of stochastic events (Scheffer et al., 2001). Furthermore, the conceptual model of catastrophic shifts emphasizes the ecosystem perspective by illustrating how external conditions can affect the resilience of equilibria by changing parameters in a stability landscape model, and further develops the modeling of the ways in which an ecosystem can respond to change in conditions (Scheffer and Carpenter, 2003). Also, the conceptual model of tipping points shows that a tiny change in a condition may cause a large shift or a small perturbation can drive the system across the boundary between the attraction basins if the system is very close to a bifurcation point (Scheffer et al., 2009), which can commonly be detected by critical slowing-down using indicators related to variability, autocorrelation, and recovery time (Carpenter et al., 2011; Dakos et al., 2008; Drake and Griffen, 2010).

Yet, where exactly a tipping point is, and whether there is a planetary-scale tipping point, are still controversial topics (Brook et al., 2013; Hughes et al., 2013; Lenton and Williams, 2013). The planetary boundary or ‘safe operating space’ concept can be expressed in two ways: (1) the potential responses from systems at equilibrium to multiple, interacting anthropogenic drivers (e.g., smooth, a step function, and hysteretic), (2) the response of the system to escalating drivers over time (Hughes et al., 2013). The concept of a “landscape trap” has been proposed, when multiple natural and anthropogenic disturbances result in synergistic interactions and generate a series of feedback processes (i.e., escalating drivers) that drive entire landscapes into an undesirable and potentially irreversible state (i.e., the response of the system). A landscape trap describes an ecosystem that has shifted into, and remained at, a highly compromised structural and functional state, and a primary goal of using the concept is to detect their onset before they are irrevocable (Lindenmayer et al., 2011). The landscape trap concept further predicts the potential outcomes of regime shifts when a positive feedback loop occurs, which does not imply a tipping point threshold. The common condition for landscape traps is human disturbances that force ecosystems to remain in an unfavorable state.

These conceptual models developed from the alternative stable states theory emphasize different parts of regime shifts. The “catastrophic shifts” model focuses on conditions in which gradual changes can result in dramatic shifts in states. The “tipping points” model further adds the concept of a bifurcation point where a catastrophic shift may occur when certain thresholds are crossed. Finally, the “landscape traps” model elaborates on the potential outcomes of regime shifts. However, they are still limited to the perspective that resilience is reflected in the size of the basin of attraction and a loss of resilience may lead to a regime shift. The dissertation instead presents an example of new understanding that regime shift can be a part of resilience.

5.2.4. Measurement of regime shift

Generally, regime shifts more likely occurred “when humans reduced resilience by removing significant ecosystem components (e.g., response diversity, whole functional groups of species, or whole trophic levels), impacting ecosystems via emissions of waste, pollutants and greenhouse gases, and altering the magnitude, frequency, and duration of disturbance regimes” (Folke et al., 2004). These human induced pressures often come with combined or synergistic effects that enforce an easier movement in the domain of attraction and make ecosystems more vulnerable to regime shifts (ibid). The conceptual model of alternative stable states suggests that regime shifts can happen as a result of changing state variables that can change ‘quickly’ in response to feedback from model dynamics, and/or changing system parameters that are either independent of, or subject only to very slow feedback from state variables within the model (Beisner et al., 2003). Different patterns in the relationship between the response of a state variable and some external control can identify three different types of regime shift: smooth or quasi-linear, abrupt or nonlinear, and discontinuous (Collie et al., 2004). Diagnosing the existence of and/or type of regime shift has become a focus (Collie et al., 2004; Scheffer and Carpenter, 2003), with researchers highlighting the importance of detecting early-warning signals of regime shifts and their indicators (Biggs et al., 2009; Contamin and Ellison, 2009; Dakos et al., 2008; Scheffer et al., 2009).

These early-warning signals include '1) critical slowing down shown as slower recovery from perturbations, increased autocorrelation and increased variation in the pattern of fluctuations, 2) skewness and flickering of fluctuations before transitions, 3) indicators for the amplitude of fluctuation and slowness in cyclic and chaotic systems, and 4) particular spatial patterns that deviate from the general pattern' (Scheffer et al., 2009). The indicators of early-warning signals were often identified according to the high-frequency signal in the spectral density of the times-series, which are associated with two key factors: the amount of inertia in the system, and the amount and type of variability intrinsic to the system and the impact of this variability on the power of an indicator (Contamin and Ellison, 2009). A powerful indicator may detect an impending regime shift with sufficient lead time to allow for an effective management intervention, but not so far in advance that an intervention is impractical (Contamin and Ellison, 2009). To improve the usefulness of indicators for averting regime shifts, Biggs *et al.* (2009) suggested that research should focus on defining critical indicator levels (or ecological thresholds), that are related to switches in ecosystem attractors, rather than detecting change in the indicators. Finally, Andersen *et al.* (2009) reviewed a variety of operational approaches to identify ecological thresholds and regime shifts.

5.3. Climate change, fire exclusion and the mountain pine beetle

5.3.1. Effects of climate change and fire exclusion on forest disturbances

Forest disturbances are changing in a more frequent and severe and less predictable manner as a consequence of climate change (Dale et al., 2001). Climate change has direct, indirect and interactional effects on forest disturbances, resulting in amplifying disturbances at a global scale and particularly in coniferous forests and the boreal biome (Seidl et al., 2017). Also, disturbance interactions under climate change may cause ecological surprises with large and nonlinear changes in ecosystem structure and functioning through linked or compound effects that alter ecosystem resistance or resilience with long-lasting results (Buma, 2015). Meanwhile, human-caused climate change has become a dominant force in driving disturbances such as fires (Harvey, 2016). Disturbances such as beetle outbreaks are also driven by interactions among climatic, biological, topographic and anthropogenic factors at multiple spatial and temporal scales (Raffa et al., 2008). Researchers have become more interested in synergistic effects on disturbances from the interactions between climate change and human impacts (Donnegan et al., 2001), or humans' modulating or overriding climatic effects on disturbances (Balch et al., 2017; Taylor et al., 2016). While multiple drivers are controlling forest disturbances across scales (Heyerdahl et al., 2001; Raffa et al., 2008), fire exclusion is one of the most-discussed human factors in influencing forest disturbances in North America (Calkin et al., 2015; Houtman et al., 2013; Parker et al., 2006). Consequently, the relative contribution from climate change and fire exclusion in driving forest disturbances has also attracted more research interest in recent years (Parks et al., 2018; Rogers et al., 2011; Taylor et al., 2016; Westerling et al., 2006).

Researchers found strong climatic controls from early spring temperatures and summer droughts on wildfires in the western United States according to the chronological coincidence between different climatic variables and fire frequency, although they also discussed spatial or temporal variation in the combined effects from human factors (Marlon et al., 2012; Trouet et al., 2010; Westerling et al., 2006). However, fire suppression has amplified the intensity and severity of fires by reducing natural fire activity, prolonging fire return interval, and gradually increasing fuel on the landscape (Parks et al., 2018; Rogers et al., 2011; Steel et al., 2015). Fire suppression and ignitions have shaped the patterns of wildland fire deficit and surplus (Parks et al., 2015), which have lessened the strong multidecadal relationship between temperature and fire (Taylor et al., 2016), and expanded the spatial and seasonal extents of fire activity (Balch et al., 2017), respectively. Since human-caused climate change has become a key driver of forest fire activity in the American West (Harvey, 2016), influences on forest disturbances from human activities may have subordinated the climatic controls.

Climatic variables temperature and precipitation are also the main factors influencing biotic disturbance. However, impacts of climate change on biotic disturbances can be more complicated than on abiotic disturbances due to the complex behavioral, physiological, and molecular interactions among biotic agents (e.g., plants and insects, or preys and predators) at multiple organizational scales. Temperature directly affects the development, survival, range and abundance of insects; mainly, higher temperatures provide more thermal budget for their growth and reproduction in the summer season in northerly latitudes and reduce mortality in temperate regions in the winter season (Bale et al., 2002). The biological impacts of the different rates of warming across latitudes are associated with the physiological sensitivity of organisms to temperature change: a slight warming in the tropics can have detrimental effects on thermally-sensitive insects while warming may enhance the fitness of the species at higher latitudes that have broader thermal tolerance and are currently living in cooler-than-optimal climates (Deutsch et al., 2008). Precipitation indirectly affects insects through modulating plant-insect relationships by changing their food quantity and quality, as higher water availability supports plant growth while droughts stress plants to be more susceptible for insect attacks. Climate change with climate warming and altered precipitation patterns is altering plant-insect interactions resulting in phenological mismatches (DeLucia et al., 2012), multitrophic readjustments (Jamieson et al., 2012), and evolutionary consequences (Rasmann et al., 2014).

As one of many human factors that impact forest disturbances, fire exclusion has influenced the spatial and temporal patterns of fires and beetle outbreaks by changing forest succession, resulting in altered forest compositions and structure. Increased density of small trees, species composition shifting to have more shade-tolerant species, and accumulation of ladder fuels and over-mature canopy layers are the successional consequences of long-term fire exclusion in fire-frequent forests (Keane et al., 2002; Parsons and DeBenedetti, 1979). Keane *et al.* (2002) have summarized the cross-scale diverse and cascading effects of fire suppression in Rocky Mountain ecosystems, including insect and disease epidemics at both stand and landscape scales. The discussion relates fire exclusion to insect outbreaks with factors that characterize susceptible forests, including tree stress induced by density, more older age classes, and continuous and homogeneous landscapes. Most of the research on the effects of fire exclusion has focused on the ponderosa-dominant or mixed conifer forests in the Cascades and Sierra Nevada where low- and moderate-severity fires occurred more frequently (B. M. Collins et al., 2011; Keeling et al., 2006; Miller et al., 2009; Steel et al., 2015; Taylor, 2010; Taylor and Skinner, 2003). However, ecosystems that have experienced infrequent stand-replacement fires with a fire return interval longer than the period of fire suppression are considered less affected by fire suppression, partially because it is less likely to suppress high-intensity fires (Arno et al., 1999), or because a shorter period of fire exclusion is unlikely to dramatically change the long fire intervals (Schoennagel et al., 2004). Therefore, quantifying the impacts of fire suppression on insect outbreaks warrants a critical assessment of ecosystems with different 'natural' fire regimes.

5.3.2. Ecology of mountain pine beetle

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) is a tiny but destructive native insect in North America. The range of MPB follows the historic host range delineated by its primary hosts lodgepole, ponderosa, sugar, western white and limber pines. Recently, MPB has expanded its change to further north into the range of jack pine (*P. banksiana* Lambert) through the lodgepole × jack pine hybrids (Coops et al., 2012; Cullingham et al., 2011; Rice et al., 2007a), and also increased its activity in whitebark pine (*P. albicaulis* Engelmann) forests (Buotte et al., 2017; Logan et al., 2010; Shanahan et al., 2016) in higher elevations. Although MPB attacks most (or at least twenty-six) of the pine species in North America (Amman and Cole, 1983; Safranyik et al., 2010), it also receives stronger resistance from some species in higher elevations, such as Great Basin bristlecone pine (*P. longaeva*) (Eidson et al., 2018, 2017). The beetle has a preference for large diameter trees (Amman and Cole, 1983) and forms multipartite symbiotic associations with blue stain fungi in its mouthparts when it attacks trees (Ojeda Alayon et al., 2017). The beetle aids the blue stain fungus to travel while the fungus helps the beetle overcome the host's defense and provides the beetle nutritional supplementation and favorable host environment for brood development. There are three species in the fungi association and it was suggested that these three different fungi caused lesions on jack pine in Alberta and they have different levels of virulence potentially linked with different adaptation in boreal temperatures (Rice et al., 2008, 2007a, 2007b). The predators and competitors of the beetle mediate its colonization at endemic levels (Tabacaru and Erbilgin, 2015), and this mediation varies across different altitudes (Krause et al., 2017).

Environmental and anthropogenic variables affect the beetle life cycle and its interactions with hosts, fungi associations, predictors and competitors across various spatial and temporal scales (Bentz et al., 2010; Raffa et al., 2008). The beetle population can develop from endemic levels to epidemic levels with suitable environment and food availability. Different stages of population development, defined in terms of population size relative to the abundance of available hosts, are controlled by biophysical thresholds and feedback mechanisms among the abiotic and biotic interactions. On an endemic level, beetles with blue-stain fungi surpass the defense threshold of weakened trees, and develop the broods within the thermal thresholds through the life stages (egg, larva, pupa and adult) while other bole-infesting bark beetle species have significant influences on the MPB establishment and survival at the stand scale (Safranyik et al., 2006). From an endemic level to an epidemic level, successful beetle colonization in large-diameter trees supports the population reaching the outbreak peaks with continuous landscape and favorable weather conditions for dispersal at the landscape scale, while after the epidemic level, adverse weather conditions or host depletion cause the outbreak's collapse (Safranyik et al., 2006). The MPB outbreak periodicity is between 30 to 40 years depending on the forest regeneration and succession process, which is also influenced by climate, fire and forest management. Climate also affects the long-term beetle-fungus-host coevolution through the population cycles.

Much research attention on the interactions between MPB and fires has been focused on whether MPB-killed trees have increased fire severity or crown fire potential, although consensus is lacking, due to the complex interactions between beetle outbreak stages, weather and burning conditions. Some researchers found that area burned was not affected by MPB outbreaks (Hart et al., 2015), that beetle outbreak and fire severity are not linked (Harvey et al., 2014, 2013) and that dry conditions rather than fuel changes associated with MPB outbreaks limit fire severity (Kulakowski and Jarvis, 2011). The simulated relationship between beetle outbreak and fire severity showed either increased or decreased crown fire potential in lodgepole pine forests after MPB infestations (Hoffman et al., 2013; Simard et al., 2011), though that work was critiqued for the inappropriate application of models (Page et al., 2014). A smaller amount of research on MPB attacks following fires has discussed whether fires have increased host susceptibility, though it contains interesting discussions on the impacts of low-severity fires on MPB outbreaks. For example, some researchers found that low-severity fires increase susceptibility of lodgepole pine to MPB while stand-replacing fires show the opposite (Kulakowski et al., 2012; Kulakowski and Jarvis, 2013), and others suggested that low-severity fires increase tree defense of ponderosa pine against MPB attacks (Hood et al., 2015). The consensus is that fire-injured trees or forests without their natural fire regimes after fire suppression are more susceptible to MPB outbreaks.

5.4. Spatial analysis and modeling

Spatial analysis is unique in statistics because spatial data structures store data objects organized by position that are used in geographic information systems (GIS). Spatial analysis is not clearly defined but is widely applied in different disciplines. The objectives of spatial analysis are to analyze patterns in spatial data and to solve geographical problems. Spatial data can be acquired from remote sensing or field-based measurements. Various methods are created in spatial analysis and modeling (SAM) by integrating statistics, GIS and spatial inquiries. Multiple examples can be found in the MPB literature: models integrated with GIS, fuzzy set theory, and cellular automata was applied to estimate forest susceptibility to MPB outbreaks (Bone et al., 2006, 2005); Moran's I statistics were employed to assess the short-term risks of MPB infestations in BC (Bone et al., 2013b); a landscape pattern index ('aggregation index') was used in a binomial regression model to examine how forest fragmentation can affect MPB-caused tree mortality (Bone et al., 2013a); and spatial overlay analysis with various temporal resolutions was applied to explore large-scale MPB-fire relationships (Nelson et al., 2016). These examples show the flexibility and diversity of spatial analysis methods, which are problem-oriented and require expert knowledge on the research problem.

Three key connected components in SAM are data, uncertainty and scale. Data quality and availability determine the appropriate variables and SAM methods. Prolific remotely-sensed data, generated with the advances of remote sensing technology, is widely used in SAM and has become an indispensable tool for large-scale landscape analysis. Scientifically developed research data, such as climatology or land use data based on first or secondary data and SAM methods, are also often further applied in SAM. The processing from data to model propagates errors, which is a main source of uncertainty. Uncertainty is the lack of exact knowledge, and it exists inherently and widely in science, which aims for increasing knowledge of the complex world by studying models of reality. In SAM, uncertainties commonly exist in spatial data quality, variable definition and selection, and model evaluation, although some classical spatial analysis techniques deal directly with questions of uncertainty (even if) in strict terms of probabilistic modeling, such as kriging and point pattern analysis techniques (Fusco et al., 2017). Assumptions are also often made in SAM due to the complexity of reality to simplify problems and methods; however, some of them cannot be satisfied also because of some intrinsic characteristics of the complex world. As such, both assumptions and uncertainties need to be addressed clearly in SAM methods. The dissertation examines and discusses the statistical and ecological assumptions of models, and addresses uncertainties in the model interpretations.

Fundamental uncertainty issues in SAM include 1) spatial data quality (i.e., lineage, positional, attribute, and temporal accuracy, logical consistency, and completeness) (MacEachren et al., 2005; Shi, 2010), 2) issues related to boundaries or scale such as the modifiable areal unit problem (Dark and Bram, 2007), and the uncertain geographic context problem (Kwan, 2012), 3) information uncertainties in cartographic visualization (MacEachren et al., 2005), and 4) limitations in our knowledge systems (Couclelis, 2003). The problem of scale at which ecological or geographical processes should be considered is critical for predictions from SAM (Chave, 2013). Changes of scale, including spatial (e.g., extent, grain, resolution), temporal (e.g., daily, decadal, centurial) and organizational (e.g., household, city, state) scales, usually change the patterns of phenomena. Problem formation, sampling design and spatial statistical analysis require careful considerations of scaling and clear explanations of the decisions implemented in SAM (Dungan et al., 2002). Applying SAM in environmental challenges, such as the prediction of ecological causes and consequences of global environmental change, requires the examination of cross-scale system variability, and the development of theories that help assimilate observations across scales, with support from different disciplines and approaches (Chave, 2013; Levin, 1992). Broadly, SAM can be defined as data analysis that involves spatial data to solve the question of ‘how much is where and why’ (Chatfield et al., 2004). In landscape ecology, it is used to understand the ecological processes that cause large-scale spatial heterogeneity.

5.5. Summary

This section reviewed the literature on 1) the theoretical framework of socio-ecological systems, introducing the important and intertwined concepts under the framework (complexity, vulnerability, resilience and sustainability); 2) the concepts and measurements of resilience and regime shift, explaining the development of both concepts with the application of the alternative stable states theory and SES perspectives; 3) a SES case study of large-scale forest disturbances, discussing the different and relative impacts of climate change and fire suppression on forest disturbances and the ecology of MPB in the background; 4) the application of SAM and its defined three structure components (data, uncertainty, and scale), connecting the SES problem formation with practical SAM solutions in general through the understanding of complexity and uncertainty. The four sections are connected so as to serve as a general research background for this dissertation in the theoretical, topical, and methodological aspects. This dissertation is an application of SES perspectives in which the resilience concept is emphasized. The resilience concept from ecology is evolving with the understanding of SES. The literature review frames the areas of interest for the following three data analysis chapters. These three chapters apply different SAM methods to answer the research questions regarding the climatic and non-climatic influences on driving MPB outbreaks.

6. Structure of the dissertation

The dissertation includes five chapters, and this introduction is followed by three data analysis chapters and a concluding chapter. The review of literature in Chapter I introduced the important concepts of SES with a focus on resilience, reviews the research background of the case study, and discusses the logic of methods. Chapters II ("climate space"), III ("species distribution modeling" or "SDM") and IV ("fire suppression") are the data analysis chapters which answer the research questions. Chapter I investigates whether MPB climate space has changed due to the geographical expansion of outbreaks by exploring the data. Chapter III models the recent MPB outbreaks using generalized additive models and generalized linear models to understand the relative contribution of bioclimatic variables to the prediction and the beetle-climate relationship in North America. Chapter IV examines the spatial pattern of fire suppression in the American West and its relationship with MPB outbreaks using fire suppression variables defined from three aspects including direct measurement of fire management, long-term impacts of fire exclusion and land use management that relate to disturbance controls.

These three chapters are linked in the data, variables, and research questions. Chapter II is the base data exploratory step for Chapter III and IV, while Chapter III and IV share common steps in variable selection and model visualization but use different approaches in data aggregation and modeling. Both Chapters III and IV utilize general additive models to inform data transformation and response curves to visualize the model predictions. Chapter III models with successive addition of variables from yearly data while Chapter IV models with successive deduction of variables from means of the yearly data. Chapter V ("conclusions") summarizes the case study based on the three data analysis chapters with diagrams of conceptual models, discusses whether the current MPB outbreak range expansion is a sign of regime shift based on the resilience literature and the case study, addresses the uncertainties and limitations in the study, and relates the management implications of the study. Chapter V also suggests the prospective research on the case study, SES research and sustainability. In sum, the dissertation examines the complexity of MPB SES and focuses on the relative impacts of climatic and non-climatic factors on MPB outbreak across scales.

CHAPTER II CLIMATIC NICHE OF THE MOUNTAIN PINE BEETLE DURING ITS RECENT RANGE EXPANSION IN NORTH AMERICA

1. Introduction

The niche is the range of climatic conditions that a species requires to maintain populations in a given region together with a range of biotic factors, including the interaction of the species with required resources and its interactions with other species (Peterson et al., 2011). This common definition emphasizes multidimensional spaces of bioclimatic variables that are typically measured at a coarse spatial resolution over a broad geographic extent (Peterson et al., 2011), which may be combined to describe the climatic conditions that occur within the distributional limits of the species (Wiens et al., 2011). While dispersal capacity and interspecific competition can change the relationship between the abiotically-defined niche and the geographic distribution (Pulliam, 2000), there remains a strong basis for studying the "climate space" as a description of the climatological constrains on the niche (Franklin and Miller, 2010). Quantifying the climatic space of a species is an important approach to understand how environments change in space and time and how the change affects species distribution patterns (Ohlemüller, 2011).

As a dominant source of disturbance to North American forests, insect herbivores are affected both directly and indirectly by climate change across scales (Ayres and Lombardero, 2000; Weed et al., 2013). Directly, insects are physiologically sensitive to temperature, and can rapidly respond to climatic variation by changing their distribution and abundance due to their high mobility, short generation time, and high reproductive potential. Indirectly, climate affects tree defenses and tolerance, as well as community interactions involving enemies, competitors, and mutualists of insects (Weed et al., 2013). And on longer time scales, climate affects the distribution and abundance of host species. Insect populations adapt differently to climatic changes through physiological and behavioral changes at various temporal scales, and/or change their geographic distribution through range expansion and local extirpation under long-term climate change (Andrew and Terblanche, 2013). At landscape and regional scales, it is evident that forest insects can expand into regions where outbreaks were historically limited, or to forest types that have previously experienced rare insect attacks, as a likely consequence of global climate change (Pureswaran et al., 2018).

The mountain pine beetle (*Dendroctonus ponderosae*, hereafter MPB), the most aggressive insect herbivore in the coniferous forests of Pacific Northwest. Climate and host availability are the two main factors determining the geographical boundary of MPB. Climate plays a major role in influencing large-scale outbreaks of MPB through three main mechanisms: larval mortality caused by abnormal cold weather (cold-induced mortality), synchronous emergence of beetle populations controlled by seasonal temperatures (adaptive seasonality), and tree-defense mechanisms affected by soil moisture (drought stress) (Creeden et al., 2014; Preisler et al., 2012). Temperatures affect multiple life history processes of bark beetles (e.g., development time, voltinism, flight, reproduction, and symbiotic associations) across multiple spatial or temporal scales (Bentz et al., 2010; Raffa et al., 2008). Specific seasonal temperatures are required to support overwintering larval survival and summer adult emergence (Amman and Cole, 1983). Drought-stressed trees are more susceptible to beetle attacks and suffer higher mortality than unstressed trees, though drought is not required to maintain large outbreaks (Creeden et al., 2014). Likewise, higher precipitation promotes tree phloem thickness that has been shown to be positively related to beetle brood production (Amman and Cole, 1983; Preisler et al., 2012). Large areas of suitable host trees of susceptible vigor, size, age and density also facilitate large-scale beetle outbreaks (Fettig et al., 2007).

Beetles expand their outbreak range under desirable climatic and non-climatic conditions. Several researchers have addressed the relationship between landscape-level beetle outbreaks and climate. Some researchers found that an increase in mean temperatures by 1 to 4 degrees increases the likely of outbreaks, whereas timing, frequency, and duration of cold snaps are associated with a decrease in outbreak episodes (Sambaraju et al., 2012). Significant decreases in temperature and extreme winter minima also lessen the likelihood of outbreaks (Sambaraju et al., 2012). Others found that minimum winter temperature and drought conditions have the largest influence on outbreak expansion, and suitable August temperatures also initiated new attacks (Preisler et al., 2012). Some researchers have also argued that different climate and weather factors may have been limiting outbreaks at different times and that these factors do not necessarily influence beetle-caused tree mortality similarly in different locations (Creeden et al., 2014). Furthermore, the levels of MPB outbreak synchrony are strongly related to the frequency of extreme cold winter temperatures controlled by large-scale climatic patterns (Fauria and Johnson, 2009; Stahl et al., 2006; Thomson, 2009). Additionally, climatic factors are not the sole influence on beetles; other factors including predators, pathogens, resources availability, habitat heterogeneity, and dispersal which also contribute to outbreaks (Aukema et al., 2008).

MPB ranges from northern Mexico to northern and central Alberta. It attacks more than twenty-six pine species in North America, and recently expanded to the range of jack pine (*Pinus banksiana*) (Cullingham et al., 2011), a novel host distributed across the north-central continent from northern British Columbia (BC) to Nova Scotia (Little, 1978). The MPB outbreak periodicity is about forty years in the Chilcotin Plateau in central interior BC, where outbreak is the most frequent in western Canada (Taylor et al., 2006). A collapse of a MPB outbreak in this region can be triggered by host depletion and extreme cold weather events (Sambaraju et al., 2012). A warming climate, particularly an increase in the frequency of milder winters, has been proposed as the main cause of northward beetle range expansion (Carroll et al., 2003; Safranyik et al., 2010). However, the full multivariate climate space of MPB using critical bioclimatic variables relevant for all life-stages of beetle development remains unexplored. In addition, most of the current literature on beetle-climate relationship has been focused on only parts of the MPB range (e.g., British Columbia or regions in the western US). In this study we investigate the climate space of MPB to fill the gap in our understanding of suitable bioclimatic conditions over the entire outbreak range of MPB. We ask two main research questions: 1) what are the climate-space constraints of beetle outbreak range expansion, and 2) whether and how has the beetle climate space changed during the recent geographical outbreak expansion?

2. Methods

2.1. Study area

To study climate space for MPB and its hosts within the continent, an equal-area grid was generated with a resolution of 10 km covering North America (Figure II-1). The study area is set as the continent to compare climate spaces within the MPB-outbreak range, within the host range and for the entire continent. The resolution of 10 km is considered as an appropriate observational spatial unit for the study extent and large scale MPB outbreak. This resolution allowed us to balance the demands of the research questions with data availability, computational efficiency, and comparisons with previous research on landscape-level of MPB eruptions.

2.2. Data preparation

We collected annual MPB outbreak extent maps from 1997 to 2016 from the United States Department of Agriculture Insect and Disease Detection Survey (IDS), from the British Columbia Ministry of Forests, Lands and Natural Resource Operations forest health project (HFP), and from the Alberta Agriculture and Forestry Forest Health and Adaptation (FHA). Polygon maps of outbreak area were converted to presence/absence maps on a 10-km resolution grid. The grid cells that are overlapped MPB polygons were identified as MPB presence resulting in the binary variable indicating the presence of a tree-killing population of MPB per cell. Because there is a one-year lag between beetle attack and the appearance of red needles (Preisler et al. 2012), the beetle outbreak year is set as one year before the mapping year (the year of red attacks) in the data analysis.

The host range data was acquired from the digitized maps of pine species (Thompson, 1999). Eight pine species (lodgepole pine, P. contorta; ponderosa pine, P. ponderosa; limber pine, P. flexilis James; pinyon pine, P. edulis Engelmann; jack pine, P. banksiana Lambert; whitebark pine, P. albicaulis Engelmann; sugar pine, P. lambertiana Dougl.;

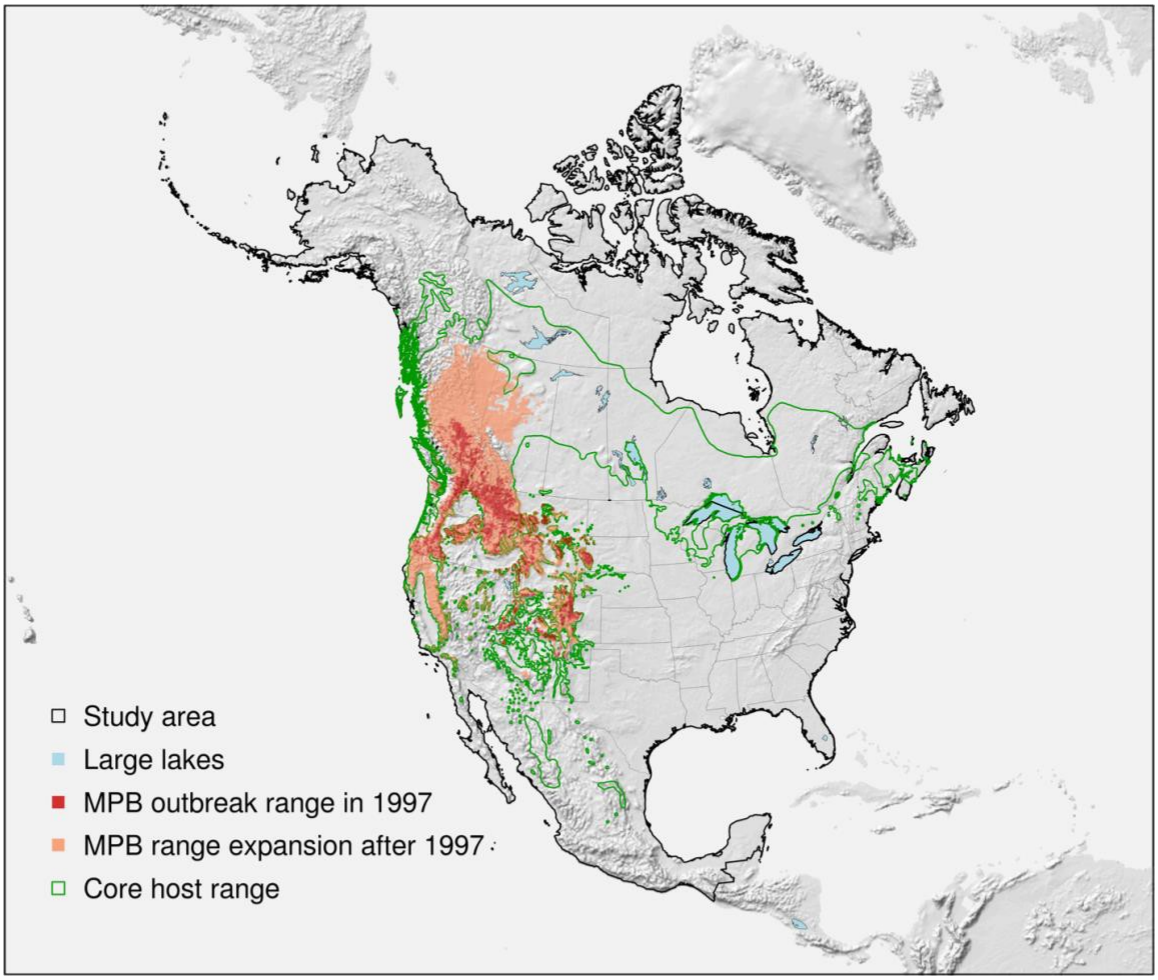


Figure II-1. Mountain pine beetle outbreak range in North America on a 10-km gird (1997 – 2016).The black boundary shows the area of interest in this study, where areas of large lakes in light blue color are excluded. The range expansion refers to the geographical expansion of MPB outbreak range from aerial mapping during red attacks. The green lines indicate the boundary of core host range in which core hosts include limber pine (*Pinus flexilis* James), lodgepole pine (*P. contorta*), jack pine (*P. banksiana* Lambert), pinyon pine (*P. edulis* Engelmann), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana* Dougl.), western white pine (*P. monticola*), and whitebark pine (*P. albicaulis* Engelmann).

western white pine, *P. monticola*) were identified as the main host species (Adams et al., 2013; Janes et al., 2014; Safranyik et al., 2010). The distribution of these host trees was represented as a binary variable on the 10-km grid as for the outbreak data, which is consistent with the coarse resolution of the host-range maps. We assumed that host range is constant over the past two decades.

We collected monthly climate data the from Climate Research Unit (CRU) including 10-arc-minute climatology (CL) 2.0 from 1961 to 1990 (New et al., 2002) and 0.5-degree time series (TS) 4.01 from 1901 to 2016 (Harris et al., 2014). Daily climate data was acquired from the Version 3 Daymet Daily Surface Weather Data on a 1-km grid for North America (Thornton et al., 2017). All the data sources including download links are provided in Appendix Table II-1. All spatial data were reprojected to a Lambert azimuthal equal-area projection and WGS84 datum centered at longitude 100W and latitude 50E.

We regridded the CRU TS 4.01 monthly data (1901-2016) to a 10-km grid following these steps: 1) monthly long-term means between 1961 and 1990 from 0.5-degree CRU TS 4.01 were computed; 2) monthly anomalies (1901-2016) were calculated from the long-term means in step 1; 3) the anomalies were interpolated to a 10-km grid using a topographically adjusted bilinear interpolation method (Praskievicz & Bartlein 2014); 4) similarly, long-term (1961-1990) means were interpolated from the 10-minute CRU CL (New et al., 2002) ; 5) long-term means (step 4) were added to the interpolated anomalies (step 3) to get the absolute data. Since daily climate data was needed to calculate some bioclimatic variables, we directly regridded 1-km Daymet data to a 10-km grid by aggregating the mean values of variables.

2.3. Computation of bioclimatic and beetle variables

We calculated 62 bioclimatic variables that have been identified as significantly affecting the survival and development of MPB (see Appendix II-2 for variable definitions and references). There are three rationales in the consideration of bioclimatic variables: cold-induced beetle mortality, beetle adaptive seasonality, and host resistance. The CRU and Daymet datasets were used for monthly and daily resolution variables respectively. The evapotranspiration-based moisture indices were calculated by using the SPLASH model (Davis et al., 2017), in which the daily fraction of bright sunshine hours as an input was computed by using a mean-preserving algorithm (Epstein, 1991). Finally, we mapped each variable for areas with beetle presence to track geographical changes of climate space (Chen, 2018a; RStudio, 2013).

To understand the spatial pattern of MPB outbreaks, we summarized the beetle outbreak history in terms of 1) the yearly alteration between presence and absence within each grid cell, 2) the maximum run of consecutive years with outbreak presence, 3) the maximum run of consecutive years with outbreak absence, 4) the first presence year after the longest absence, 5) the first absence year after the longest presence, 6) the mean length of continuous presence, and 7) the sum of presence in each grid cell and the surrounding eight grid cells (i.e., beetle persistence).

2.4. Exploratory data analysis

Univariate plots of bioclimatic variables were first used to explore data distribution. Strip charts, density plots, and boxplots were used to compare the range and density among continental, host and MPB climate spaces, and differences in climate between MPB presence and absence and host absence, respectively. In addition, we applied the function ‘auc’ using the pROC package in R (Robin et al., 2011) to quantify the potential of bioclimatic variables with an area under the curve (AUC) value in differentiating beetle presence and absence. Plots of the bivariate climate-spaces were then created to examine the climatic limits and the constraint variables for MPB. Climate space was plotted using the ggplot2 package in R (Wickham, 2016). Thirty-six bioclimatic variables were paired according to the data distribution of each variable and correlation between variables to better visualize in climate space. For example, binary or highly correlated variables cannot display clearly climate space. “Union climate space” (UCS) plots were constructed by merging data across all years (1996 – 2015), showing the limits of current MPB climate space. “Time-series climate space” (TSCS) shows a series of similar plots for each year, thus revealing the changes of climate space over time. In both type of plots, the underlying distribution of geographic space is shown as variably-sized dots on a grid underlying the shading for host presence and beetle outbreak presence density. If beetle climate space overlaps with much of the dominant host climate space, then beetle presence is not highly selective for a given climate space. However, if a climate space is marked by large areas of host climate space outside of beetle outbreaks (e.g., visually more 50% of large dots are uncovered by the beetle climate space), we considered the climate variables as "constraint variables". Similarly, constraint variables are expected to show a much narrower peak in beetle climate space than the peak in host climate space in a density plot. Such variables also should show more differences between the climatic conditions in beetle presence and absence. We also summarized bioclimatic variables that have records of thresholds in the literature to examine the consistency of climatic constraints between our findings and other research.

To examine whether climatic constraints of outbreak area have changed over time, we used quantile regression of the four constraint variables versus year. The quantiles examined are 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, and 0.95. To understand whether climatic conditions have changed during the geographical expansion, we focused on the bioclimate every three years during the period of major expansion (1996 to 2008), and the bioclimate between expanded areas and core areas where expanded areas are those where the length of maximum continuous absence is equal or higher than 10 years, shown in Appendix Figure II-1-M2, and core areas are those where the beetle persistence index is equal or higher than 80, shown in Appendix Figure II-1-M6. We also compared the difference of bioclimatic quantiles between a three-year period (2006 through 2008), when the number of outbreak range grid cells was increasing yearly toward the peak outbreak, and another three-year period one decade before (1996 through 1998), and between expanded and core areas using a bootstrapped inference. We first determined the number of iterations by replicating the quantiles from a sample of 5000 until the mean of the difference in the 95th quantile between the two periods or areas has stayed relatively constant. Then we iterated the differences of the examined quantiles in the two comparison cases. Next, we used the distribution of difference from iterations to infer its significance. If the number of zero is located within the 95th percentile, it is considered that the difference in the examined quantile is not significant. Finally, we examined the recent beetle climate space from the perspective of long-term trends of bioclimate. Due to the length limit of paper, we selectively plotted bioclimatic variables by including constraint variables and comparative variables in the representation of the three rationales at the long-term scale, and only showed examples of climate space plots and bioclimatic maps in the results in the paper. Other results are shared through the RStudio shiny sever.

3. Results

3.1. Spatial patterns of mountain pine beetle outbreaks during recent years in North America

Since 1997, there was a massive expansion in the MPB outbreak range northward to northern BC and Alberta and southward to southern California (Figure II-2). Larger areas of new outbreak occurred in 1999 in central and northern BC and in 2007 in northern and central BC and Alberta. The northward expansion continued until 2014, while the southward expansion has become intense since 2006. After the outbreak range reached its peak in 2008, a collapse of epidemic beetle populations started in central BC. Summary statistics from the 1997-2016 outbreak history reveal distinct spatial patterns (Appendix Figure II-1, maps M1 to M6). The outbreaks that persisted in central BC over the recent two decades are shown as a continuous presence (M1, M5 and M6). New outbreaks occurred at the edges of the host range in the American West, northern BC and Alberta (M2). The northern range expansion began and ended in the later decade of the study period, at the same time when large areas of the outbreak range started to collapse (M3, M4). During the period of 1997 – 2016, the outbreaks persisted in the interior regions of BC and Black Hills in South Dakota (M5). Most of the expanded regions cover northern BC and western and northern Alberta (red areas on M2), while the core regions are within the internal range of lodgepole and ponderosa pines extending from western US to central and northern BC (red areas on M6).

3.2. Climate space associated with the current beetle outbreak range and its dynamics

The northern range edge of MPB outbreaks was constrained by cold winter temperatures. For example, on annual maps of outbreak progression, the average duration of a cold snap (i.e., a minimum of four continuous days of average winter temperatures at or below -20 °C; Acs), normally has a value of 0 days within the outbreak range (Figure II-3). As the beetle outbreak range expanded further north from 1996 to 2006, Acs decreased in as beetle outbreak expanded, though a small proportion of northern beetle range also covered areas with an Acs longer than 4 days. Overall, a certain proportion (i.e., totally 34% of outbreak-presented grid cells) of the range covers colder areas where Acs is longer than 4 days (Table 1). The beetle outbreaks expanded to the cold areas where early or late cold snaps occurred (see Figure II-3 caption), with 9 to 10 percent of presence grid cells (Ecs and Lcs in Table 1), but rarely reached the areas with a number of days with a minimum temperature below or at -40 °C during winter time, with 5 to 6 percent of outbreak-presented grid cells (winter40 in Table 1).

High temperatures also constrain the outbreak range. No beetles were present in grid cells without at least one day above or at 18.3 °C in August during the outbreak year, and the outbreaks predominantly occurred in the areas with summer temperatures lower than 40 °C, despite a smaller range of beetle outbreaks reached the areas without optimal summer temperature (12% of presence grid cells). Although bioclimatic thresholds during peak and non-peak years are similar, the differences in bioclimatic thresholds between core and expanded areas indicate that MPB has expanded into colder regions, rather than into warmer regions, before expansion (Table II-1).

Consistent with the above patterns, variables related to monthly-based minimum temperatures (JanTmin, MarTmin, Tmin) have distributions indicating that they differentiate between outbreak and non-outbreak areas (Appendix Figures II-2 and II-3). In addition, variability of summer monthly temperatures (Tvar) and cumulative summer precipitation (summerP2) are similar to the minimum temperatures in having a narrower peak in MPB climate space than in host climate space (Appendix Figure II-3) and is more contrasting between outbreak presence and absence (Appendix Figure II-4). Many other bioclimatic variables are weaker than Tvar (AUC=0.725) to differentiate between outbreak and non-outbreak areas (e.g., maxAugT, OptTsum, pt.coef) using strip charts (with AUC values), density plots, and boxplots (Appendix Figure II-2, II-3, and II-4).

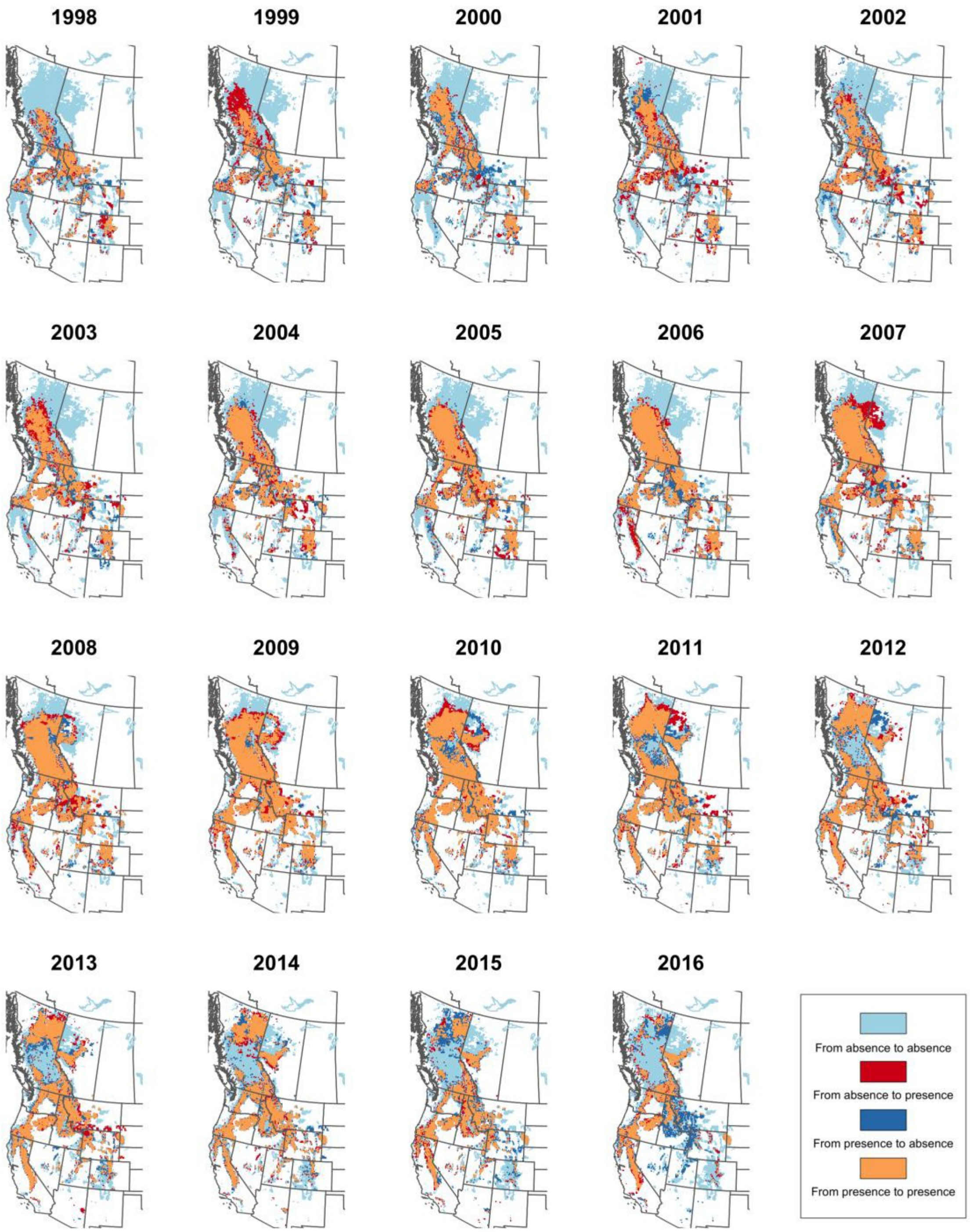


Figure II-2. Time-series maps of mountain pine beetle outbreak alteration between absence and presence within the recent outbreak range in North America. The grey line indicates the boundary of states in the United States and provinces in Canada, while the light blue line delineates the large lake areas.

Union climate spaces (UCS) are useful to display bivariate relationships of outbreak and host species in the context of the limits of bioclimate in North America (Figure II-4). The UCS plots shows how the point density in host climate space overlaps with beetle climate space. The boundaries of UCS show that monthly mean of daily minimum temperatures (e.g., JanTmin and MarTmin), seasonal temperature variation (Tvar), and summer precipitation in beetle climate space are more constrained in host climate space than variables like maximum drop in winter temperature (max.drop), six-year cumulative Oct-Aug precipitation (PPT), and coefficient of variation in Apr-Jun daily precipitation (cv.gsp). These four variables (JanTmin, MarTmin, Tmin and Tvar) also show high density areas in host climate space that do not overlap with beetle climate space; these four "constraint variables" are selected for additional analyses. Beetle climate space is also clustered to lower values of degree days (ddAugJun and ddAugJul). It is also interesting to note that evapotranspiration-related variables such as water deficit and moisture index are more significant at controlling the host range (large dots in background of Figure II-4) compared to temperature and precipitation alone.

Time-series climate space (TSCS) also shows constraints in minimum temperatures and seasonal temperature variation (Chen, 2018b; RStudio, 2013). Low summer precipitation is preferable for MPB outbreaks, but summer precipitation is not considered as a constraint variable of beetle climate space because it covers the dominant or common host climate space (i.e., high density spots in TSCS shown with larger dot sizes in Figure II-5). For example, Tvar in Figure II-5 is restricted between 5 and 10 but cumulative summer precipitation shows beetle abundance in the high-density region of host climate space (i.e., common host climate space, or dominant host climate space). According to TSCS, beetle climate space has not reached some common host climate space in regions with cold winters and springs and wet summers.

In a different way from TSCS of showing beetle climate space change, quantile regression results in Figure II-6 show that the median values of observations in beetle climate space have largely been stable during 1996-2015, except that Tvar has increased

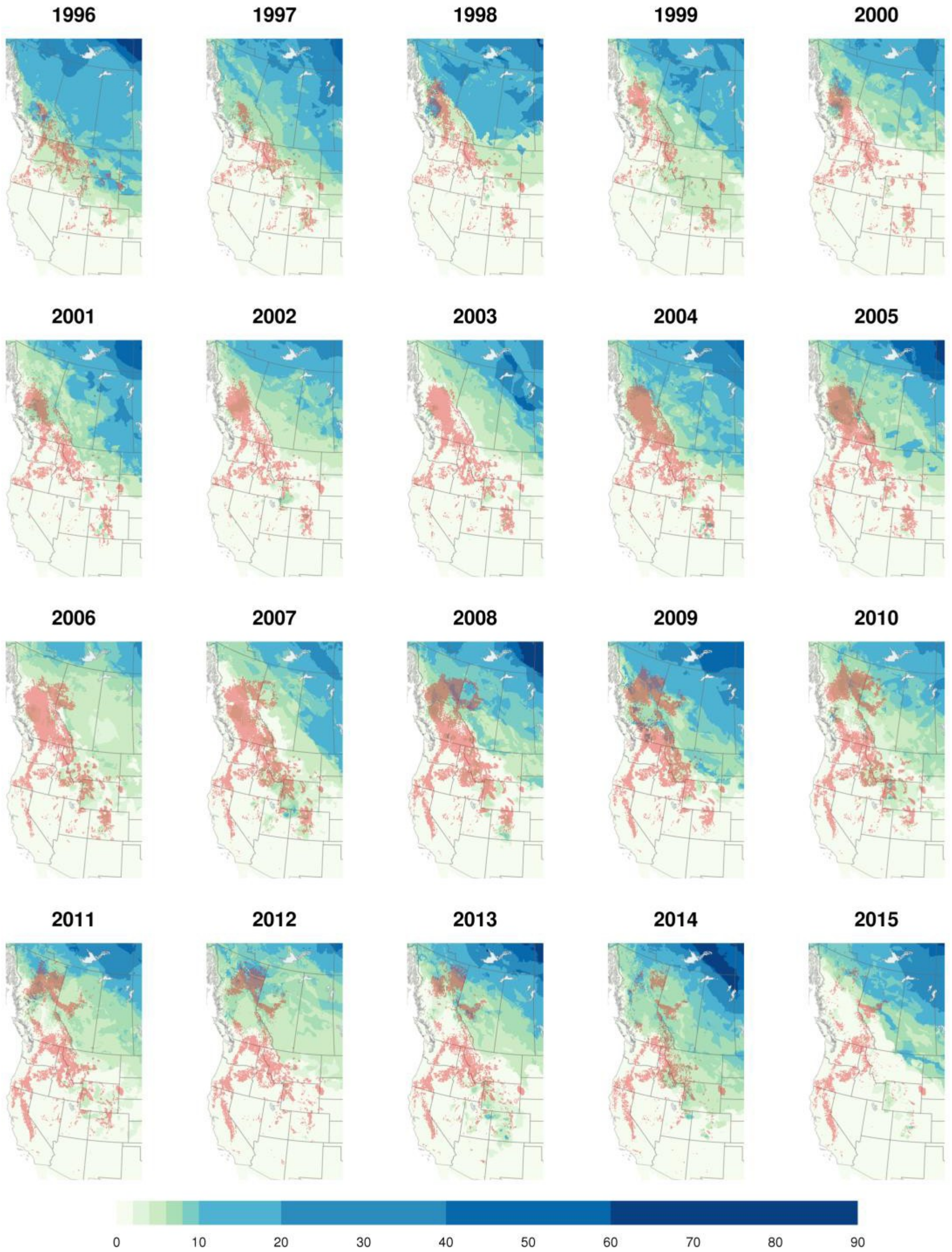


Figure II-3. Time-series maps of average duration of a cold snap in days (Acs) with yearly mountain pine beetle presence as red shading green color. A cold snap is defined as a minimum of four continuous days of mean daily temperatures at or below -20 °C during winter. Maps of other bioclimatic variables including early cold snaps (Ecs) and late cold snaps (Lcs) can be found in Chen 2018a. Both Ecs and Lcs are binary variables with 0 indicates an absence of early or late cold snap and 1 indicates otherwise. The detailed descriptions of bioclimatic variables can be found in Appendix Table II-2.

slightly over years. The lower quantiles in winter and spring minimum temperatures have decreased, while the higher quantiles in minimum temperatures and temperature variation increased. During the expanding periods from 1996 to 2008, MPB climate space shows mild fluctuations every three years in the inter-quartile range with medians align fairly well, although temperatures in the peak years are slightly lower (Appendix Figure II-5). Nevertheless, the expanded areas are significantly colder than the core areas with lower minimum temperatures and higher temperature variation.

Specifically, negative differences in the lower quantiles 0.05 and 0.1, and positive differences in the higher quantiles 0.9 and 0.95 are shown in monthly mean minimum temperatures (Figure II-6). The winter temperatures during peak years (2006 – 2008) are 1 °C lower in the cold limits and 2 °C higher in the warm limits than nonpeak years (1996 – 1998). Between peak and nonpeak years, the stability of beetle climate space shown in minimum temperatures from winter to spring moved from lower to higher quantiles (e.g., insignificant quantile difference occurred in the 0.25 quantile of JanTmin and the 0.75 quantile of MarTmin), while seasonal temperature variations (Tvar) significantly increased in all quantiles except the low end of range. Minimum temperatures are more than 4 °C colder and seasonal temperature variation is more than 2.5 higher in the expanded areas than in the core areas. However, the long-term climatic changes show that climate has recently become warmer and drier and the seasonal temperature variation is also lower in the current beetle outbreak range (Appendix Figure II-6). Winters are noticeably warmer, and summers are generally drier in the current beetle affected regions than in the host range. As such, the current outbreak range remained warmer than historical records in these regions, although the beetles moved to colder climate space compared with the one before expansion.

Table II-1. Proportion of beetle-affected grid cells within the proposed bioclimatic thresholds in the current beetle range, during the peak and nonpeak years, and in the expanded and core areas.

Variable	Definition	Criterion	All	Peak years (2006-2008)	Nonpeak years (1996-1998)	Expanded areas	Core areas
ddAugJun	degree-days (DD) above 5.5 °C from 1 August to 30 June	> 305 DD	1.00	1.00	1.00	1.00	1.00
ddAugJul	degree-days above 5.5 °C from 1 August to 31 July	> 833 DD	0.98	0.98	0.99	0.98	0.99
Acs	the average duration of cold snaps during winter	≤ 4 days	0.66	0.69	0.49	0.35	0.70
Ecs	early cold snap in the Fall	absent	0.91	0.85	0.95	0.68	0.95
Lcs	late cold snap in the Spring	absent	0.90	0.93	0.98	0.69	0.93
Ncs	number of cold snaps during winter	zeros	0.55	0.53	0.40	0.30	0.59
Oct20	days with a ≤ -20 °C temperature in October	≤ 4 days	1.00	1.00	1.00	1.00	1.00
Oct30	days with a ≤ -30 °C temperature in October	0 days	1.00	1.00	1.00	1.00	1.00
Oct40	days with a ≤ -40 °C temperature in October	0 days	1.00	1.00	1.00	1.00	1.00
OctMin	minimum daily temperature in October	> -40 °C	1.00	1.00	1.00	1.00	1.00
Jan20	days with a ≤ -20 °C temperature in January	≤ 4 days	0.68	0.66	0.56	0.36	0.74
Jan30	days with a ≤ -30 °C temperature in January	0 days	0.75	0.75	0.64	0.43	0.80
Jan40	days with a ≤ -40 °C temperature in January	0 days	0.95	0.94	0.94	0.85	0.97
JanMin	minimum daily temperature in January	> -40 °C	0.95	0.94	0.94	0.85	0.97
Mar20	number of days with a ≤ -20 °C temperature in March	≤ 4 days	0.88	0.91	0.96	0.61	0.93
Mar30	number of days with a ≤ -30 °C temperature in March	0 days	0.92	0.99	0.99	0.76	0.95
Mar40	number of days with a ≤ -40 °C temperature in March	0 days	1.00	1.00	1.00	0.98	1.00
MarMin	minimum daily temperature in March	> -40 °C	1.00	1.00	1.00	0.98	1.00
winter20	number of days with a ≤ -20 °C temperature during winter	≤ 4 days	0.46	0.43	0.36	0.26	0.48
winter30	number of days with a ≤ -30 °C temperature during winter	0 days	0.67	0.67	0.61	0.36	0.71
winter40	number of days with a ≤ -40 °C temperature during winter	0 days	0.94	0.94	0.93	0.80	0.97
winterMin	minimum daily temperature during winter	> -40 °C	0.94	0.94	0.93	0.80	0.97
maxAugT	frequency of ≥ 18.3 °C in August	≥ 2 days	1.00	0.99	1.00	1.00	1.00
OptTsum	days with summer temperatures between 18 °C and 30 °C	> 0 days	0.88	0.94	0.91	0.87	0.88
summerT40	days with summer temperatures > 40 °C	0 days	1.00	0.99	1.00	0.99	1.00

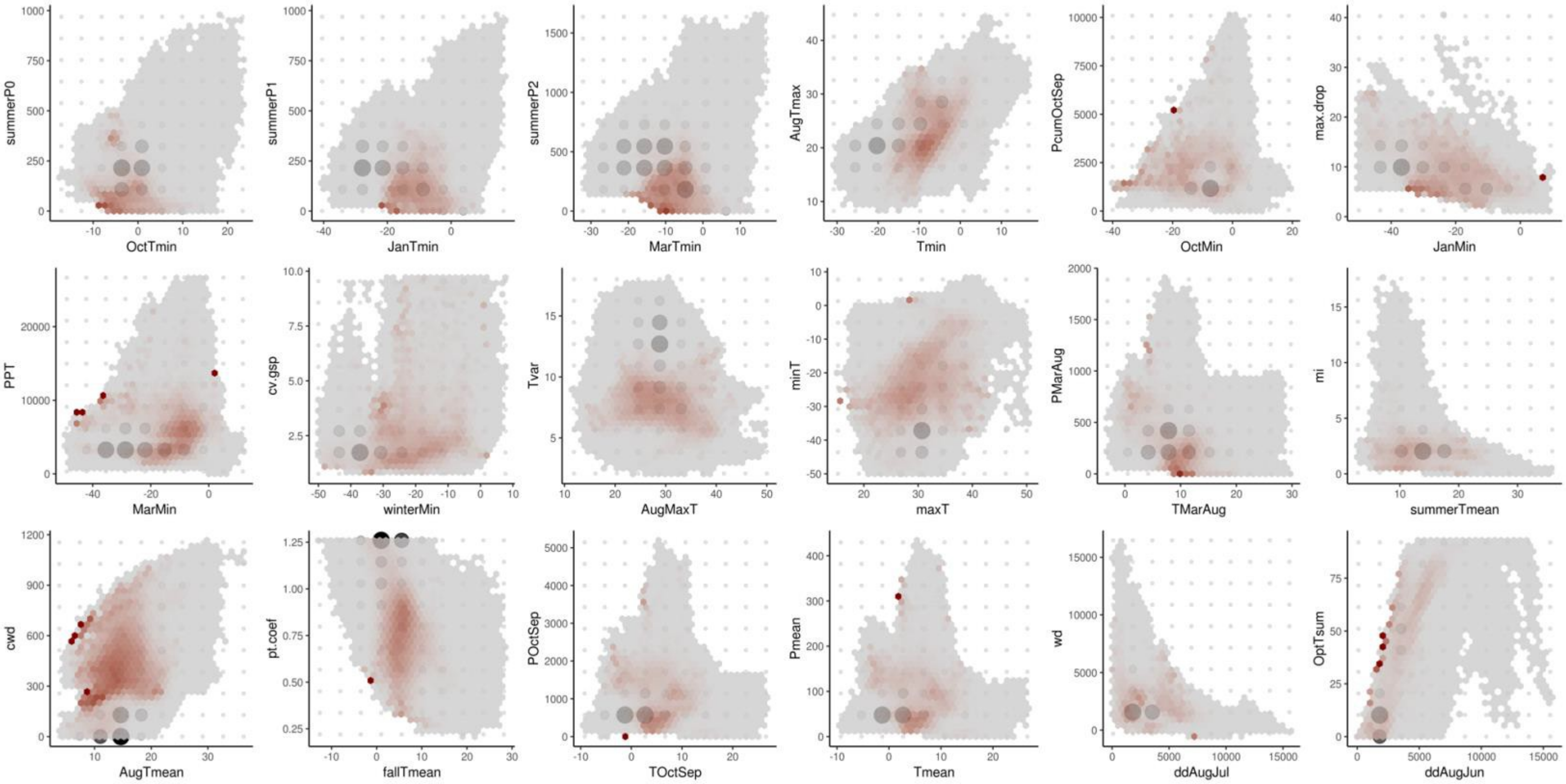


Figure II-4. Union climate space of beetle outbreaks and host tree species for various pairs of bioclimate variables. Data are merged across all years of annual climate and beetle outbreak history from 1996 to 2015. The grey shadow shows the boundary of host climate space, which also shows zero to very low beetle presence in host climate space. The dots beneath the shadow show the density of grid points within the host range (i.e., the amount of geographic space). The dark red color in hexbin indicates the proportion of host-range grid cells with a beetle outbreak, and a darker red color indicates a higher proportion within the bin, same as Figure II-5. Variable pairs were selected to avoid highly correlated scatter plots.

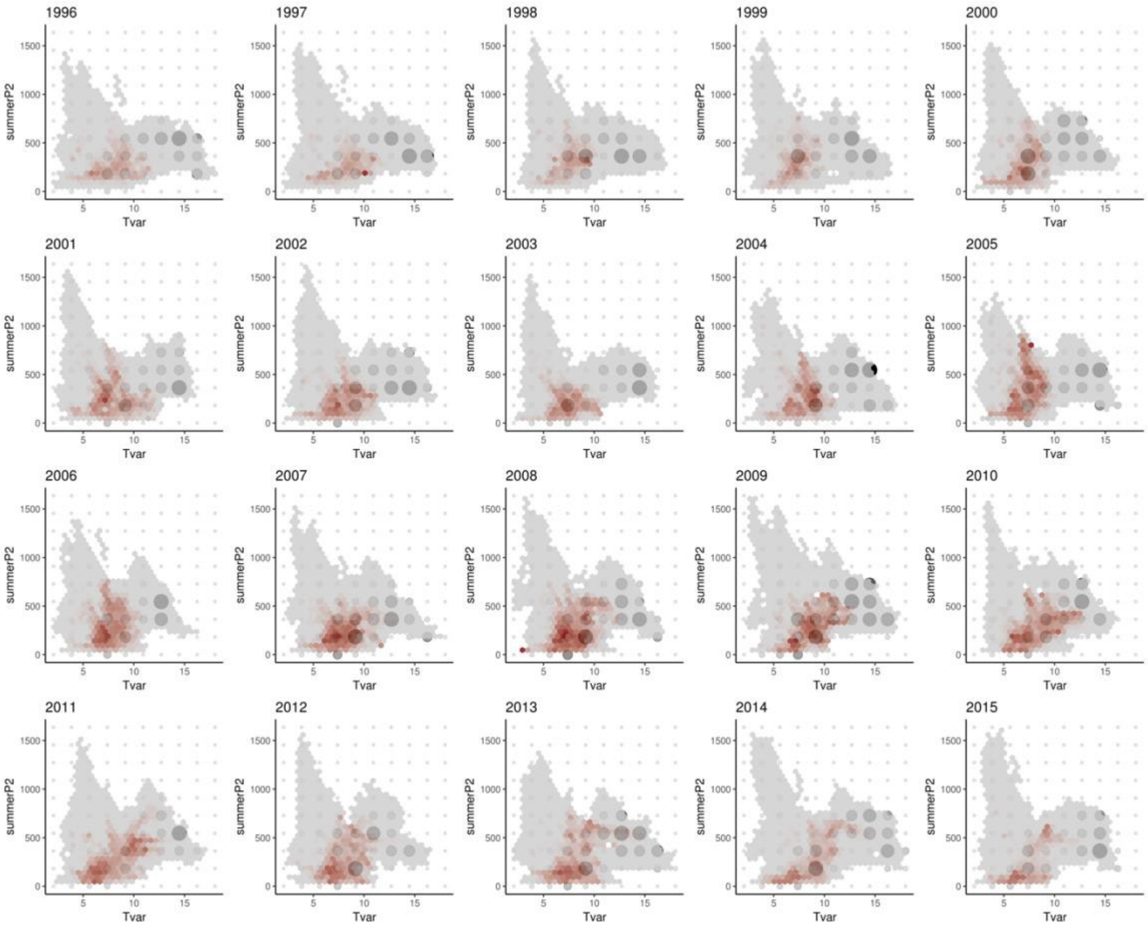


Figure II-5. Time-series climate space of cumulative summer precipitation (summerP2) versus seasonal temperature variation (Tvar).

4. Discussion

4.1. Climate space limits and constraint variables within the current beetle outbreak range

Species ranges are commonly constrained by climate due to their physiological tolerance to the environment and due to climatically-mediated biotic interactions. As a poikilothermal species, MPBs depend on temperature for the environmental cues to complete their life cycle, in which there are three main thermal requirements. First, heat--in terms of day-degrees--is required during beetle development from egg to teneral adult (Amman and Cole, 1983). Historically, the northern and eastern climatic limits to MPBs were set by growing degree-days greater than 833 (during the growing season and on a 5.5 °C base; Safranyik et al., 2010). Our results showed that more than 98% of MPB-

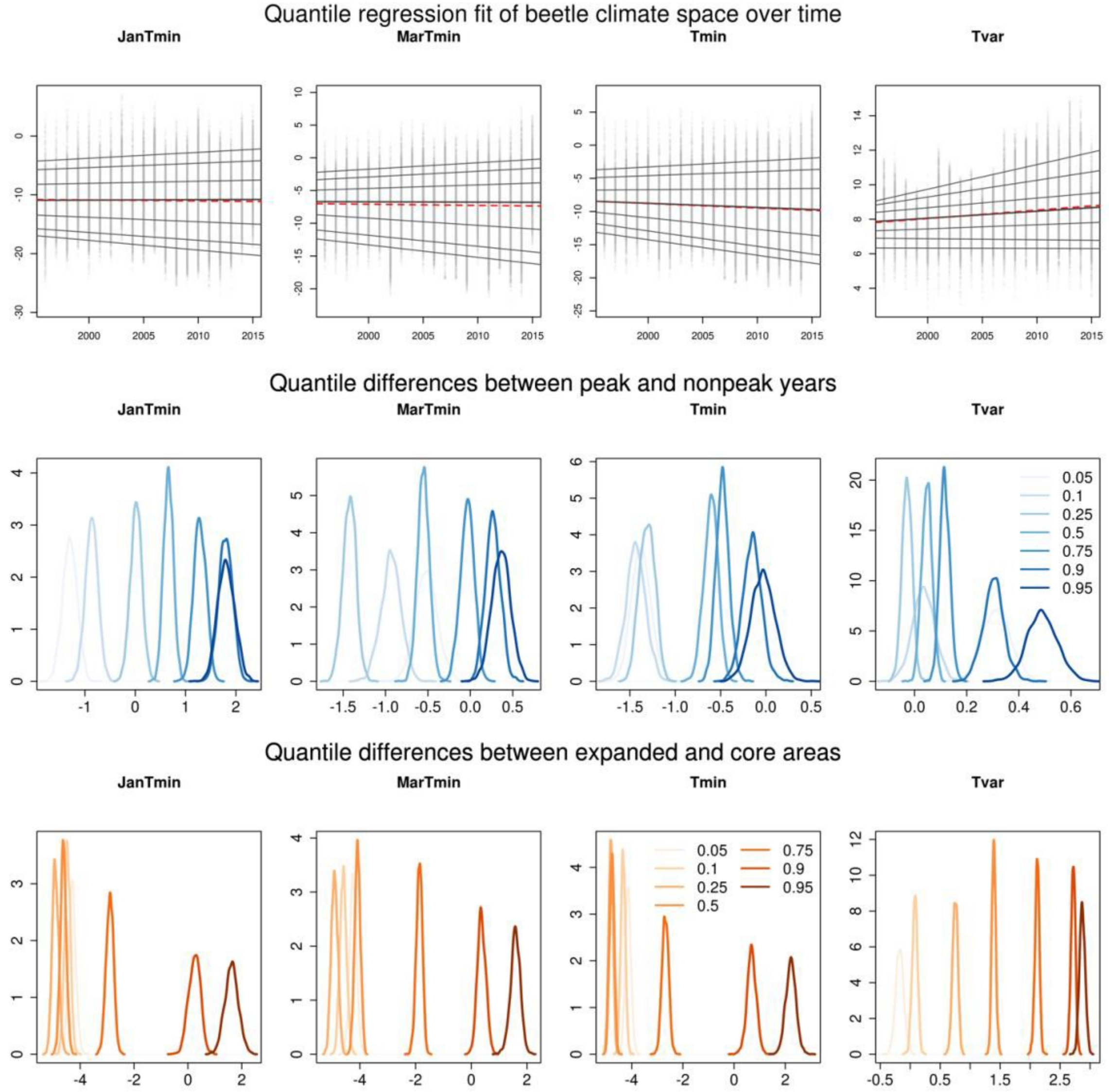


Figure II-6. Dynamics of beetle climate space using constraint variables during 1996 and 2015.The constraint variables are average minimum daily temperatures in January, March, and from November to March, and seasonal temperature variation during the beetle life cycle (August to July). In the quantile regression fit of the constraint variables, each plot shows a scatterplot of the bioclimatic data on beetle outbreak range and year. Superimposed on the plot are the 0.05, 0.1, 0.25, 0.75, 0.9, 0.95 quantile regression lines in gray, the median fit in solid black, and the least squares estimate of the conditional mean function as the dashed red line. All quantile regression fits are significant except for Tvar at 0.05 quantile. Quantile differences (QD) of the constraint variables are shown between peak years during 2006-2008 and nonpeak years during 1996-1998 in blue colors, and between the defined expanded and core areas during the recent two decades in orange colors. In the QD plots, the x axis shows the difference of temperature (°C) or temperature variation, and the y axis shows the density of each quantile difference.

affected grid cells are within that degree-day thresholds, which is largely consistent with the previous research. Second, August temperature is considered to relate to the mechanistic process of beetle dispersal. It is assumed that the peak of emergence and flight will be protracted, and mass-attack success reduced when the frequency of maximum daily temperatures equal or higher than the lower threshold for flight, approximately 18.3 °C, is less than two days during August (Safranyik et al., 2010). However, when August temperature is too high, emergence and flight may be diminished (Amman and Cole, 1983). We found that August (or summer) temperature is generally not a constraint in the current beetle climate space at the examined scale, since the related beetle climate space overlaps with host climate space. Third, cold-induced mortality is also a key factor controlling beetle population dynamics (Régnière and Bentz, 2007) and climatic warming has been associated with the recently intensified beetle activity (Aukema et al., 2008; Bentz et al., 2010; Safranyik et al., 2010). The minimum temperature was at or below the mortality threshold -40 °C in 21% of beetle-affected grid cells in the expanded regions (Table II-1) and nearly reached at -50 °C at the extreme in our study (Table II-2).

It seems implausible that beetles can surpass the experimentally determined lethal temperatures, however, several factors should be considered in this discussion. Local bioclimatic conditions within the 10 km grid and the phloem temperatures likely provide a thermal environment within the threshold. Beetles have geographical variation in their thermal responses to the local environments and adaptive behaviors such as diapause can increase the probability of avoiding climatic extremes (Powell and Bentz, 2009). Beetle populations require 2-year to complete life cycle at higher elevations during cold years, as opposed to 1-year at low-to-mid elevations (Bentz et al., 2016). The landscape levels of colds dismiss the local variation of temperature and thus hide the varied beetle adaption information. Also, phloem temperatures were generally warmer when temperature lows occurred and did not drop before below-freezing temperatures persisted for more than 24 hours (Schmid et al., 1993). Despite uncertainty in the actual phloem temperatures, the extreme cold in beetle outbreak range is rare.

Similarly, cold snaps frequently occurred in the current MPB outbreak range and the frequency of winter temperatures below or at -20 °C for more than four days was also found to be common. This may indicate that the threshold of -20 °C or even -30 °C is not a practical setting for the lower limit of winter daily temperature within current beetle climate space at large-scales. Furthermore, some minimum daily temperatures in beetle climate space can also reach the lower limits in host climate space, while monthly average of minimum temperature has limited the beetle in a warmer host climate space. Continuous low temperatures probably have more controls in MPB outbreak synchrony than sporadic daily temperature minimums within the critical thresholds. It could also indicate that monthly-based minimum temperature variables are more suitable as a predictor for large-scale beetle outbreak presence.

Seasonal temperature variation as another climate space constraint variable is highly correlated with minimum temperature variables. Beetle outbreaks predominantly occurred in a climate space with lower temperature variation that corresponded with warmer temperatures. Seasonal temperature variation, coupled with differing developmental thresholds for different life stages, is sufficient to synchronize the seasonality of a poikiliothermic organisms (Powell et al., 2000). Limited summer precipitation during the outbreak, in which droughts increase tree stress and tree resistance to beetle attacks is weakened, is a desirable condition for beetle outbreaks, but summer precipitation is not a constraint in beetle climate space due to its prevalence throughout common host climate space. The TSCS patterns of summer precipitation in the previous, current or both years of the outbreak are relatively similar, although summer precipitation levels prior to the outbreak year was suggested to have a positive effect on the size of brood that emerges in the current year, while two-year cumulative summer precipitation was indicated to have a negative impact due to drought-induced tree stress (Preisler et al., 2012). Our climate space analyses suggested that summer precipitation, particularly during the year of outbreak, mainly remains an influential factor on tree resistance to beetle attacks.

Table II-2. Bioclimatic extremes in the current mountain pine beetle range and number of beetle-affected grid cells within the extremes.

Variable	Description	Low extreme	High extreme	No. grid cell
JanTmin	monthly average daily minimum temperature in January	-29.3 °C		1
MarTmin	monthly average daily minimum temperature in March	-23 °C		1
Tmin	mean of monthly average of minimum temperature from November to March	-24.6 °C		1
summerT40	number of days with maximum temperatures higher than 40°C during summer		11 days	3
AugMaxT	maimum of daily maximum temperature in August		43.9 °C	1
maxT	maximum daily temperature from August to July		43.2 °C	1
max.drop	the largest drop in daily average temperature during winter	24.6 °C		1
Jan40	number of days with minimum temperatures at or below -40 °C in January	8 days		3
Mar40	number of days with minimum temperatures at or below -40 °C in March	6 days		4
winter40	number of days with minimum temperatures at or below -40 °C during winter	13 days		1
JanMin	minimum of daily minimum temperature in January	-49.4 °C		1
MarMin	minimum of daily minimum temperature in March	-46.2 °C		1
winterMin	minimum of daily minimum temperature during winter	-49.4 °C		1

4.2. Dynamics of climate space during the recent beetle geographical expansion

Mountain pine beetle has expanded both northwards and southwards since 1997, and its climate space has expanded slightly towards both warmer and colder space. With considerable evidence from the literature to support the hypothesis that warming climates marked the expansion of beetle range, we expected climate space to remain stable. Our findings from quantile regression are consistent with our assumption of stable climate space in the majority of observations; however, the species also expanded its climate space to include regions with higher seasonal temperature variation and lower winter temperature. The expanded regions cover a large area in northern BC, central and western Alberta, and multiple spots in western US, resulting in expansion of climate space in both high and low quantiles of winter and spring temperature and summer precipitation. However, the southern expansion did not change the lower quantiles of Tvar but the northern expansion increased the higher quantiles of Tvar over time.

Overall, climate space has reached colder space than the climate space in core beetle outbreak range during the expanding years. Given that long-term climatic changes rather than recent climate space dynamics are consistent with beetle outbreak range expansion, our interpretation is that the northern expanded regions have become warmer recently and surpassed certain temperature thresholds including degree days and minimum monthly winter temperature, to support beetle development due to long-term climate change; however, these regions remain colder than pre-expansion MPB-adapted climate. This is generally consistent with previous threshold-based conceptual models (Cooke and Carroll, 2017; Raffa et al., 2008). Since MPB expanded in northern areas yearly (Figure II-7), even when temperature decreased in these areas (Figure II-8), it is more likely that MPB has adapted to colder weather, rather than that time lags between yearly climatic change and beetle dispersal caused MPB to remain in colder regions.

However, it remains unclear whether the beetle has adapted to colder weather recently, or the historical climate space has not expanded its cold tolerance limits because of other factors such as fire suppression and biotic interactions that may have overcome climatic impacts at a different scale. For example, the effect of warmer climates at the landscape and regional scales can be overwhelmed by the effect of competition for resources within trees at the site level (Goodsman et al., 2018). While MPB invaded the novel host range, it was suggested a new match between the climate and ecophysicological effects of host species that may constitute a trade-off between increased host suitability and winter mortality, in which rapid development to less cold tolerant pupal and adult stages by broods in novel hosts prior to winter (Rosenberger et al., 2017a). The beetle may have gradually adapted to climate change by increasing its cold-tolerance thresholds, while the novel hosts have not evolved to resist the invaded insect (Raffa et al., 2013). Historical fire suppression combined with the effects of surface fires and low site productivity have contributed to MPB outbreaks by generating susceptible lodgepole pine forests (Aukema et al., 2008; Taylor and Carroll, 2003). Moreover, geographical variation in beetles' physiological responses to climatic influences suggested that MPB has different thermal requirements in completing its life cycle across geographical space (Buotte et al., 2017; Weed et al., 2015) and likely adapted in colder climate when it expanded northwards, possibly through facultative diapause in overwintering adults (Lester and Irwin, 2012).

Though droughts accelerate MPB outbreaks, the beetle climate space in the expanded regions has significantly higher summer precipitation than the conditions in core range areas, a less preferable condition. However, the long-term climate change showed a noteworthy decrease in summer precipitation, which is also much lower in beetle affected regions than in the host range, and an exceptional peak of six-year cumulative growing season precipitation, which showed a well-aligned beetle-host climate space dynamic in the current outbreak range during recent years (Appendix Figure II-6). These combined climatic conditions have created a desirable environment for beetle development by promoting phloem growth prior to outbreak and reducing tree defensive abilities during outbreak. Furthermore, water deficit and moisture index have largely remained stable during the expansion (data not shown), indicating that the increasing precipitation may have been associated with increases in potential evapotranspiration, and still resulted in reducing the resistance of pines. Similarly, we also cannot eliminate other non-climatic factors such as biotic interactions and forest governance that may have contributed to the beetle expansion in this discussion.

4.3. Caveats in applying climate space to understand effects of climate on beetle expansion

Climate space analyses are associated with caveats, that they rely on the accuracy of climate (and species) data and it is hard to determine whether the species can track their suitable climate space or occupy new climate space due to the hidden information in their migration, dispersal and adaptation capacity (Ohlemüller, 2011). We employed climate space as a tool to explore the current climatic constraints for MPB to invade the complete host range and changes of climatic conditions when MPB expanded its outbreak range. We consider it meaningful to understand climate space limits and dynamics for further research on effects of climate on species range expansion. At this juncture, we suggest caveats in applying climate space for this purpose from three main perspectives. First, uncertainty exists in MPB outbreak extent maps from aerial mapping as well as the use of spatial interpolation and aggregation of climate data from different sources. Some limitations of aerial survey data were listed in previous research (Aukema et al., 2008). We did not manipulate the aerial survey data because standard criteria for corrections, due to lack of detailed documents on data explanations and ground-truthing, have not been developed, and there is a lack of common variables to compare the severity of outbreaks and aerial mapping data quality. Although we cannot exhaust all the possible errors propagated from data collection to climate space, it is still applicable to identify the constraint variables and climatic change patterns at the studied scale, since the error is not systematic.

Different modeling methods and resolutions in the climate data sources CRU and Daymet may create inconsistency in the absolute values of same variables, although the spatial and temporal patterns of both datasets are largely consistent. Second, effects of scale in climatic impacts, particularly influences of local climates, cannot be well understood from coarse 10-km resolution data. Climate space summarizes large-scale climatic constraints and changes; however, it ignores the possible impacts of various bioclimates at local scales. Many topographic, forestry and insect population factors are unknown in the interpretation of climate space. Third, it can be arbitrary to determine the climate space constraints due to high correlation among bioclimatic variables. For example, minimum temperatures, seasonal temperature variation and growing degree days are highly correlated in our case. We included as many data criteria as possible to select the most important constraint variables, by using beetle abundance in host climate space in the time-series climate space (Figure II-5), peaks in the density plots of bioclimate (Appendix Figure II-3), and different climatic conditions in beetle presence and absence (Appendix Figure II-4), to determine that minimum temperatures and seasonal temperature variations are the current climate space constraints and suggest that both are important for two different reasons, cold tolerance and seasonal synchronization. Lastly, we emphasize the need to take the equilibrium between climate space and species distribution into consideration, and that disequilibrium can exist due to habitat availability, intraspecific competition and dispersal (Pulliam, 2000).

5. Conclusions

We introduced climate space as a data exploratory method to understand impacts of climate change on mountain pine beetle outbreaks. According to the conclusion from previous research that beetles have expanded to historically colder areas that have recently become suitable for beetle development (Bentz et al., 2010; Safranyik et al., 2010), we tested whether MPB has been tracking changes of climate and stayed in the same climate space or has moved to a different climate space during the geographical expansion. We created a 10-km grid and applied spatial interpolation and aggregation to compute over sixty bioclimatic variables that are reported to be crucial for MPB development and outbreak in North America. We then visualized bioclimatic variables to plot climate space and compared beetle and host climate space to reveal constraint variables: 1) mapping bioclimatic variables with MPB outbreak presence; 2) different univariate plots to compare range, density and divergence of climate space data; 3) union climate space combined data from 1996 to 2015 to show climate space limits of MPB; 4) time-series climate space to show yearly beetle abundance in host common climate space over the twenty years. Other bioclimatic variables are summarized within thresholds or mapped to visualize climatic limitations or changes. We also used quantile regression to examine climate space dynamics and compared beetle climate spaces during expanding years and between expanded and core outbreak range using a bootstrapped inference in the differences of quantiles. Additionally, we selectively calculated long-term changes in bioclimates to have a better understanding of climate change impacts on MPB outbreaks.

We found that minimum temperatures and seasonal temperature variation are the best variables at differentiating the bioclimatic conditions between beetle outbreak presence and absence. These variables were identified as constraint variables. In contrast, summer precipitation is not considered as a constraint variable even though lower summer precipitation is preferred, since beetle climate space fully occupied the core host climate space. The beetle climate space has been relatively stable in that median bioclimates remained unchanged and the changes in the below or above quantiles are small. However, we considered climate space also expanded to both warmer and colder areas during expanding years and climate space in the expanded areas are with significantly lower temperatures and higher temperature variation. Long-term climate change has contributed to the recent beetle expansion while only by combining short-term climate space dynamics with local bioclimatic conditions can we explain beetles' moving to northern regions. We concluded that climatic warming has moved MPB to historically colder climate space with influences from non-climatic factors (e.g., beetle-host coevolution, competition, dispersal, and host susceptibility). Finally, we discussed the caveats in the application of climate space including data uncertainties, effects of scales, and potential subjectivity in variable selection.

CHAPTER III AMPLIFIED CLIMATIC EFFECTS ON MOUNTAIN PINE BEETLE OUTBREAKS IN NORTH AMERICA

1. Introduction

A major way that climate change has affected forests is by altering the timing, intensity, frequency and extent of disturbances (Dale et al., 2001), causing significant ecological and economic impacts to forest ecosystems (Ayres and Lombardero, 2000; Weed et al., 2013). Anthropogenic amplifying impacts of global change, including forest management, human-caused carbon emissions (Logan and Powell, 2001; Raffa et al., 2008), and disturbance interactions influenced by climate change (Buma, 2015), may have driven cross-scale complex systems to be more unpredictable, and ecosystem resilience may be debilitated through more pathways. The recently expanded mountain pine beetle (*Dendroctonus ponderosae*, MPB) outbreaks in the eastern boreal forests of North America were widely attributed to climate change (Carroll et al., 2003; Cullingham et al., 2011; Safranyik et al., 2010), and were also affected by fire suppression during the last century, which made old pine forests more susceptible (Ono, 2004; Taylor et al., 2006; Taylor and Carroll, 2003). In this study, we aim to reassess the relative contribution of climatic factors relative to non-climatic factors in driving the unprecedented MPB outbreaks in North America.

The influences of various climatic factors on MPB are well studied. Temperature is the dominant climatic control of beetle development since critical life stages of the beetle - from egg hatch to larval overwintering to adult emergence - require appropriate thermal conditions (Bentz et al., 1991; Powell et al., 2000). Cold-induced mortality is one major factor preventing MPB expanding its range, a process in which non-cold-harden parts of beetle populations are killed by extreme low temperatures (Régnière and Bentz, 2007). Eggs are not well-adapted in cold (Bleiker et al., 2017). Overwintering adults may lower their metabolic rates to adapt lower supercooling points (Lester and Irwin, 2012). To survive exposure to cold in an invaded range, beetles may have rapidly developed less cold-tolerant stages prior to winter in novel hosts (Rosenberger et al. 2017b). Though warm temperatures and lower precipitation are favorable conditions for MPB outbreaks (Chapman et al., 2012), and extreme cold weather events reduce the probability of outbreaks (Sambaraju et al., 2012), climate change has geographically varied impacts on beetles. This is due to differences in the local thermal environments (Weed et al., 2015), the physiological responses of beetles to the environments (Bentz et al., 2014; Bentz and Powell, 2014), interactions between beetles and host species (Chapman et al., 2012; Dooley et al., 2015; Esch et al., 2016), the temperature tolerance of the blue-stain fungi associations (Rice et al., 2008), and forest management strategies (Seidl et al., 2009).

Current research on the beetle-climate relationships commonly propose warm winters and higher year-round temperatures are positively correlated with increased beetle infestations (Buotte et al., 2016; Creeden et al., 2014; Preisler et al., 2012; Sambaraju et al., 2012), which corresponds to beetle cold tolerance (Régnière and Bentz, 2007). Thus, large-scale spatiotemporal patterns of MPB outbreaks are closely related to climatic and weather patterns. Beetle cold-mortality events are associated with the synoptic-scale circulation and large-scale climate modes such as the shift between Pacific Decadal Oscillation (PDO) and Arctic Oscillation (AO) (Stahl et al., 2006). Some researchers claimed that spatial synchrony of MPB outbreaks resulted from regional patterns of extreme cold temperatures related to PDO and AO phases (Fauria and Johnson, 2009). Moreover, droughts-stressed host trees and boost the intensity of beetle attacks (Creeden et al., 2014; Preisler et al., 2012). Beetle pressure, defined as “the magnitude of a mountain pine beetle population affecting a stand as determined by the number of currently infested trees and their proximity to the stand being assessed” (Shore et al., 2000), was also evaluated in a landscape analysis of MPB outbreaks, showing spatial autocorrelation related to dispersal mechanisms (Aukema et al., 2008, 2006). Beetle dispersal is affected by population size, host connectivity and wind directions (Chen and Jackson, 2017; Robertson et al., 2009).

Previous landscape analysis of MPB outbreaks focused on regional patterns (Chapman et al., 2012; Creeden et al., 2014; Preisler et al., 2012; Safranyik et al., 2010; Sambaraju et al., 2012) without examining the whole species range and particularly missed the expanded range in the east of Rocky Mountain range. We reevaluate the beetle-climate relationships within the current species range using a species distribution modeling (SDM) framework. Species distribution models relate field observations to environmental factors based on statistically or theoretically derived response surfaces and rely on the assumption that the modeled species or community is in equilibrium with the environment and the ecological niche is temporally and spatially constant (Guisan and Thuiller, 2005). Challenges and uncertainties consistently remain in the wide application of SDMs, and are embedded in data sampling, variable selection, parameterization, and model evaluation and selection (Araújo and Guisan, 2006); and some criticisms focused on implausible assumptions have often been misplaced due to the uncritical use of these methods (Araújo and Peterson, 2012). Using SDM to predict impacts of climate change on species invasion requires the appropriate selection of spatial scale and interpretation of model results with consideration of the limitations involved (Pearson and Dawson, 2003). Particularly, incorporating spatially autocorrelated processes in SDMs has been suggested to improve the modeling of range expansion (De Marco et al., 2008).

In this study, we apply generalized linear regression combined with generalized additive modeling, which is also a machine learning process, to predict large-scale MPB outbreak probability using multi-year aerially mapped tree mortality to answer the following research questions: 1) how has climate change contributed to the recent MPB range expansion in North America? 2) what is the relative importance of climatic and biotic predictors in the model prediction? We present the annual prediction maps to compare with the observations and address the limitations of our models, to discuss the associated uncertainties, and provide insight on the climatic and non-climatic controls of the massive MPB outbreak of the last 20 years.

2. Methods

2.1. Data and variables

We used forest health aerial mapping data from the United States, British Columbia (BC) and Alberta to identify mountain pine beetle outbreak presence on a 10km grid annually for the period of 1997-2016. We intersected the raw beetle data in a polygon or point format with the area of 10km grid cells to identify outbreak presence, and the rest of study area was marked as absence. The beetle outbreak year was set as one year before the mapping year due to a one-year lag between beetle attack and the appearance of red needles (Preisler et al., 2012). Climate data were derived from the Climate Research Unit (CRU) 10-minute climatology 2.0 (New et al., 2002), 0.5-degree time series 4.01(Harris et al., 2014), and the10-km grid Daymet Daily Surface Weather Data (Thornton et al., 2017). The ranges of the eight main host species were collected from Little 1978. The sources of the above datasets and detailed steps in the computation of bioclimatic variables and the generation of beetle and host presence/absence data were addressed in Chapter II. We also used the continental forest age map of North America (Pan et al., 2011) and global tree density map (Crowther et al., 2015; Glick et al., 2016) for stand age and forest density variables by aggregating the mean values on 10km grid.

The 47 bioclimatic variables used for modeling were related to seasonal temperature, cold events, heat load, and drought stress on beetle survival (Appendix Table III-1). These bioclimatic variables were selected in Chapter II by removing the variables that are less distinguishable between MPB outbreak presence or absence. We further screened variables in the modeling steps. Beetle pressure variables were defined from time and space aspects, including the beetle outbreak presence on the same grid cell in the previous two years and the summary of beetle outbreak presence on the grid cell and its neighboring eight grid cells. The number of years prior to the current outbreak for beetle pressure was determined by the autocorrelation of a time-series of number of grid cells with beetle outbreaks during 1997-2016 using the functions “acf” and “pacf” in R. Beetle pressure variables are also considered as variables that take both spatial and temporal autocorrelation into account. Vegetation dynamic variables including tree density and stand age are selected for the understanding of possible impacts of forest governance on beetle outbreaks. For example, the legacy of fire suppression has accumulated old and large host trees in dense forests that are more susceptible to beetle attacks (Taylor and Carroll, 2003). Additionally, we included latitude, longitude and elevation for location variables. The beetle pressure, vegetation dynamic and location variables are used to examine the impacts of non-climatic factors. The selected predictors are listed in Table III-1 and further explanation of the variables is in Appendix Table III-1. We also included interaction variables among different factors to understand the potential impacts of local climatic and biological conditions.

Table III-1. Predictors related to climate, vegetation, and beetle pressure in generalized linear models.

Factor	Variable group	Variables
Climate	Seasonal temperature	Tmean, Tvar, fallTmean, TOctSep, TMarAug, ddAugJun, ddAugJul
	Heat	AugTmax, AugMaxT, maxAugT, OptTsum, summerTmean, maxT, AugTmean
	Cold	Tmin, minT, JanTmin, OctTmin, MarTmin, Acs, max.drop, OctMin, Jan20, JanMin, Mar20, MarMin, winterMin
	Water deficit	Pmean, summerP0, summerP1, summerP2, POctSep, PcumOctSep, PMarAug, wd, vpd, cwd, mi, PPT
Vegetation	Tree density	density
	Stand age	age
	Host presence	vgt
Beetle pressure	Beetle presence in the previous years	btl_t1, btl_t2
	Neighboring beetle presence in the previous years	sum9_t1, sum9_t2, sum9_diff

Table III-1 (continued)

Rationale	Data source
Seasonal temperatures synchronize the beetle life cycle Summer temperatures particularly August temperatures are associated with beetle dispersal Extremely low temperatures can cause larva mortality Water conditions are related to both tree growth and drought stress	CRU, Daymet
Denser forests are more susceptible to insect outbreaks	Glick et al. 2016
Old trees are more susceptible to insect outbreaks	Pan et al. 2011
The mountain pine beetle has host preference	Little 1978
Beetle presence in the same grid cell in the previous two years is correlated with beetle presence in the current year Beetle presence in the neighboring grid cells in the previous two years is correlated with beetle presence in the current year	IDS, HFP, FHA

Notes: Data sources were described in Chapter II.

2.2. Modeling steps

The extent of the study area is delineated as a rectangular region encompassing the MPB outbreak range, from northwest British Columbia to southeast Arizona and the Black Hills in the East (Figure III-1). The modeling steps described below include generalized additive models (GAM) and generalized linear models (GLM). Both methods are widely applied in SDM due to their less subject to the constraints of assumptions. We consider GLM is simpler to apply in the prediction of beetle outbreak probability using large dataset than GAM, which is not appropriate for the size and complexity of the dataset but important to examine non-linear relationships. Therefore, we first used GAM as a tool on subsets of the data to explore reasonable variable transformations, then used GLM because of its computational efficiency for large data sets. The total data points include annual climate and beetle data during 1996 and 2015, and the stand age and tree density data that was repeated annually.

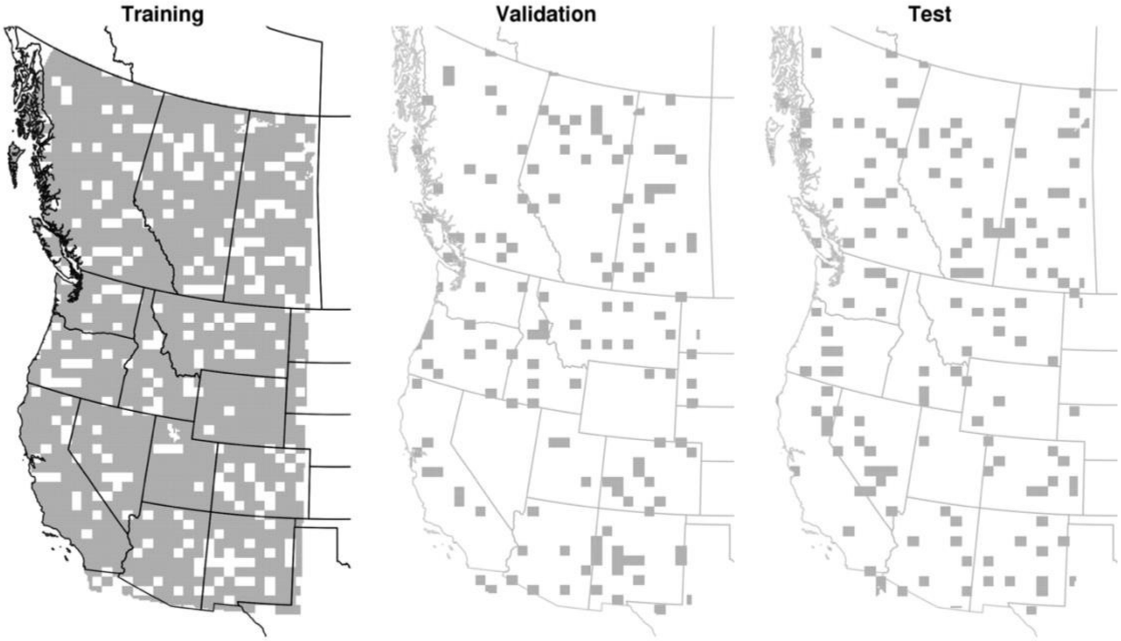


Figure III-1. Study extent and randomly sampled blocks.

To explore potential nonlinear relationships between the predictors and beetle outbreaks, we initially used GAM to suggest potential transformations. Owing to the large number of data points (790,328, or 777,265 when missing values present) and potential predictors

(> 263), we explored the model space by repeatedly sampling 10% of the total data points for each of nine randomly selected variables, always including at least one variable from each of the following categories: climate, host species, location, and previous outbreak presence. The group of climatic variables was split into six groups (No. 1- 6 in Appendix Table III-2) to include different impacts of extreme temperatures and water conditions in the random selection of variables. Variables in each group explain similar biological processes, and variables among different groups were less correlated. GAMs were fitted using the 'mgcv' package, and the 'te' smoother was used, because of its computational efficiency (Wood, 2017; Wood et al., 2016). GAMs were run on 100 resamplings of the data. Response curves that appeared consistently for each variable were transformed in order to be used in a full logistic regression model. To simplify the models, nonlinear effects were modeled as either quadratic or cubic transformations of the raw variables (see Appendix Figure III-1 for further details).

Beetle outbreak presence was then modeled as the response in logistic regression models variable using GLM. To reduce the influence of spatial autocorrelation, we assigned a block index to each group of neighboring grid cells such that the entire grid was divided into a 30 × 60 block matrixes, with each block around 65 × 60 square kilometers. The blocks were then randomly sampled with 80% of the blocks assigned to training data and the remainder divided into 10% validation data and 10% test data (Figure III-1). The percent of presence in each of the three datasets is ca. 13%. The model matrix for the full model included the raw variables, their transformations where applicable, and interaction terms where appropriate. All predictors were then scaled to z-scores (i.e., by subtracting the mean and dividing by the variance). In exploring the model space, we performed logistic regression on all available variables and random subsets of the variable and used model accuracy on the test set as the criterion for model selection. L1 regularization (i.e., lasso regression), a compromise between variable-subset selection and ridge regression (Guisan et al., 2002), was used to reduce the number of variables and to minimize overfitting and optimized using the validation set. To further summarize the effects of the model, confusion matrices were logged, and relevant statistics were derived (sensitivity, specificity, f-score), as well as ROC curves and area under (AUC). Models were fit in

Python 3.6.7 using the “LogisticRegression” function from the scikit-learn library (Pedregosa et al., 2011).

To convert the continuous probability-of-presence values to simple a binary presence/absence variable, all probabilities higher than a certain value were assigned as “presence”. This value was the threshold that maximized the model accuracy, which is defined as the percent of accurately predicted presence and absence grid cells in the total number of grid cells. We compared predictions with the observations to reveal the spatial patterns of commission and omission errors and mapped the errors. The selected model was then fitted in R without scaling the predictors to obtain the Akaike information criterion (AIC), *p* values for coefficients and the model as a whole, using the “glm” function. The *r2* value was obtained using Nagelkerke’s method (Faraway, 2016; Nagelkerke, 1991) using the “NagelkerkeR2” function, and the adjusted *r2* value was calculated from that. The formulas of different metrics are listed in Appendix Table 3. To understand the relative impacts of climatic and biological factors, we present and summarize five models with successive addition of variables: 1) Model 1 with only single bioclimatic variables; 2) Model 2 added transformed bioclimatic variables, location variables, and interactions between location variables and climatic variables to Model 1; 3) Model 3 added beetle and host presence variables, interactions between location variables and beetle variables, and interactions between beetle variables to Model 2; 4) Model 4 added stand age and tree density and their interactions with bioclimatic variables and the difference of neighboring beetle presence in the previous two years to Model 3.

In order to cross validate the performance of the models on novel data, model performance metrics based on confusion matrices are reported for the withheld test set, not the data set that was used to train the model. Although accuracy was our primary criterion for model selection, AIC and r-squared are also presented for comparison. We used the model coefficients from the best lasso models with the scaled predictors in order to compare the relative effects of each predictor on beetle presence. We also provided the coefficients from the same model fitted using the raw (unscaled) units, and without L1 regularization, so that coefficient effects can be compared in their original units, and *p* values may be compared. Finally, for each predictor in the bioclimatic and non-climatic variables, we plotted a response curve to show how the variable predicts the MPB outbreak probability, applying Model 4 with the input data as sampled 100 values from low to high equivalently within the 95% quantiles in the examined predictor and constant values with the median in other predictors. We interpreted the relationship between each predictor and MPB outbreak probability incorporating effects of other predictors from the bivariate plots with consideration of data density and multilinearity.

3. Results

3.1. Predictions of mountain pine beetle outbreak probability

The highest overall accuracy found in the models is 0.94 with an AUC of 0.97 in the Model 3 and 4 (Table III-2). The AIC was nearly halved (221953) in Model 4 in which bioclimate, spatial components, beetle pressure (autocorrelation), vegetation and interactions were all considered, from 410261 in Model 1 in which only bioclimatic variables were included. Although including stand age and tree density in Model 4 did not increase the overall accuracy or AUC, the sensitivity improved from 0.777 in Model 3 to 0.791 in Model 4. Similarly, the adjusted r2 increased from 0.418 in Model 1 to 0.719 in Model 4. The performance of the four models with different variable settings are summarized in Table III-2.

The actual presence of MPB outbreaks largely overlaps with the predictions of a probability > 0.5 among models (Figure III-2; Appendix Figure III-2 - 5). With the highest accuracy among the models with the same number of observations, Model 3 shows large omission errors in northern BC and Alberta in 1998, 2006, 2009 and 2010 (Appendix Figure III-6). Models from 1 to 4 present an increasing outbreak probability eastward. In Model 1 that includes only bioclimatic variables, notable underpredictions include some smaller areas around the Black Hills, southern Montana, northern California, Arizona during some years and some larger areas in northeastern BC and central Alberta since 2009, where predicted probability of presence was nearly 0. Model 1 largely failed to predict the eastward expansion of beetle outbreaks in the Alberta

Table III-2. Model performance from the four models.

Model	Predictors	No. observations	No. parameters
1	bioclimatic variables	790328	38
2	added transformed bioclimatic variables, location variables, and interactions between location variables and climatic variables to model 1	790328	198
3	added beetle and host presence variables, interactions between location variables and beetle variables, and interactions between beetle variables to model 2	790328	210
4	added stand age and tree density and their interactions with bioclimatic and beetle variables to model 3	777265	263

Table III-2 (continued)

Optimal threshold	Accuracy	Sensitivity	Specificity	Recall	F-score	Kappa statistic	TSS	AUC	AIC	R squared	Adjusted R squared
0.499	0.888	0.609	0.909	0.329	0.427	0.371	0.518	0.879	410261	0.418	0.418
0.457	0.901	0.632	0.933	0.529	0.576	0.512	0.565	0.925	325485	0.565	0.565
0.543	0.939	0.777	0.961	0.726	0.751	0.716	0.738	0.969	226539	0.717	0.717
0.543	0.939	0.791	0.957	0.704	0.745	0.710	0.749	0.969	221953	0.719	0.719

region, from 2006 to 2008. Although the probability of presence did increase in this region, the probability was < 0.21 for most of this region. With the optimal threshold 0.499 (Table III-2), Model 1 predicted absence everywhere within the study extent (Figure III-3).

By including more bioclimatic predictors and interaction terms between bioclimate and location, the predictions from Model 2 improved noticeably, especially during the expansion period since 2006 (Figure III-2; Appendix Figure III-3). Predicted outbreak probability in northern BC and eastern Alberta was also nearly 0, largely agreeing with the observed absence. While the occurrence of true positives increased, the occurrence of false positives also increased. For example, high probabilities of presence were predicted in California in the early years, and in central BC in the later years. Both Model 1 and 2 predicted increasing outbreak probability in California from 1998 to 2006, and Model 2 also predicted presence with a high probability from 2001. However, false negatives continue to occur in several regions (e.g., Montana, Wyoming, South Dakota, northern BC and Alberta). With the optimal threshold 0.457 (Table III-2), Model 2 shows clusters of omission errors in northern outbreak range, Rocky Mountains, Black Hills, Blue Mountains, and southern Cascades (Figure III-3).

Model 3, which includes beetle-related predictors that account for spatial and temporal autocorrelation, increased the prediction accuracy in these regions (Figure III-2; Appendix Figure III-4). Also, Model 3 predicted beetle outbreak presence and absence more accurately than Model 1 or 2 for all years (Appendix Figure III-4). Despite the improved accuracy overall, Model 3 failed to predict the northern expansion in 1998 and 2006 and performed worse with lower probabilities than Model 2 in these regions. However, the diminishing presence in central BC was more correctly predicted in Model 3, although lower probability of outbreak remained in some regions during later years. Model 4 slightly improved the proportion of false negatives in the 2006 beetle expansion; however, the accuracy did not change from Model 3 overall (Appendix Figure III-5).

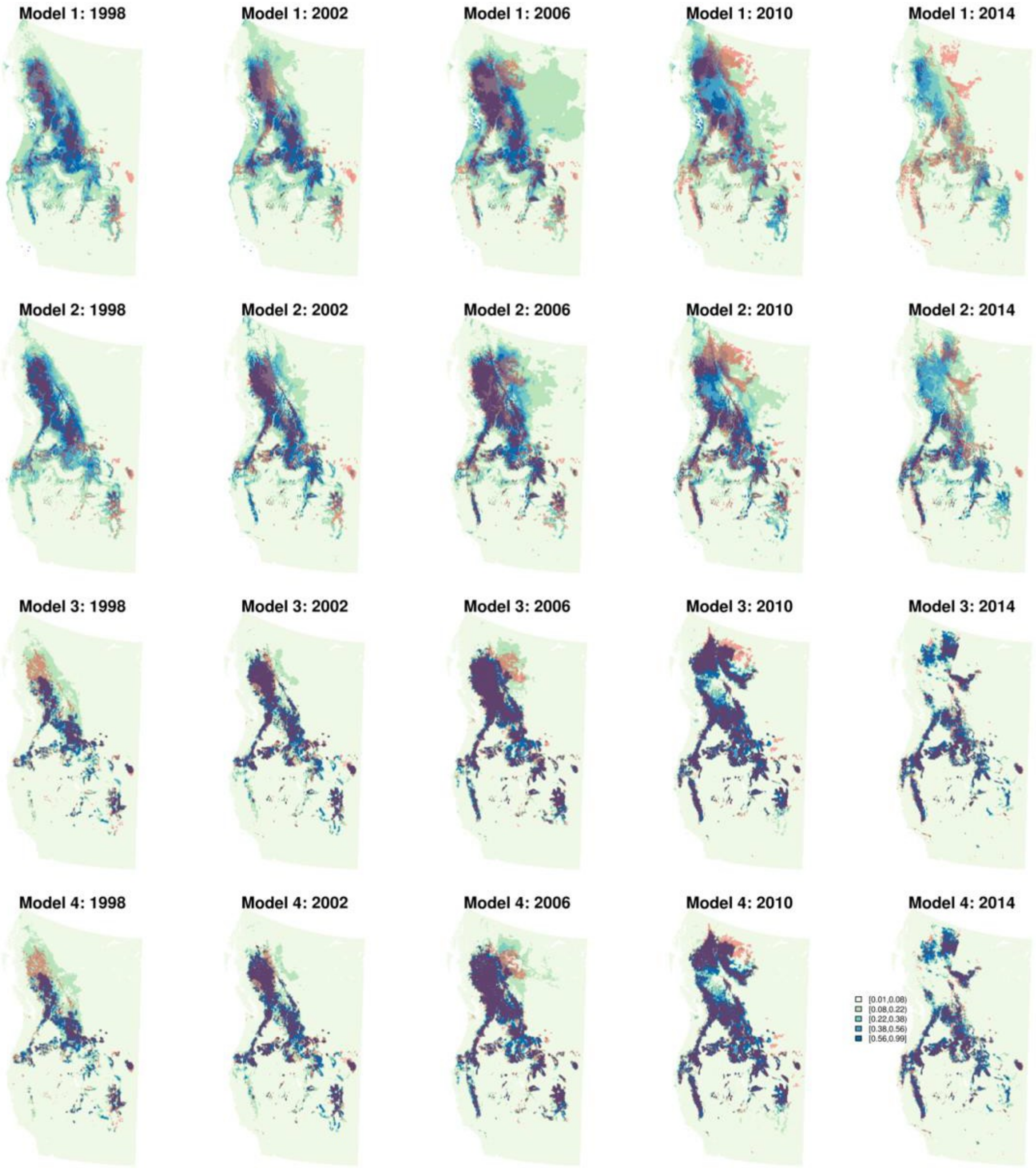
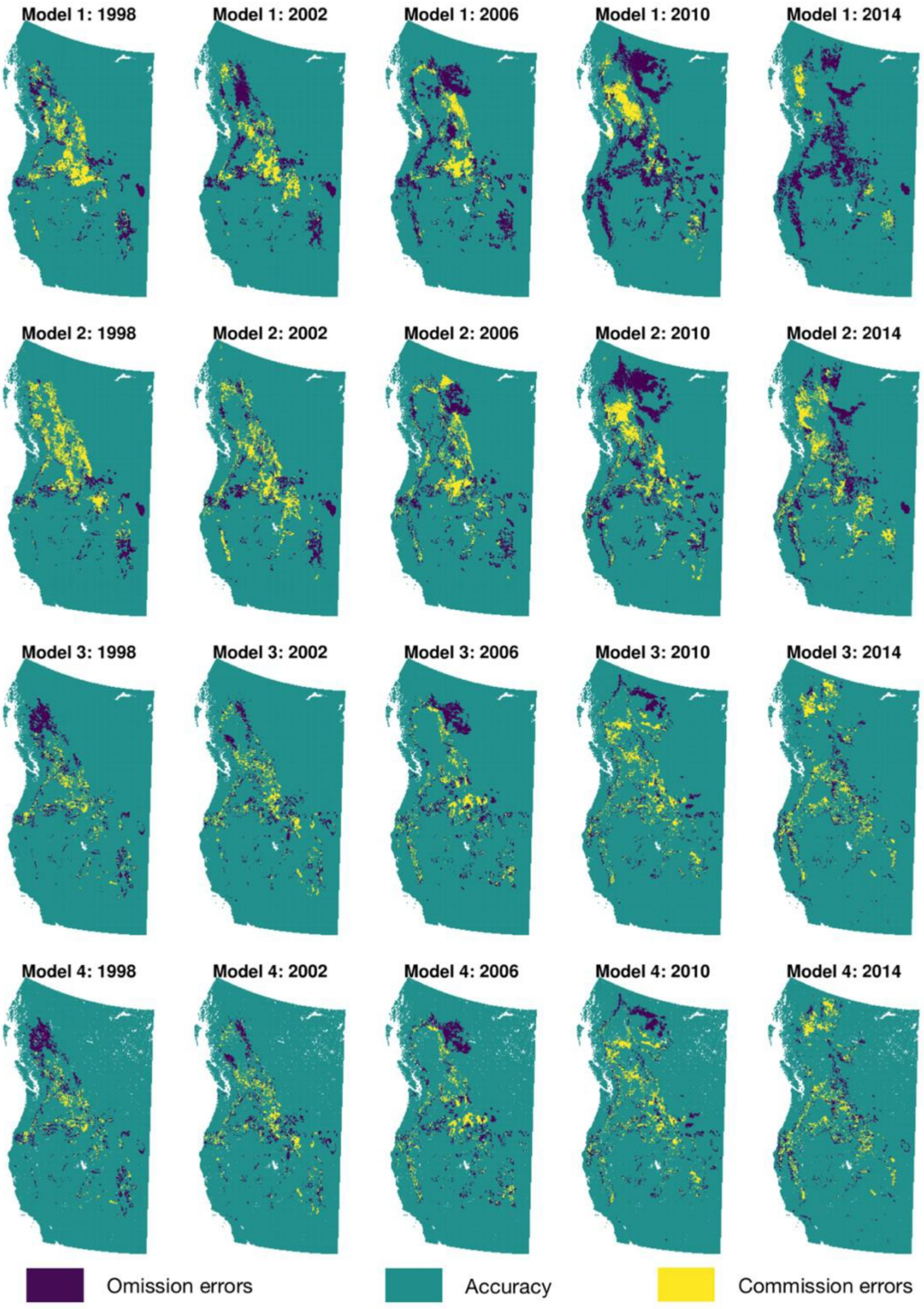


Figure III-2. Predictions of MPB outbreak probability every four years from 1998 to 2015 in Model 1 (with only bioclimatic variables), Model 2 (included transformed bioclimatic variables and interactions between bioclimatic variables and location variables to Model 1), Model 3 (added spatial autocorrelation variables to Model 2), and Model 4 (added stand age, tree density and their transformation and interactions with bioclimatic variables and beetle pressure to Model 3).

Figure III-3 (next page). Prediction accuracy of MPB outbreak probability every four years from 1998 to 2015in Model 1 (with only bioclimatic variables), Model 2 (included transformed bioclimatic variables and interactions between bioclimatic variables and location variables to Model 1), Model 3 (added spatial autocorrelation variables to Model

2), and Model 4 (added stand age, tree density and their transformation and interactions with bioclimatic variables and beetle pressure to Model 3), using the threshold of probability that maximizes accuracy.



Finally, the comparison between the predictions of beetle expansion from Model 1 to Model 4 shows how the additional variables contribute to the prediction (Figure III-2). All models predicted a northward and eastward outbreak range expansion with different levels of probability, and the probability is higher than 0.5 only after taking beetle pressure variables into account. The comparison between the spatial patterns of commission and omission errors from Model 1, 2 and 3 in 2006 at their optimal thresholds (Table III-2) also shows some consistency in Alberta and parts of western US. Without including beetle pressure variables, both Model 1 and 2 predicted the beetle outbreak presence poorly. Model 3 did well in the predictions of the main outbreak range, however, the beetle expansion in 2006 remained largely omitted in Model 3. A larger range of beetle outbreak than the observations was predicted in the northern and central Rocky Mountains (BC, Idaho, Montana) in all the models.

3.2. Influential variables and their effects to the beetle outbreak predictions

When using only bioclimatic variables to predict outbreaks in Model 1, temperature variables have a greater predictive power than moisture variables (Appendix Table III-4). However, moisture variables increase their predictive power when the variable includes effects from other variables on the prediction in their transformation or interaction terms in other models. Similarly, tree density is more influential in the interaction terms between tree density and climatic conditions including seasonal temperature and vapor pressure deficit. Unsurprisingly, the difference of neighboring beetle presence in the previous two years, which explains spatiotemporal autocorrelation, significantly improves the predictions.

When exploring a large range of values for the L1 (lasso regression) penalty hyperparameter (i.e., C value) on the validation set, we found that beetle pressure variables, host presence, stand age, and the interaction term of the three location variables (longitude, latitude, elevation) were always retained. The interactions between elevation and precipitation, and the interactions between density and August temperature were also selected from the Model 4 lasso regression with a C value of 0.0001 (very strong penalty).

When the same regularization strength was applied to Model 2, in which beetle and tree variables were excluded, vapor pressure deficit, cumulative climatic water deficit, and summer temperature were always with a higher coefficient than the cold-related variables such as mean of monthly average of minimum temperature from November to March and number of days with minimum temperatures at or below -20 °C in January.

After including the effects of other variables, growing season temperature, annual mean temperature, degree days, mean August temperature, and vapor pressure deficit predicted the highest MPB outbreak probability (Figure III-4). The probability increased with the increase of seasonal mean temperature and vapor pressure deficit, but MPB outbreaks were predicted very unlikely when degree days higher than 4000 °C or mean August temperature higher than 20 °C. Similarly, the increase of January minimum temperature and minimum daily temperature were associated with a decrease of MPB outbreak probability. However, the probability is relatively lower than what seasonal mean temperature predicted. The rest bioclimatic variables are much less influential than seasonal temperature and vapor pressure deficit, generally associated with a probability lower than 0.1.

The location variables predicted the highest beetle probability among the non-climatic variables, with optimal conditions for MPB outbreaks in lower longitude and latitude, and higher elevation (Figure III-5). These location variables are not influential in the MPB predictions of the eastern (> -115°W) or northern (> 45°N) areas, or lower elevations (< 1000m). Beetle outbreak probability is positively correlated with stand age, tree density and beetle pressure (difference between neighboring outbreak presence prior to the outbreak year), although the probability is commonly lower than 0.1 after taking the impacts of climatic conditions into consideration.

4. Discussion

4.1. Relative roles of climatic and non-climatic factors contributing to the beetle expansion

Three main climatic factors expressed as cold, heat and water conditions influence beetle life cycles and population levels directly and indirectly (see Chapter II). Winter temperatures and annual degree days set the basic thresholds for larval survival, egg hatch and being univoltine, summer temperatures are the constraints for adult emergence and dispersal, and water deficit affects the host resistance to beetle attacks (Preisler et al., 2012; Safranyik et al., 2010). We found that climatic factors predicted a potential expansion in northern BC and eastern Alberta, which was caused by warming winter temperatures. This is consistent with previous research that warming average annual temperature synchronized a semivoltine population into a univoltine population (Logan and Powell, 2001), and increased winter temperatures became favorable for brood development in the historically cold regions (Carroll et al., 2003). However, warming winters cannot explain the outbreak range expansion in southern regions where temperature conditions have been suitable for beetle survival and development (Buotte et al., 2017; Weed et al., 2015). Also, longer number of cold days in higher elevations did not limit beetle outbreak probability, which is likely explained by variables other than temperature (Rosenberger et al. 2017b).

Seasonal temperature and August temperature are more influential predictors than winter temperature, indicating that heat conditions associated with flight may have become a more important factor contributing to beetle expansion, since winter temperature is not a limitation. Similarly, the heat cycles in summer temperature can capture the major emergence peaks at the landscape scale (Chen and Jackson, 2015). Furthermore, vapor pressure deficit and cumulative climatic water deficit that describe tree defensive capacities have also facilitated mass beetle attacks. Summer temperature and its influence on vapor pressure deficit was considered as a primary driver of host susceptibility (Oneil, 2006). Finally, large-scale climatic conditions combined with other local factors (e.g., topography, tree density and beetle pressure) explain better beetle probability than climate only. Broad-scale climatic conditions between outbreak presence and absence are not significantly distinct within the study extent (Chen, 2018a), thus accuracy was subject to the extent and prevalence in Model 1.

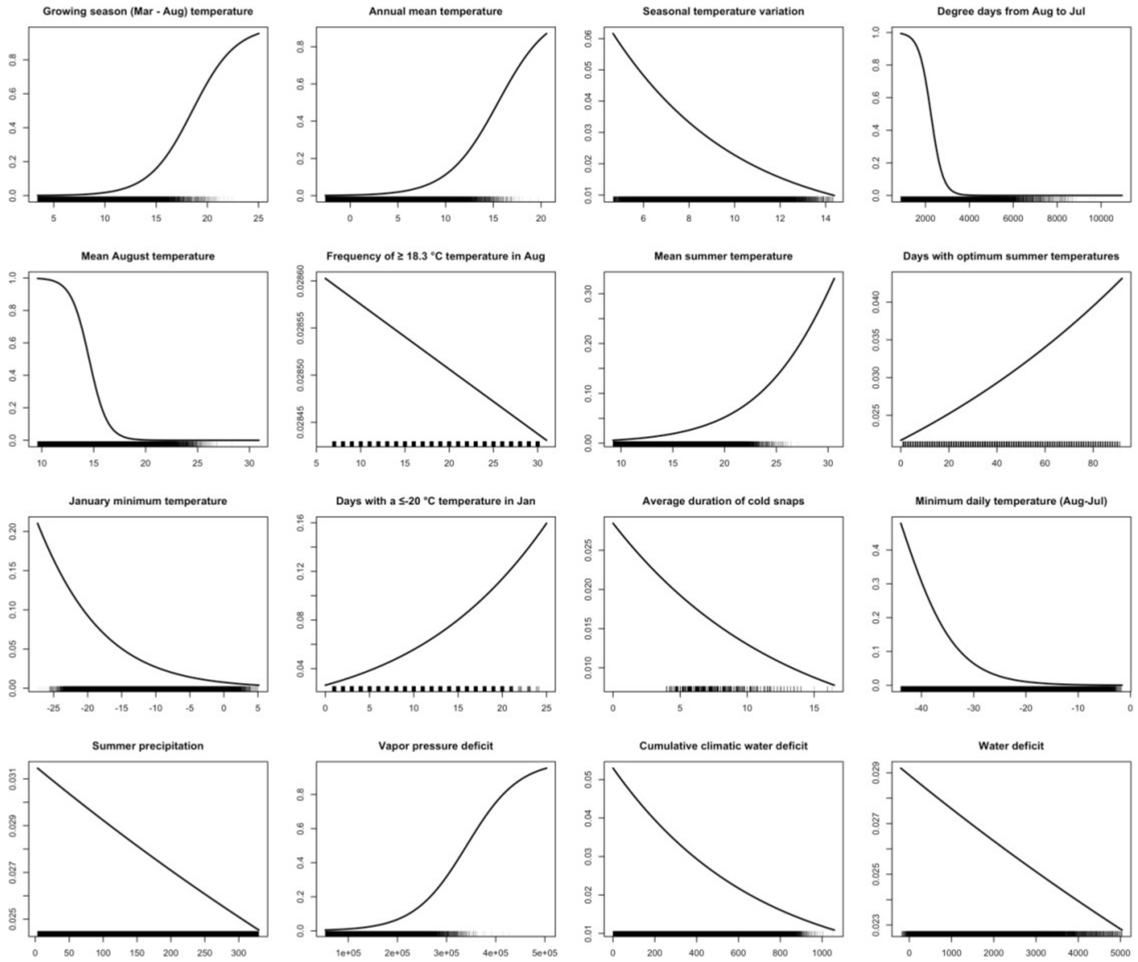


Figure III-4. Response curves between bioclimatic variables (x-axis and title) and MPB outbreak probability (y-axis).The x axis shows the continuous values of each predictor within the 95% quantiles, while the y axis shows the predicted beetle outbreak probability from Model 4 with a setting of median values for the rest predictors. The rug shows the data distribution of each predictor, same as Figure III-5.

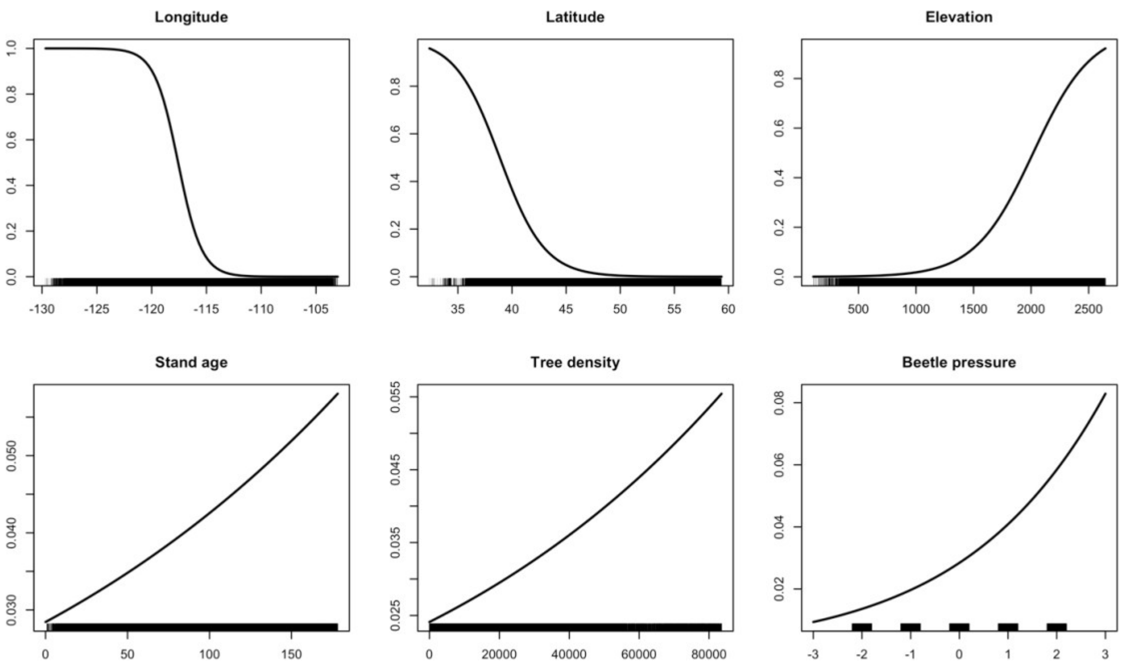


Figure III-5. Response curves between non-climatic variables (x-axis and title) and MPB outbreak probability (y-axis). Beetle pressure variable is the difference in the beetle outbreak presence summary of the nearest eight grid cells and the center grid cell in the previous two years.

Location variables account for the spatial dimensions of beetle outbreak range and localized climatic conditions. Beetle outbreaks synchronized within the host range for centuries (Jarvis and Kulakowski, 2015), and the thermal optimum for phenological synchrony shifted recently and was predicted to expand from middle elevations to lowest and highest elevations (Bentz et al., 2016). Including effects of longitude, latitude and elevation as well as their interaction terms with climatic and biotic variables in the training data increased the overall accuracy of test data and beetle expansion probability in our study, likely due to MPB spatial synchronization and its largely staying in the same climate space while expanding the outbreak range (see Chapter II). These static variables serve as helpful proxies for current climatic conditions, and can be used as a mask to localize beetle range (Stanton et al., 2012) over the yearly time step of data. On the other hand, these location variables can also show a changing species-climate relationship over space (i.e., local adaptation). Moreover, a meta-analysis of published data also showed that location variables mainly determined the relationship between tree diameter and

MPB attacks (Björklund and Lindgren, 2009). Therefore, local environmental conditions remain influential.

Beetle pressure variables reflecting population attraction, competition and dispersal are increasingly influential on the predictions, especially when beetle populations reach an epidemic level. These variables increase the explanation of spatial and temporal autocorrelation, and the outbreak probability increased with the increase of beetle pressure measured by neighboring past outbreaks prior to the current outbreak in our case. From Model 1 to Model 3 with an increase of probability in the expansion, we speculate that climatic suitability has increased initially in the newly attacked regions and created opportunities for MPB infestation, then the local beetle population at endemic levels dispersed and increased its size to push and expand the red attack, coupled with host availability and suitable landscape characteristics. Although the relative importance in the roles of topographic and biotic predictors changed at the different stages of outbreak (Walter and Platt, 2013) and beetle pressure is probably a more important predictor on large-scale beetle outbreaks, climatic conditions remains influential throughout the expansion. Beetle emergence and flight was found to be associated with distinct climate conditions that are beneficial to initiate long-distance dispersal (Chen and Jackson, 2017), and the initial range expansion and invasion was also characterized by aerial deposition along a strong north-west to south-east gradient, followed by additional aerial deposition and localized dispersal to continue expansion (de la Giroday et al., 2012a).

Forest density and stand age are related to MPB host preference in large trees and thus influence host availability and susceptibility that diametrically facilitate beetle development. Stand density index (SDI) was a widely used measure of susceptibility (Anhold and Jenkins, 1987; Negrón et al., 2017; Perkins and Roberts, 2003). It is an indicator of tree stress due to competition of space and water (Mitchell et al., 1983; Negron and Klutsch, 2017). Some research found that both basal area of large ponderosa pines and SDI were correlated with increased MPB attacks and trees generally more likely to be attacked in denser stands (Negron et al., 2008). Although tree density was suggested to be a more important predictor at a local scale (Björklund and Lindgren, 2009), we found that the interaction terms between tree density and climate are more influential in the predictions at a large scale. Stand age, which is correlated with diameter (Björklund and Lindgren, 2009), has been used to detect the influence of fire exclusion on stand susceptibility to MPB infestations (Taylor and Carroll, 2003). In our model, however, stand age was not the most weighted predictor in our final model but due to some strong correlation between predictors remained influential with a strict regularization, since stand age also indicates host availability. Additional variance explained (and the reduced AIC) from Model 3 to 4 showed the contributions of these forest stand characteristics to the MPB outbreak expansion. These variables are related to forest management, such as long-term fire suppression that can increase stand age and tree density (Taylor et al. 2006).

Our study suggests that warmer temperatures have triggered more beetle infestations at the outset and the populations propagated with more susceptible host trees locally, and eventually expanded the range globally. This agrees with the Moran effect caused by the spatial correlation of regional climates (Aukema et al., 2008; Peltonen et al., 2002), but also coincides with climate change. However, with an increasing influence of beetle pressure on a landscape level during the peak MPB emergence, local climatic conditions in denser stands likely created a habitable environment for the beetle in the colder regions outside of core climate space (see Chapter II). Moreover, host trees in the recently expanded regions were less able to resist to MPB attacks due to lack of co-evolutional defense systems (Raffa et al. 2013; Rosenberger et al. 2017a), MPB also displayed behavioral variations within different thermal environments (Bentz et al., 2014) or utilized different cold tolerance strategies in novel hosts or colder regions (Lester & Irwin 2012; Rosenberger et al. 2017a). More importantly, changes of disturbance regimes due to a fire exclusion paradigm have increased the amount of susceptible pines to MPB infestations in BC and Alberta (Ono, 2004; Taylor et al., 2006; Taylor and Carroll, 2003). Thus, it is very likely that complex systems of biotic interactions within a suitable environment expand beetle spread at smaller scales due to strong feedback of MPB populations triggered by a small change of climate (Cooke and Carroll, 2017). Finally, host depletion or a return to cold temperatures, likely combined with intraspecific competition (Goodsman et al., 2018), became a primary limitation when outbreak range retreated in central BC during later years.

4.2. Applying species distribution modeling in understanding large-scale insect outbreaks

Applying species distribution modeling requires critical examinations of its ecological, data, and statistical components and their harmony (Austin, 2002). Basic challenges in doing that exist in identifying ecologically representative scales, data, and variables, choosing appropriate modeling techniques and their evaluation methods, and measuring uncertainties produced from the limitations of data, modeling techniques and current knowledge. Critics of SDM predominantly discussed how the assumptions associated with its application commonly mismatch with the ecological reality. Our case study provides an example of large-scale insect outbreak in which we identified relative contributions of predictors to the eruptive beetle infestations and uncertainties in our predictions using SDM. This case study also involves two main differences from common SDM case studies. First, the presence of beetle populations captured by tree mortality implies both the presence of MPB and the epidemic beetle population level. Second, the yearly temporal resolution of presence data was combined in the modeling, which process considers both temporal and spatial autocorrelation. We discuss the merits and limits of the case study from its addressing ecological assumptions and uncertainties caused by data and models.

We summarized how this study addressed the relevant ecological assumptions associated with SDM in Appendix Table III-5. Common misassumptions in SDM are that species are at equilibrium with their current habitats, and biotic interactions and evolutionary variation over space and time are largely ignored. Despite including relevant predictors to the model that has significantly increased model performance (e.g., spatial variables and their interaction terms, which weighted climatic variation with localized conditions, and beetle pressure and forest conditions, which explains partially biotic interactions), our model failed to completely predict the northern expansion in Alberta with the optimal probability threshold. This indicates that climatic or non-climatic factors that were excluded in the models may have played the dominant role to the northern expansion, and this expansion states a disequilibrium between beetle outbreaks and climatic factors. As discussed above, these factors might be a combination of beetle dispersal connected with population size and wind conditions, beetle adaptive behaviors in colder areas, less-defensive systems in novel host species, and susceptible landscape characteristics.

Spatial autocorrelation (SAC) related assumptions implied in SDM are often connected with the dispersal mechanisms. Spatial synchrony of MPB outbreaks, which addresses correlated population fluctuation over wide geographical area (Peltonen et al., 2002), is another factor of spatial autocorrelation. In our models, the clusters in the spatial patterns of errors in training data reduced with the increase of accuracy from Model 1 to Model 3, however, they remained relatively high. Dispersal of MPB varies with climatic conditions, beetle population dynamics, host, and landscape. Generally, short-distance is the dominant dispersal mode particularly during rapid invasion, determined by the active responses of the beetle to chemical and physical cues, while long-distance is more important at the early stage of the beetle outbreak, often facilitated by winds above the canopy (Chen and Walton, 2011; Lundquist and Reich, 2014; Robertson et al., 2009). Beetle populations were found more synchronous with larger geographical area during epidemic years than incipient years (Aukema et al., 2006), which may be associated with large-scale climatic patterns such as Pacific Decadal Oscillation and Artic Oscillation (Fauria and Johnson, 2009). We acknowledge that spatial autocorrelation exists and may bias the accuracy and inflate the significance of coefficients, however, we applied a block sampling method to minimize the spatial autocorrelation in the test set by limiting the number of neighboring grid cells in the training and validation sets. Moreover, from the ecological point of view, spatial autocorrelation is inherently prevalent due to dispersal, and it is nearly impossible to disentangle stochastic and process-introduced SAC (Dormann, 2007; Dormann et al., 2007).

Multicollinearity among the key bioclimatic variables is also unavoidable in our case study, which can inflate variance of regression parameters, potentially causing inaccurate model parameterization and significance of predictors (De Marco and Nóbrega, 2018;

Dormann et al., 2013; Graham, 2003). However, “multicollinearity does not reduce the predictive power or reliability of the model as a whole” (Midi et al., 2010, p. 255), since “the main use of the model is to predict new cases within the range of the sampled data” (Dormann et al., 2013, p. 29). Predictive models were used to show the beetle-climate relationship in a better fit. We have examined the correlations among bioclimatic variables and randomly grouped the key variables with lower correlation in the models, and found that including all variables remained the highest accuracy with regularization through lasso regression, which made collinearity less of an issue (Guisan et al., 2002). We also considered correlated variables in groups that explain the same ecological process, which lessened the trouble of interpretations. Applying a principal component analysis (a common method to reduce collinearity), however, increased the interpretation difficulty in our case. Other sources of uncertainties including choices of modeling techniques and model selection methods were also explored; however, an exhaustive discussion of the SDM uncertainties is out of the scope of current study. We suggest applying SDM carefully and integrating ecological knowledge with the methods based on case studies.

5. Conclusions

Climate change has impacted forest disturbances through changing the disturbance regimes and disturbance interactions, but the climatic influences on the recent expansion of MPB outbreaks are not simply results of increased beetle infestations from increased winter temperatures. We applied species distribution modeling techniques combining generalized additive models and generalized linear models with four groups of variable combinations to reveal the relative contributions of climatic and biotic factors to the prediction of beetle outbreaks. The highest accuracy occurred in the models that include beetle-related predictors accounting for spatial and temporal autocorrelation. We found that climatic variables closely related to beetle dispersal and host resistance are more influential than the cold related variables for the prediction. Seasonal temperatures and their interactions with spatial predictors and tree density more strongly predicted the MPB outbreak probability. Although increased probability in the boreal forests of eastern Rockies was found in our models, the probability remained low, and an expansion of outbreaks in this region was not completely predicted at the beginning. Including beetle pressure variables significantly increased the outbreak probability in the expanded range during the later years. Our interpretation of the models is that slight climatic warming introduced epidemic beetle populations into high density forests that eventually amplified the impacts of climate change.

Assumptions associated with SDM were evaluated in our case study. Geographical variation of beetle responses to climate change, beetle dispersal mechanisms, and biotic interactions were not fully addressed in our models. We argued that suitable data related to specific dispersal process and interactions among beetles, hosts and biological associations is not available at the study scale; however, research at smaller scales supports our interpretation that the beetle has behaviorally adapted to the expanded range coupled with weakly coevolved new hosts and susceptible landscape resulting from long-term fire suppression. Although we cannot completely reduce spatial autocorrelation, we have evaluated our models appropriately to better understand the recent beetle expansion. Future research on the cascading effects of climate change that combined with anthropogenic factors is warranted.

CHAPTER IV EXPLORING FIRE SUPPRESSION ACROSS THE AMERICAN WEST AND ITS RELATIONSHIP WITH MOUNTAIN PINE BEETLE OUTBREAKS

1. Introduction

Fire suppression, an effort to suppress the spread of fire and mitigate its negative impacts on the society, involves the direct extinguishment of flames or the indirect containment of fire spread to within a limited area by deploying fire suppression resources (crews, vehicles, and aircraft) (Duff and Tolhurst, 2015). Fire suppression in the American West, pursued aggressively since 1910 and more effectively with aerial supports since the 1940s, is incentivized through the Forest Fires Emergency Act and the availability of emergency funds (Berry, 2007). Fire suppression policies evolved after ecologists recognized the positive role of burning in the 1960s (Stephens and Ruth, 2005), after which some fires caused by lightning were allowed to burn on some public lands (parks and wilderness), and the application of prescribed fires occurred under controllable conditions. However, with residential development near forested areas -the Wildland Urban Interface (WUI)- in the 1990s (Hammer et al., 2007), fire control has become more demanding due to additional assets at risk and less flexible management options. In addition, long-term fire suppression has contributed to increased fuel loads on public lands, causing more intense fires that are more difficult and costly to suppress (Arno and Brown, 1991; Donovan et al., 2004). As such, expenditures on fire suppression continue to increase substantially, while fire size and area burned in the US have not diminished.

The ecological effects of long-term fire control have been observed in ecosystems in various ways. Evidence of the cascading effects of fire exclusion has been found in the Rocky Mountain ecosystems across scales (Keane et al., 2002). Specifically, fire suppression can contribute to an accumulation of surface and crown fuel, can convert shrublands to woodlands or forests (Lenihan et al., 2008), or create more fire-prone grassland and shrubland ecosystems through the introduction of exotic annual grasses (Calkin et al., 2015). It can increase tree density (Parsons and DeBenedetti, 1979), and reduce vegetation diversity, particularly in the pine-dominated forests in which structure and composition were historically shaped by natural fire disturbances (Taylor, 2007). Some species that have adapted to frequent, low-intensity fires, such as ponderosa pine, longleaf pine and giant sequoia, also had lower levels of reproduction due to fire suppression (Berry, 2007; Sturtevant et al., 2004). Fire suppression can restructure landscapes by controlling the succession of dominant tree species in terms of species abundance, age structure and spatial pattern (Chang et al., 2007; Wang et al., 2007), the results of which vary across different spatial and temporal scales (Baker, 1993, 1992) and may be restored by reinstating natural fire regimes (Baker, 1994). Moreover, fire suppression can shift fire regimes by prolonging fire return intervals and increasing fire intensity, risk, and the chance of catastrophic fires (Chang et al., 2007; Liu et al., 2009; Shang et al., 2007; Wang et al., 2007).

Fire and insects are the two most important factors in shaping the coniferous forest composition and structure in western North America. Changes caused by fire control in landscape and fire regimes influence the abundance and spatial continuity of susceptible host trees, and thus the potential for insect outbreaks. These changes are a likely contributing factor to the often dramatic increases in outbreak intensity and spatial-temporal synchronicity (Mccullough et al., 1998). Interest in understanding fire-insect interactions has been shown in a large body of literature and continues to grow (Jenkins et al., 2014; Parker et al., 2006; Simard et al., 2008). While the effects of outbreaks on fire has received significant attention, the effect of fire suppression on insect outbreaks has not been widely researched with quantitative methods. There are three possible paths through with fire suppression could have affected beetle outbreaks. First and more commonly assumed, fire control increased spatially extensive areas of dense and old forests which are more susceptible to beetle attacks (Mccullough et al., 1998; Naficy et al., 2010). This is due to both beetles' preferring large trees (Taylor and Carroll, 2003) and the increased competition for space and water within forest stands that has weakened the defense systems of host trees (Mitchell et al., 1983; Negron and Klutsch, 2017). A second possibility is that surface and crown fuels accumulated due to fire exclusion, which led forests to be more fire-prone and thus fire injuries happened to reduce tree resistance to beetle outbreaks (Keane et al., 2002; Mccullough et al., 1998). Finally, long-term absence of fires weakened the defense systems of host trees that have adapted to different fire regimes, because lack of low-severity fire relaxes resin duct defense in fire-adapted ponderosa forests (Hood et al., 2015), and lack of replacement-severity fires may have increased the susceptibility of lodgepole pine to MPB (Kulakowski et al., 2012). In any of these scenarios, we expect that increased beetle outbreaks could result from decades of fire suppression. For example, changes in species compositions, tree diameter, and age structure were shown to affect beetle susceptibility in western Canada (Taylor et al., 2006; Taylor and Carroll, 2003).

The mountain pine beetle (MPB, *Dendroctonus ponderosae*), has killed millions of acres of pine trees yearly and particularly increased its affected area in the American West in recent years. While much attention has been given to the role of climate in promoting recent MPB outbreaks (Bentz et al., 2010; Logan et al., 2010), there is no broad assessment of fire suppression and its relationship with MPB outbreaks across the American West. In this study, we aim to utilize available fire and tree data to evaluate fire suppression and its consequences on vegetation dynamics and fire regimes, and thus its relationship with MPB outbreaks, to answer the following research questions: 1) how has fire suppression contributed to MPB outbreaks in the American West? 2) what are the relative roles of climatic and non-climatic factors in driving MPB outbreaks across spatial scales?

2. Methods

2.1. Study area and mountain pine beetle affected area

The western United States is well studied in regard to fire-climate relationships and the impacts of human activities such as fire ignition and suppression on landscape disturbances. Since fire exclusion policies and practices can be impacted by national boundaries within the mountain pine beetle (MPB) outbreak range, and also due to data availability, we selected the American West, which includes the complete or partial territory of western 17 states, and covers the complete MPB range in the US, as our study area for large-scale spatial analysis (Figure IV-1). We consider this spatial extent appropriate for studying the ecological process of MPB outbreaks and to observe the

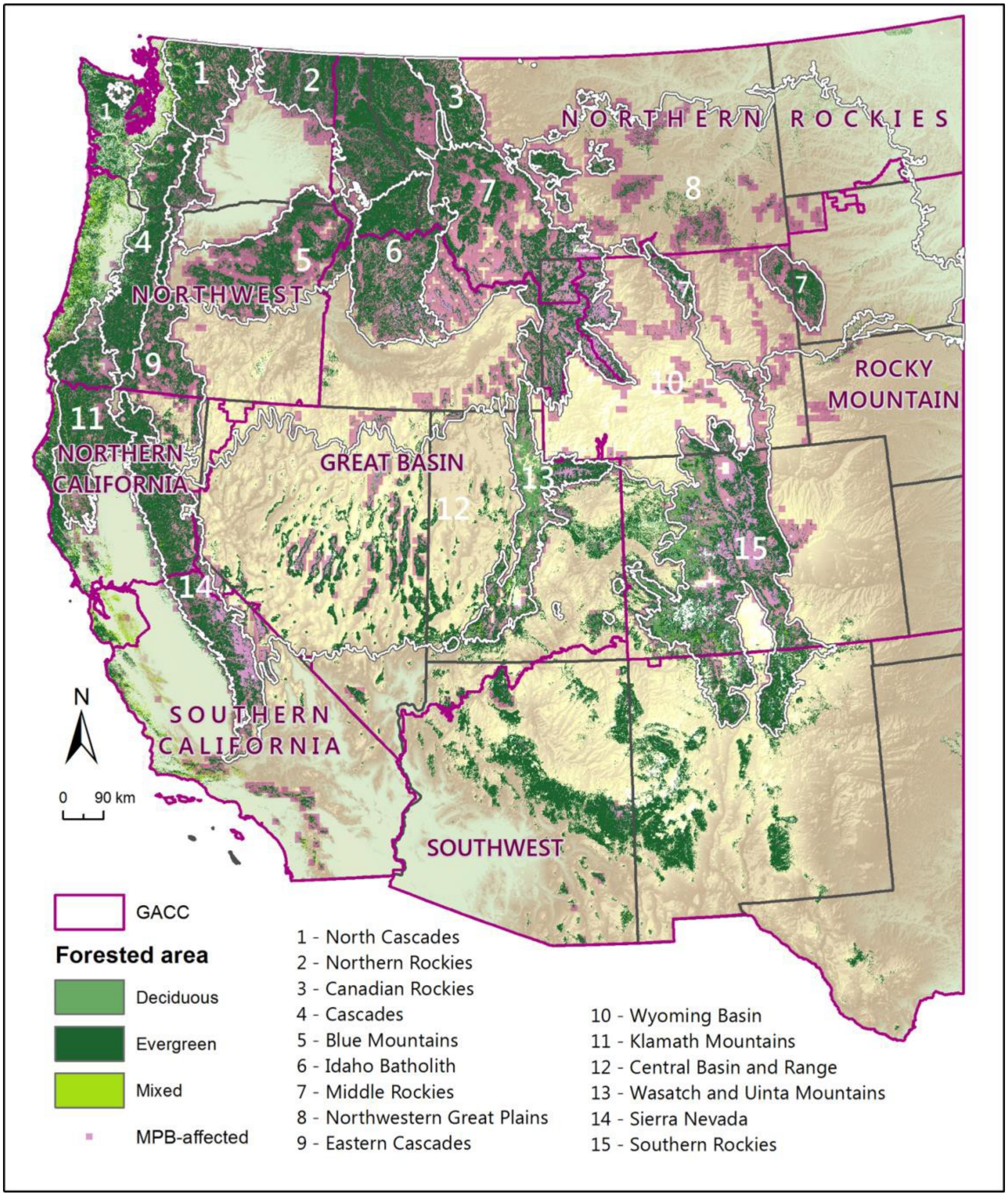


Figure IV-1. Study area with the boundaries of ecoregions, geographic area coordination centers (GACC) and states. The resolutions of elevation and land cover are both 30 meters. The MPB-affected regions are on a 10km grid. The white line shows the boundaries of ecoregions and the dark greyline shows the boundaries of states.

spatial patterns and ecological outcomes of fire suppression (Miguet et al., 2016; Wheatley and Johnson, 2009). We included the boundary of Geographic Area Coordination Centers (GACC) and Level 3 Ecoregions to present the spatial pattern of fire suppression. The MPB outbreaks are measured as acreage experiencing tree mortality. The study area was limited to areas experiencing at least some MPB outbreak.

2.2. Data preparation

We utilized Climate Research Unit (CRU) 10-minute climatology 2.0 (New et al., 2002), 0.5-degree time series 4.01(Harris et al., 2014), and 1-km grid Daymet Daily Surface Weather Data (Thornton et al., 2017) to generate climate data and then calculated the critical bioclimatic variables on a 10km grid using a topographically-adjusted bilinear interpolation method (Praskievicz & Bartlein 2014). The detailed steps in the interpolation of climate data were addressed in our previous work (see Chapter II). We gathered the MPB data from the Insect and Disease Detection Survey (IDS) maps of the United States Forest Service (USFS). The annual average of beetle affected acres from 1997 to 2016 was calculated on the 10km grid using available data and served as the response variable in the statistical analysis. For the forest stand variables (Table IV-1),we aggregated Forest Inventory and Analysis (FIA) data collected from the forest plots in the western 17 states from USFS (FIA, 2019), stand age data (Pan et al., 2011) and tree density data (Crowther et al., 2015; Glick et al., 2016).

To directly and indirectly estimate the management of fires, we first gathered fire containment cost information from 1999 and 2016 in the Situation Report (SIT) – 209 Application on the National Fire and Aviation Management Website (NWCG, 2019). Key information from SIT209 includes fire identification, coordinates, containment costs and containment acres. We also combined the corrected coordinates from the Fire Program Analysis Fire-Occurrence Database (FPA-FOD) (Short, 2017) with SIT209 using unique fire identification numbers. The Federal Wildland Fire Occurrence Data was used to identify naturally caused fires that were managed during 1980 and 2016 using the fire type and fire cause information. We downloaded the LANDFIRE fire regime data (LANDFIRE, 2019) including mean fire return interval, vegetation condition class, percent of replacement severity, percent of mixed severity, and percent of low severity fires and downscaled the source data from 30m by resampling at 10km and labeling cells according to the majority class. We also used the Protected Areas Database of the United States (PAD-US) Data from the National GAP Analysis Project (GAP, 2019) to identify protected forests with different management strategies. Data sources, details and usages are provided in Appendix Table IV-1.

2.3. Variable selection

In Chapter II, we calculated 62 bioclimatic variables annually; here we use the mean from 1996 to 2015 of the same variables. To reduce the number of variables, we first screened bioclimatic variables by removing the variables that are less distinguishable between MPB outbreak presence or absence (e.g., number of days with summer temperatures > 40 °C is zero in both) (see Chapter II), or whose significance in contributing to the prediction in our previous model was minimal (e.g., the coefficient ranks in the lowest among z-scored predictors in the model) (see Chapter III). The remaining list of bioclimatic variables included in this study is listed in Appendix Table IV-2, and the maps of these variables are shown in Appendix Figure IV-1. Furthermore, we used four categories of variables, which all are expected to reflect effects of fire suppression on stand structure or are related to jurisdictions that have different histories of logging and fire suppression. The four categories include: (1) recent fire suppression (variables quantifying the effectiveness of fire control), (2) forest stand and (3) fire regime (metrics for long-term fire control), and (4) forest protection (related to land use and fire management). The first factor is a direct assessment while the last three factors are indirect evaluation of fire control. The detailed justification, descriptions and computation of fire-suppression variables are listed in Table IV-1, and additional steps in variable selection are addressed in the statistical analysis section.

More specifically, variables representing recent fire suppression included: unit fire suppression costs (computed from suppression costs and acres and both are also listed in Table IV-1), containment duration (the duration of fire control activities), and fire-out duration (the duration of burning), number of fires suppressed, percentage of suppressed fires, and mean fire size of suppressed fires. We computed the percentage of trees that are older than 80 years and percentage of trees that are larger than 12 inches in diameter, both of which are more susceptible to MPB attacks (Gibson et al., 2009). Variables measured by percentage (or noted as ratio) range from 0 to 1, with 0.5 indicating 50%. Forest stand age (i.e., time since the last stand-replacing fire) is generally considered to reflect disturbance history (Kulakowski et al., 2012), and old forest stands are less likely to have experienced major disturbances recently. Denser forests were often a result of long-term fire control (Keeling et al., 2006), and thus, tree density was also included to examine the potential influence from fire suppression on forests.

Variables that are related to the long-term influence of fire suppression on fire regimes and thus vegetation dynamics (Miller et al., 2009; Steel et al., 2015) include: vegetation condition class (VCC), mean fire return interval (MFRI), and fire severity (including percent of low-severity fire, percent of mixed severity fire and percent of replacement-severity fire). These are all categorical variables ranging from low to high. To link the recent fire management with the potential long-term effects of fire suppression, we compared beetle-affected acres and recent fire suppression variables among vegetation condition classes to examine the possible patterns between these variables and vegetation departure. Forest protection status is also related to the suppression of disturbances, for which GAP status 1 indicates disturbances are allowed to proceed, whereas statuses 2 ("disturbance events suppressed") and 3 ("subject to extractive or OHV use") indicate disturbances are more prone to be suppressed.

Finally, the spatial coverage of these fire suppression variables varies due to data availability, which further determines variable selection methods in the statistical analysis section. We calculated the sample size of these variables within MPB-affected areas. The number of grid cells with missing data was used to categorize the variables as having larger or smaller samples, with 8% missing being the threshold, as we considered stand age to be indispensable.

Table IV-1. Description of fire suppression variables.

Factor	Variable name	Data type	Unit	% NA grid cells*	Model	Variable included in GWR
recent fire suppression	suppression costs	continuous	dollar	74.5	n.a.	*a, b*
	suppression acres	continuous	acre	74.5	n.a.	*a, b*
	unit suppression costs	continuous	dollar/acre	74.5	n.a.	*a, c*
	containment duration	continuous	day	59.3	n.a.	*a, c*
	fire out duration	continuous	day	47.2	1	*a, c*
	number of fires suppressed	continuous	fire	47.0	1	*a*
	ratio of suppressed fires	ratio	n.a.	47.0	1	*a*
	fire size of suppressed fires	continuous	acre	47.0	1	*a*
forest stand	ratio of old trees	ratio	n.a.	13.4	1, 2	*a*
	ratio of large trees	ratio	n.a.	8.6	2	*a*
	stand age	continuous	year	8.0	2, 3	mStdAge
	tree density	continuous	trees/acre	0.6	1, 2, 3	density
fire regime	vegetation condition class	ordinal	percent	7.3	2, 3	vcc
	mean fire return interval	ordinal	year	3.4	2, 3	mfri
	percent of low-severity fires	ordinal	percent	3.1	2	*d*
	percent of mixed-severity fires	ordinal	percent	3.0	2	*d*
	percent of replacement-severity fires	ordinal	percent	3.0	1, 2, 3	prs
forest protection	disturbance events allowed	binary	n.a.	0.0	1, 2, 3	GAP1
	disturbance events suppressed	binary	n.a.	0.0	n.a.	*d*
	subject to human activities	binary	n.a.	0.0	2, 3	GAP3

Table IV-1 (continued)

Description (computation of variables on the 10km grid)
the median value of total containment costs from the recorded fires occurred within the 10 km grid
the median value of total containment acres from the recorded fires occurred within the 10 km grid
the median value of unit containment costs calculated from dividing containment costs by acres
the duration in days from the discovery date to the date when the fire was controlled, and the median value is summarized
the duration in days from the discovery date to the date when the fire was declared out and the median value is summarized
summary of number of naturally caused fires in which the appropriate fire management response was taken
the percent of managed fires in the total number of naturally caused fires during 1980 and 2016
mean fire size of the managed naturally-caused fires
number of trees older than 80 years divided by the total number of trees by plot and the median value is summarized
number of trees larger than 12 inches divided by the total number of trees by plot and the median value is summarized
mean forest stand age on a 10km grid extracted from points at 1 km resolution and adjusted by the forest inventory data
mean tree density on a 10km grid extracted from points at 1 km resolution
the majority of vegetation condition class at 30 km resolution is summarized
the majority of mean fire return inverval at 30 km resolution is summarized
the majority of percent of low-severity fires at 30 km resolution is summarized
the majority of percent of mixed-severity fires at 30 km resolution is summarized
the majority of percent of replacement-severity fires at 30 km resolution is summarized
the boundary of GAP status 1 indicating that disturbance events are allowed intersects with the 10 km grid
the boundary of GAP status 2 indicating that disturbance events are suppressed intersects with the 10 km grid
the boundary of GAP status 3 indicating regions subject to extractive or OHV use intersects with the 10 km grid

Table IV-1 (continued)

Rationale	Dataset
containment costs indicate the amount of resources invested in fire extinguishment	SIT-209
containment acres reflect the size of fires and the effectiveness of fire suppression	SIT-209
the resources per acre invested to contain fires	SIT-209
containment duration reflects fire size and the effectiveness of fire suppression	FW FOD
fire out duration reflects fire size and the effectiveness of fire suppression	FW FOD
number of natural fires suppressed reflect fire and fire suppression frequency	FW FOD
percent of suppressed fires reflect fire suppression strength and fire frequency	FW FOD
fire size of the suppressed fires indicates fire frequency and the effectiveness of fire suppression	FW FOD
older trees are likely larger and resulted from absence of fires	FIA
mountain pine beetle prefers large host trees which more likely live with high frequency and low intensity fires	FIA
forest stand age is connected with the disturbance history, e.g. replacement fires initialize secondary succession	FSA, FIA
the consequence of fire exclusion is often associated with denser forests	GST
fire suppression and other human activities influence vegetation condition class which categorizes vegetation departure	LF-VCC
mean fire return interval is prolonged because of fire control	LF-MFRI
the increase of percent of low-severity fires increases the frequency of fire suppression	LF-PLS
different levels of fire frequency and intensity may subject to different impacts of fire suppression	LF-PMS
the increase of percent of replacement-severity fires increases the difficulty of fire suppression	LF-PRS
fire control is lessened in the GAP status 1 regions	PAD-US
fire control is strengthened in the GAP status 2 regions	PAD-US
fire control is strengthened in the GAP status 3 regions	PAD-US

2.4. Statistical analysis

Due to the large number of variables and the heterogeneity in their range and spatial coverage, we used a three-step process (1-3) to develop our models. A model with a better fit is preferred. (1) The first step was to use generalized additive models (GAM) to infer transformations that best captured the nonlinear relationships between predictors and the response. (2) The second step was to use a bootstrapped linear regression to remove the unstable variables in the visualization of beetle-fire-suppression relationship from predictive models in the third step. (3) The third step was linear regression with stepwise reduction to predict beetle-affected acres. K-folds cross-validation (with k=5) was employed to fit the model in the third step to avoid overfitting and the Akaike information criterion (AIC) was the model selection criterion. (4) The selected models from the third step were used to visualize the relationship between fire suppression and MPB infestations and to interpret the relative importance of fire suppression variables in the prediction. (5) We then used the final fitted model with the largest spatial coverage in a geographically weighted regression (GWR) model (Brunsdon et al., 1996; Fotheringham et al., 2002) to identify the local significance of climatic and non-climatic contributions to the MPB predictions. Finally, we organized the GWR results in a k-means cluster analysis to map the regions where climatic variables were more influential to MPB outbreaks. We elaborate on each of these steps below.

(IV) *Using GAM to Estimate Nonlinear Transformations—*

In this step, we began with a full model that included nonparametric smooths of each of the variables. We applied a stepwise removal of variables in an iterative process, using the generalized cross-validation value to determine goodness of fit. We plotted the predictors in the final GAM with the response variable to detect the nonlinearity. To reduce the complexity of the model, we approximated the GAM fits using linear, quadratic, logarithmic or exponential transformations. The same transformation terms for each variable were used for subsequent modeling. In the linear models below, appropriate normalization of the response variable for a better fit was also applied by conducting the Tukey's Ladder of Powers (Mangiafico, 2016).

(2) Bootstrapped Regression to Remove Unstable Variables—

This is a step to examine the robustness of datasets. We started with all data in the fire suppression variable categories (Table IV-1). The sample size of the model was initially constrained to the variable with the smallest spatial extent: ‘unit fire suppression costs’ (data missing in 74.5% of MPB-affected grid cells). The coefficients of variables were assessed using bootstrapped regression with 1,000 resampling iterations (with replacement) to determine their significance, by examining whether a coefficient of 0 occurred in the 95% bootstrap confidence interval. If all of the variables in the same dataset were detected as insignificant, the dataset was removed; otherwise, the entire dataset was used in the next step. The removed variables in this step were not shown in the response curves (addressed below).

(3) Stepwise Model Reduction Using Cross-validation—

The insignificance of suppression costs led to the removal of SIT-209 in this step. The rest datasets in Table IV-1 are with variables retained from bootstrapped regression. However, as several of these variables were missing large amounts of data (e.g., data missing in 47% of MPB-affected grid cells), in order to maximize the use of available data, we ran multiple models retaining different subsets of the final variables. Model 1 started with all variables in the retained datasets in the full model; Model 2 started with the removal of variables in FW FOD from Model 1; and Model 3 started with the removal of variables in FIA from Model 2. Each of these models was then reduced using cross-validation and stepwise reduction based on AIC, built in the R package “caret” (Max et al., 2019). The predictors in each of these models were also converted to z-scores to enable direct comparison of the coefficients. These selected models and their differences in data usage are shown in Appendix Table IV-3.

(4) Visualization and Model Interpretation—

Each model fitting process in (2) and (3) initially included all possible predictors and samples in a multiple linear model, but only the variables that were not excluded from bootstrap or stepwise regression were presented in a response plot to show the partial effects of fire suppression factors on beetle outbreaks. To visualize the effects of each variable on the response, we plotted the predicted values over the middle 95% of the range of each predictor's values while holding all other variables constant at their median values. We refer to these plots as the "response curves", which portray the collective effect of all terms including the given predictor on the predicted response. We interpreted the response curves with a consideration of correlation between predictors and using the z-scored rank and p values in Appendix Table IV-3 as a reference.

(5) GWR and K-Means Clustering to Assess Local Effects—

Model 3 (z-scored) covered with the largest spatial extent among the three models was used in GWR to examine the significant contributors of beetle affected acres locally using the same model. A fixed bandwidth was determined by cross-validation, using the value that minimized the root mean square prediction error (Bivand, 2017). We mapped the coefficients from GWR, the calculated p values and adjusted p values using the Bonferroni correction method (Byrne et al., 2009). To approximately map out the regions with more (or less) influence from climatic factors, we employed a k-means clustering method (Hartigan and Wong, 1979; Lloyd, 1982) on the GWR coefficients. We began with the elbow method to determine a reasonable range for the number of clusters and then used the silhouette method (Rousseeuw, 1987) to identify the optimal number of clusters. Two clusters were selected from the process to reduce the uncertainties of clustering. Boxplots were used to compare the coefficients between clusters. Interpreting the signs of GWR coefficients in each climatic variable within clusters, however, need to combine with other correlated variables or infer from Model 3 on a global model with consideration that a smaller *p* value indicates the 'real' relationship between the correlated climatic variables with MPB outbreaks. We also summarized the characteristics of the two clusters using maps of fire suppression and MPB data and boxplots of GWR coefficients. Results were selectively shown in the maps and boxplots of GWR coefficients due to the article length limit, and the complete results were shown and explained in Appendix figures. The selected variables are representative and ecologically important.

3. Results

3.1. Regional patterns of beetle-affected acres and fire suppression

During the past two decades, the tree mortality acreage caused by MPB outbreaks in the western US has been greater in the Idaho Batholith, Middle Rockies and Southern Rockies ecoregions, particularly in the higher-elevation regions, than in most areas of the Cascades and Sierra Nevada (Appendix Figure IV-2). The most severely affected regions in the middle and southern Rockies are associated with relatively higher forest stand age and percentage of old trees, and relatively less continuous high tree density and percentage of large trees (Appendix Figure IV-3), whereas forests in the northern Rockies, Cascades, Klamath Mountains, and the northern Sierra Nevada have higher tree density. More large trees are clustered in the Sierra Nevada, northeastern Blue Mountains, and southern Idaho Batholith, where MPB-affected acreage is relatively smaller.

Within the MPB-affected regions, the spatial pattern of fire suppression costs is more clustered in northern Rockies, Northwest, and California GACC (Appendix Figure IV-4), although high fire suppression costs, fire size of suppressed fires, and containment duration can be found in most of the study area with fewer grid cells. A cluster of grid cells with lower fire suppression, fewer number and ratio of fires suppressed, and longer fire-out duration without containment duration is found in Idaho Batholith. Higher number and percentage of fires suppressed are predominantly located in lower-elevation regions (e.g., western northern Rockies, northwestern Great Plains, and northern Klamath Mountains), where MPB-affected acreage is relatively smaller. By comparing with stand age and percentage of old trees, these variables show that recent fire suppression corresponds less with the spatial patterns of MPB-caused tree mortality.

Higher vegetation departure (> 50%) largely occurred in the eastern Cascades slopes and foothills, Wasatch and Uinta Mountains, southern Rockies, and parts of middle Rockies (Appendix Figure IV-5). These regions are associated with more frequent and smaller fires in the recently controlled fires (Figure IV-2). Very low vegetation departure (< 17%) occurred in the regions with less frequent but larger fires. Approximately 43.3% of MPB-affected regions experienced mid-level (34-50%) vegetation departure. The total and unit suppression costs are higher in the vegetation condition classes in which MPB-affected acres are also higher. Among different VCC, the average stand age, tree density and ratio of old trees are similar, although the recent fire control is different.

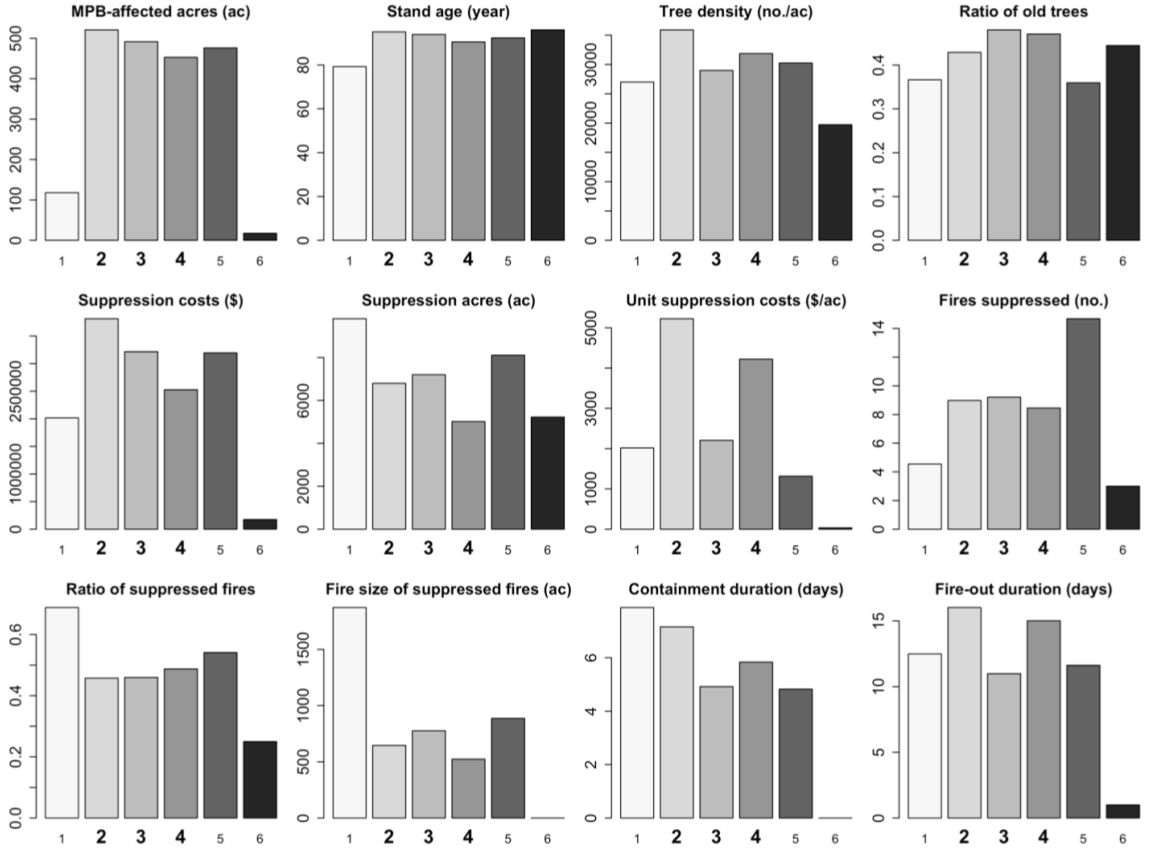


Figure IV-2. The average values of fire-suppression variables (y-axis and title) within areas of MPB-affected forests by grid cells, across six levels of vegetation condition class (x-axis).The six levels of vegetation-departure condition class range from very low (1) to very high (6) in greyscale. The percentage of the vegetation-departure condition class affected by MPB are 6.6, 28.8, 43.3,15.3, 5.8, and 0.1 for condition classes 1 to 6, respectively. Those condition classes most affected by MPB (class 2, 3, and 4) are marked in a bold in the x-axis labels.

The majority of grid cells with beetle infestations are in a mixed-severity fire regime. Mixed-severity fires with a wide range of MFRI characterize the dominant fire regime in the northern and southern Rockies and Cascades. Replacement-severity fires with a

MFRI longer than 150 years are prevalent in the middle Rockies in Wyoming, while low-severity fires are more frequent in the Sierras, eastern Cascades, Blue Mountains, and parts of the northern Rockies and Black Hills where the MFRI is less than 50 years (Appendix Figure IV-5). The clusters of high MPB-severity area can be found in areas with either fire regime.

3.2. Relationships between fire suppression variables and beetle-affected acres

Model 1 revealed that the number of fires suppressed has a positive response and the ratio of suppressed fires and the mean fire size of suppressed fires have a negative response to MPB-affected acres (Figure IV-3; Appendix Table IV-3). Forests with a higher percentage of large trees were less infested by MPB, while the positive relationship between the percentage of old trees and MPB-affected acres is not significant in Model 2. However, a significant positive relationship exists between the predicted MPB-affected acres with stand age, tree density and vegetation condition class respectively in Model 3. The positively correlated mean fire return interval and percent of replacement-severity fires has the opposite trends with the response variable in Model 3, while the latter predictor has a smaller p value and a higher rank in the z-scored order, which suggests a quadratic-like relationship between fire severity and the predicted MPB-affected acres. Mixed-severity fires are associated with higher MPB predictions, while increasing or decreasing a certain percent of replacement-severity fires reduces the predicted value. Lastly, increased MPB-affected acres are predicted with the absence of GAP 1 status (disturbance events are allowed) and the presence of GAP 3 (subject to human activities).

3.3. Spatially-varied influences of bioclimatic and non-climatic factors on beetle outbreaks

Although bioclimatic variables commonly have higher coefficients than non-climatic variables in the z-scored multivariate models (Appendix Table IV-3; adjusted R squared ranges from 0.50 to 0.52), the significance of bioclimatic variables is consistently

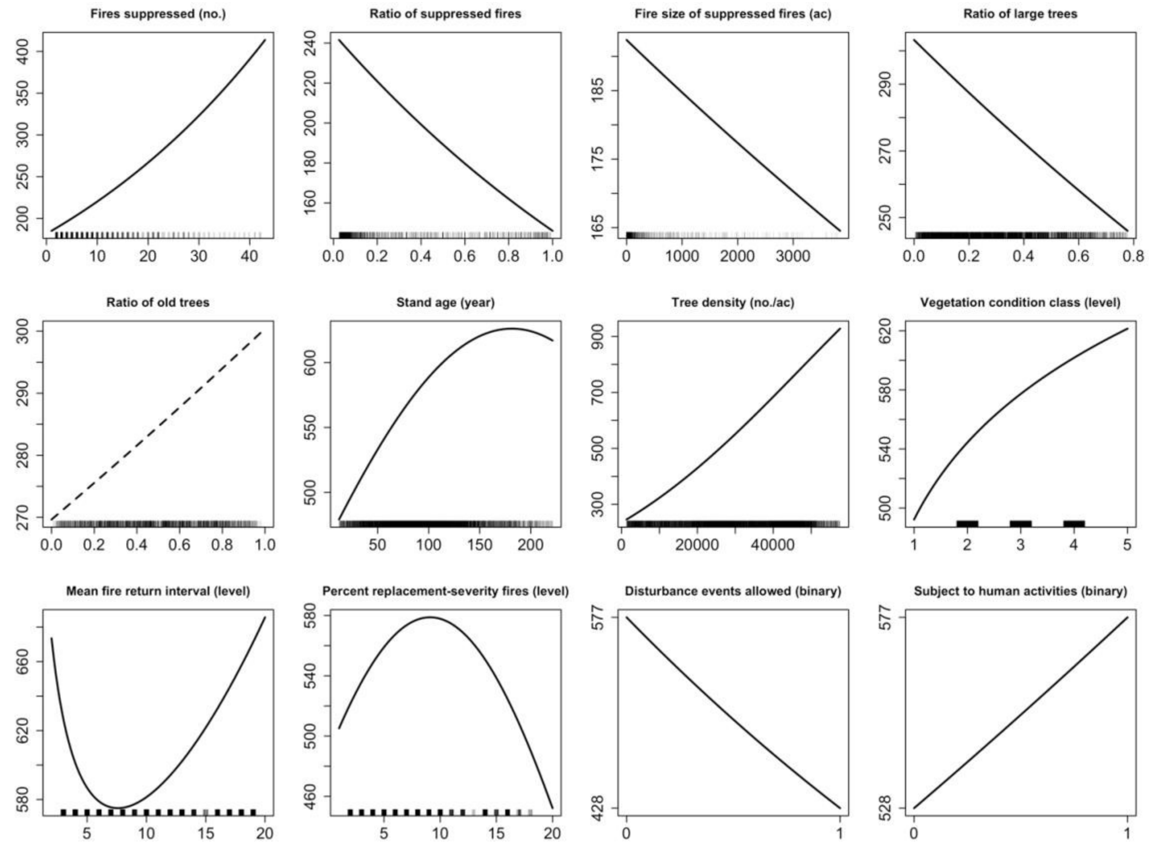


Figure IV-3. Partial effect of fire suppression variables (x-axis and title) on the predicted MPB-affected acres (y-axis).The x axis shows the continuous values of each predictor within the 95% quantiles, while the y axis shows the predicted beetle affected acres from models with a setting of median values for all other predictors. The rug shows the data distribution of fire suppression variables. A dashed line indicates that the relationship is not significant in a multivariate model. Due to the varying spatial coverages of the fire suppression variables, three models were applied. The variables, ‘fires suppressed (no.)’, ‘ratio of suppressed fires’, and ‘fire size of suppressed fires (ac)’, are from model 1. The variables, ‘ratio of large trees’ and ‘ratio of old trees’, are from model 2. The rest variables are from model 3. Detailed results of the model coefficients are listed in Appendix Table IV-3.

missing in a large part of the Rockies, as indicated by the coefficients and p values from the GWR results (Figure IV-4, Appendix Figures IV-6-7; quasi-global R squared is 0.81). The widespread MPB-affected regions were not significantly predicted using bioclimatic variables suggested by adjusted p values at a local level (Appendix Figures IV-8). In contrast, variables related to topography, forest stands, and land use management have significant coefficients in larger clustered areas, particularly in the Rockies. The coefficients of elevation and tree density are both globally and locally positive, and significant p values are shown in the central and southern Rockies (Figure IV-4). We also found negative coefficients of GAP status 1 in the northern Rockies, and positive coefficients of GAP status 3 with significant adjusted p values in Wasatch and Uinta Mountains. Mean temperature during the MPB life cycle is positively correlated with the beetle-affected acres in some higher-elevation areas of the Rockies, in the Sierras and Black Hills, however, the relationship is not significant. Strong negative influences of temperature and positive influences of precipitation occurred in a very small area of the Rockies and Sierras.

The two k-means-identified clusters (Figure IV-5) show a strong cluster in most of the Rockies regions, the northern Cascades and the Sierras (Cluster 1) and a weak cluster in Klamath and Blue Mountains and the middle and southern Rockies (Cluster 2). By comparing the boxplots of coefficients among clusters, we found that Cluster 1, with median values of the coefficients within the cluster are close to zeros, is less influenced by climatic variables than Cluster 2, in which the interquartile range of climatic coefficients mostly stay outside of zeros (Figure IV-6). The GWR coefficients of elevation, stand age and tree density are mostly positive, while negative coefficients in GAP 1 (disturbance events allowed) are mostly negative in both clusters. Different from non-climatic factors, climatic factors are less consistent in the medians and signs of coefficients between the two clusters. Distinct patterns of fire regimes and the recent fire controls in each cluster are missing (Table IV-2). Although the three different fire regimes (low-, mixed-, and replacement-severity) existed in both clusters, northern Idaho Batholith, where lower fire suppression costs, longer fire out duration and less fires suppressed occurred, was included in Cluster 2.

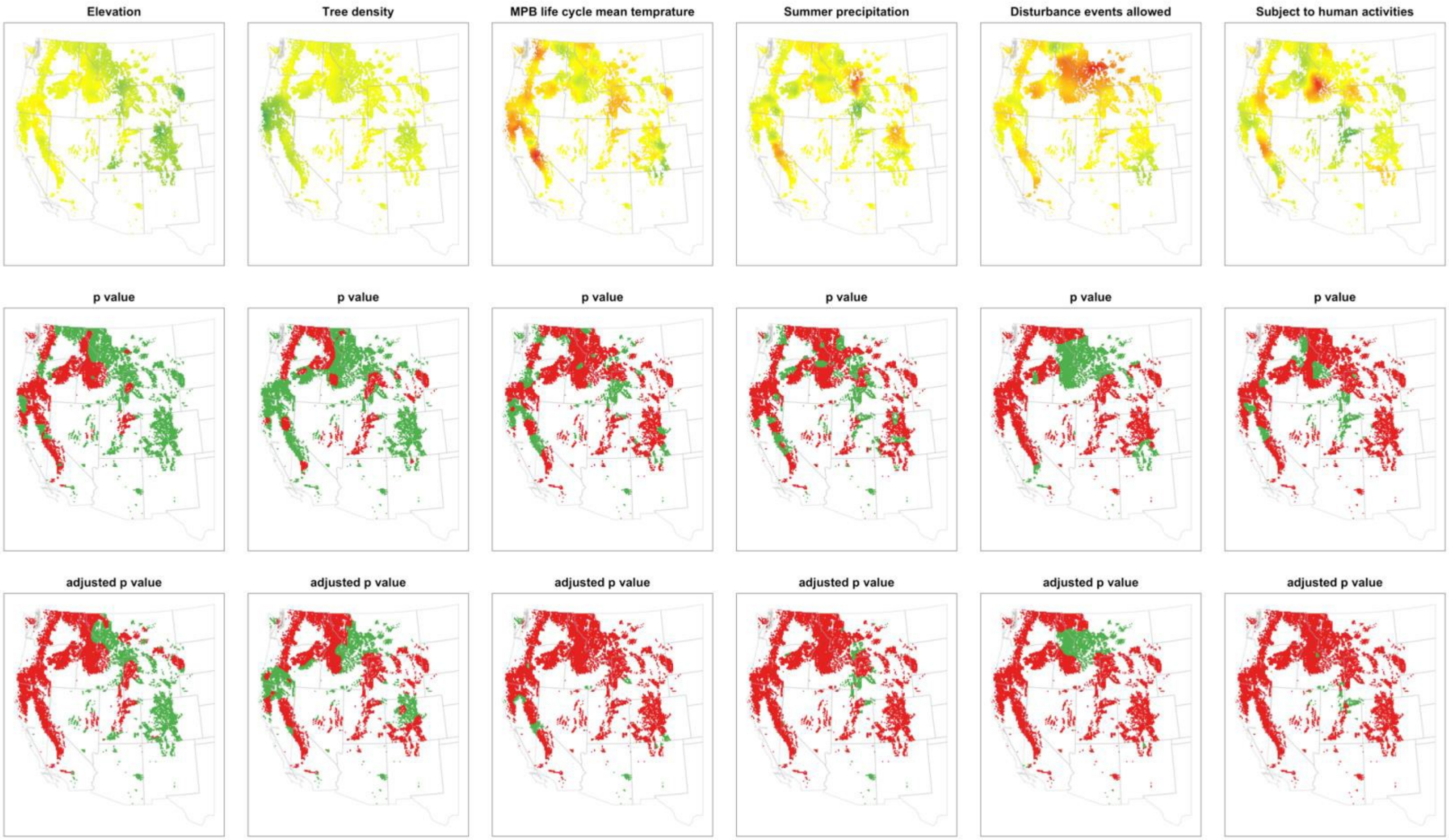


Figure IV-4. Geographically weighted regression coefficients, p values and adjusted p values from the selected variables. Each column shows information for the same variable. The first row shows the GWR coefficients from negative to positive colored with the gradient from red to green, with the yellow color indicating the midpoint zero. The second row shows the unadjusted p values of each variable and the last row shows the respective adjusted p values using the Bonferroni correction method. Significant p values are shown as green, while insignificant p values are shown as red.

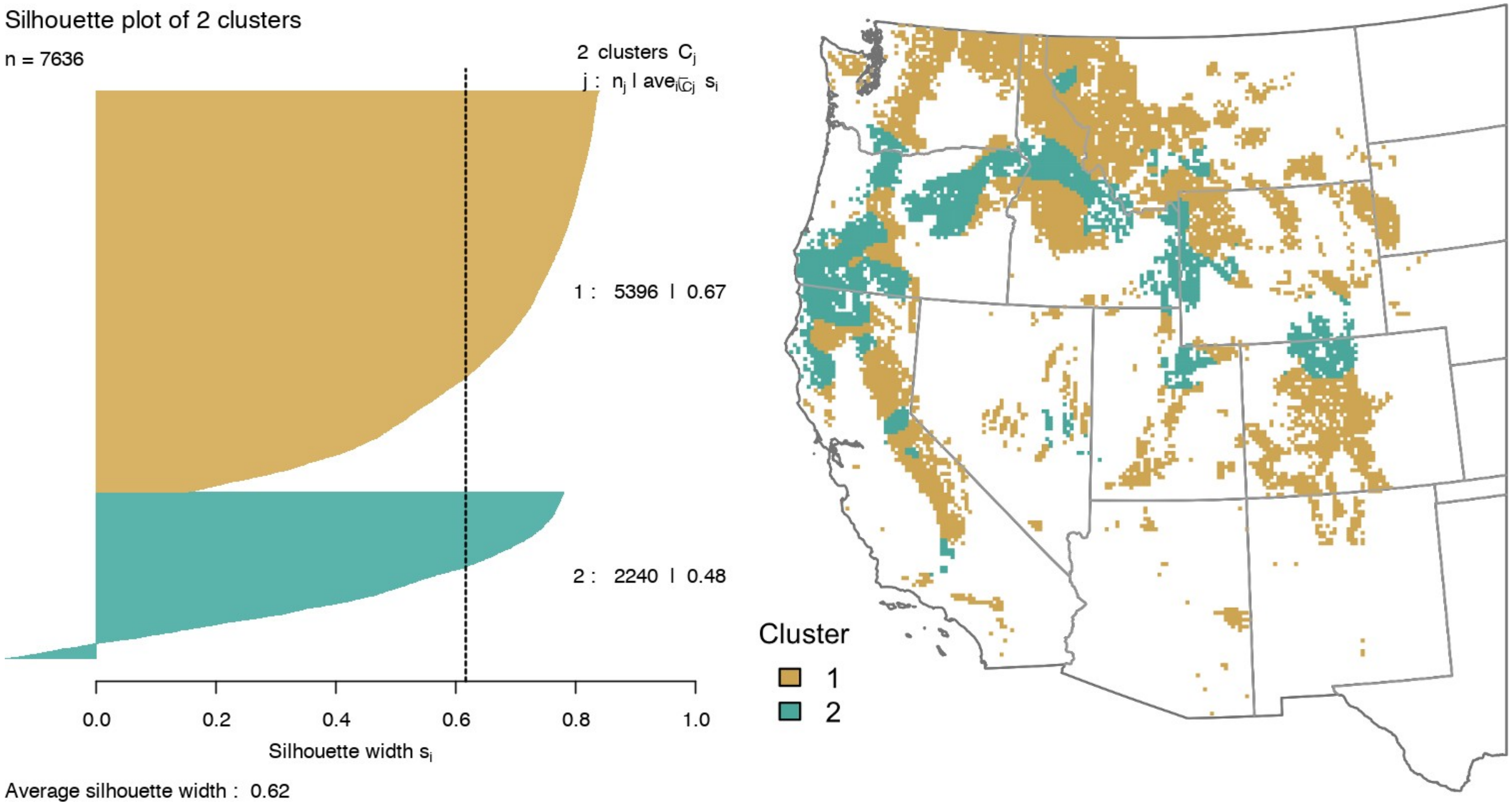


Figure IV-5. Map of the two clusters from GWR coefficients (right) according to a silhouette plot (left).Cluster 1 shows a strong clustering and less climatic influence with median values of climatic coefficients close to zeros within the cluster, while cluster 2 shows a weak clustering and more climatic influence with the interquartile range of climatic coefficients mostly stay outside of zeros within the cluster. The comparisons of GWR coefficients between the two clusters are selectively shown in Figure IV-6 and completely shown in Appendix Figure IV-9.

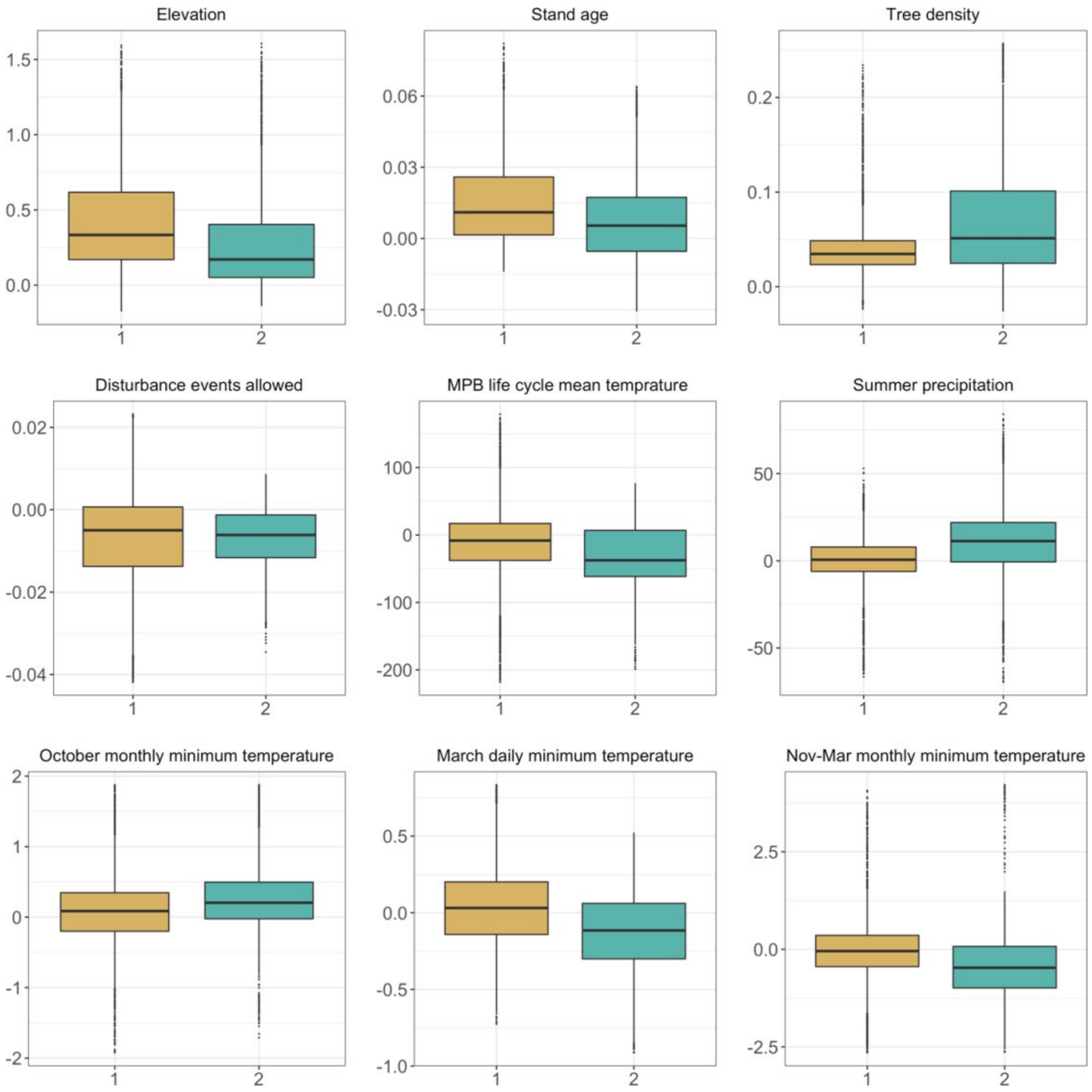


Figure IV-6. Boxplots of the GWR coefficients (y-axis) from the selected variables in the two clusters (x-axis).The predictors are z-scored in the GWR model and thus the coefficients are also comparable between variables. Boxplots of the GWR coefficients from all the other variables are shown in Appendix Figure IV-9.

Table IV-2. Summary of the clusters among the geographically weighted regression coefficients of the selected variables.

Comparisons	Cluster 1	Cluster 2
Geographical areas	northern Cascades, most of the Rockies and Sierras	parts of Klamath and Blue Mountains, middle and southern Rockies
Spatial coverage	larger	smaller
Elevation	relatively higher	relatively lower
Climatic influence	weaker	stronger
Clustering	stronger	weaker
Fire regimes	mostly mixed-severity fires; frequent low-severity fires in Black Hills; rare replacement-severity fires in northern Rockies	frequent low-severity fires in Klamath Mountains; rare replacement-severity fires in middle Rockies in Wyoming; mixed severity fires in Blue Mountains and southern Rockies
Fire suppression	many areas with a high ratio of fires suppressed and higher fire suppression costs; some areas with a longer fire out duration in northern and middle Rockies	lower fire suppression costs, longer fire out duration and less fires suppressed in northern Idaho Batholith; high ratio of fires suppressed in Klamath Mountains
Low MPB-severity areas	northern Rockies and northwestern Great Plains	Klamath and Blue Mountains
High MPB-severity areas	the Rockies and southern Sierras	middle and southern Rockies

4. Discussion

4.1. Fire-beetle interactions, fire suppression and their influences on beetle outbreaks

The two significant forest disturbances fires and insect outbreaks in the American West interact through modifying the susceptibility of vegetation to one another with changes in the amount, diversity and compositions of trees. Our evaluation of the defined fire suppression variables supports the argument of a positive feedback from long-term fire suppression to beetle outbreaks. Fires can have both positive and negative feedbacks on the subsequent insect outbreaks, in which fires can directly incinerate insects or predispose trees to beetle attacks. In the short-term, beetle outbreaks can increase in the recently-burned area if there is a sufficient amount of fire-damaged trees and beetle population size, and a matched timing (Gibson and Negrón, 2009). In the long-term, however, host species that have adapted to different fire severities have developed their own defense strategies to beetle attacks. For example, ponderosa pines living in a fire-prone environment are more resistant to beetle outbreaks than lodgepole pines with thin bark after low-severity fires (Hood et al., 2015; Kulakowski and Jarvis, 2013), on the contrary, stand-replacing fires reduce susceptibility of lodgepole pines to beetle outbreaks by regenerating less-susceptible young stands (Kulakowski et al., 2012). Therefore, a long-term absence of fires in both ecosystems is expected to affect tree defense to MPB outbreaks.

Fire control can also interrupt fire-beetle interactions by restraining the combustion of trees and promoting overmatured forests. We evaluated fire control from fire ignitions and spread, fire regimes, and forest succession after fire exclusion. The estimation of fire suppression effectiveness (i.e., success of containment), particularly in the control of large fires, is challenging because of its complex relationships with the fire environment (e.g., fire weather, fire spread and intensity) and human decision-making in that environment. It was positively connected with a longer period of low fire spread, more number of previous spread intervals, fewer timber fuel types, and perhaps less constraints on firefighting resources (Finney et al., 2009). Although fire size was not a significant predictor of the successful containment of large fires (Finney et al., 2009), it tracked well with fire suppression expenditures (Calkin et al., 2005; Liang et al., 2008) and the majority of fires were contained before they grew to a large size (Calkin et al., 2005). As such, we consider fire suppression costs better capture the effective suppression of small and frequent fires than the containment of large fires. Similarly, fire suppression effectiveness very likely decreases with the increase of fire size, containment and fire-out duration.

In our study, fire suppression costs, containment duration and fire-out duration were considered insignificant as predictors of MPB outbreaks in our bootstrap regression process, although both higher average suppression costs, lower containment duration and MPB-affected acres per grid cell were found in the regions with a mid-level vegetation departure. Considering the positive correlation between number of fires suppressed and MPB-affected acres from our model, and that there were similar geographic patterns for lightning-caused fires between early and contemporary fire suppression (Collins et al., 2019), we speculate that the recent management activities on frequent fires is a continuation of historical fire control and rendered forests more susceptible to beetle infestations. The increased fire size of suppressed fires, positively correlated with the potential fire behavior risk and fire suppression difficulty (Rodríguez y Silva et al., 2014) and thus linked with lower fire suppression effectiveness, was predicted to reduce MPB-affected acres. This corresponded with lower number of fires suppressed and longer containment duration in the regions with a very-low level vegetation departure. It is also unsurprising that larger recently burned area with more trees fire-consumed would have reduced host availability to support MPB outbreaks.

A significantly positive correlation between MPB-caused tree mortality and stand age, tree density and vegetation condition class suggested that the increased beetle outbreaks can be a consequence of the long-term fire control. This judgement came from multiple lines of evidence of denser coniferous forests, changed age structure, and other vegetation departures resulting from fire exclusion in the western United States: e.g., the Cascades (Taylor, 2010), the Sierra Nevada (B. M. Collins et al., 2011), and the Rocky Mountains

(Gallant et al., 2003; Keeling et al., 2006; Naficy et al., 2010). The vegetation dynamics eventually shift fire regimes by prolonging the fire return interval and increasing fire size and severity (Bekker and Taylor, 2010; Everett et al., 2000; Miller et al., 2009). Meanwhile, fire-prone forests resulting from fire exclusion are more susceptible to beetle attacks. We found that prevalent areas with mixed-severity fires are subject to higher beetle infestations, which may be explained by the superimposed or compounding effects of suppressing low-severity and replacement-severity fires. However, increasing the percent of replacement-severity fires (> 50%) was suggested to decrease the predicted MPB outbreaks. This agrees with the hypothesis that young stands (< 100 – 150 years old) regenerated from stand-replacing fires are less susceptible to MPB outbreaks than older stands at a stand scale (Kulakowski et al., 2012). Although increased percent of replacement-severity fires often resulted from fire exclusion (Keane et al., 2002), some regions with high severity fires recurring at intervals longer than the period of active fire exclusion, particularly at higher altitudes, may have escaped the impacts of fire suppression (Cocke et al., 2005; Noss et al., 2006).

Forest protection strategies that allowed disturbances to proceed significantly reduced the MPB infestations, while the opposite trend occurred in the areas where intensive management is allowed. GAP status 1 regions where fires are allowed to burn commonly overlap with wilderness and roadless areas where forest management practices are much less intensive, which is also relevant to the historical forest management patterns (Bradley et al., 2016). On the other hand, GAP status 3 regions subject to intensive management activities such as timber harvest, non-commercial thinning, and grazing, were associated with lower fire probabilities (Starrs et al., 2018). Although the influences of different management activities on MPB outbreaks cannot be completely excluded, the positive correlation between GAP status 3 and MPB-affected acres more likely resulted from higher fire suppression effectiveness in the GAP status 3 regions, since other management practices often reduce forest density and thus increase the resistance of forests to beetle attacks (Negrón et al., 2017; Stark et al., 2013).

4.2. Relative contribution of climate change and forest management on beetle outbreaks

It is undeniable that climate change has a global-level effect on insect outbreaks (Logan and Powell, 2009; Pureswaran et al., 2018; Weed et al., 2013), primarily linked with the increasing environmental habitability for insect survival and reproduction from climatic warming, and partially connected with drought stressed host trees that became more vulnerable. We too found that bioclimatic variables, such as annual mean temperature and summer precipitation, generally have higher weights in the prediction of beetle outbreaks using a z-scored and unweighted model. However, in a locally-weighted model, the influences of non-climatic factors such as topography and forest management became more prominent in determining forest susceptibility to beetle infestations. We found that elevation, tree density and GAP status 1 are significant predictors of MPB-affected acres in the middle and southern Rockies ecoregions, while climatic factors are not locally significant. This finding is consistent with our previous research using mainly bioclimatic variables to predict beetle probability, in which scatter or clustered omission errors were shown in some peripheral areas of the current MPB range, including these ecoregions in the Rockies (see Chapter III). The clustering of less climatically-influenced regions is stronger than the clustering of more climatically-sensitive regions from a cluster analysis of GWR coefficients, implying that effects of climate change have been buffered or amplified by local biophysical conditions and/or anthropogenic activities (Raffa et al., 2008).

Influences of long-term fire suppression on the MPB outbreaks have also been discussed in previous research in Canada (Ono, 2004; Taylor et al., 2006; Taylor and Carroll, 2003) and are not exceptional in the American West. The unprecedented MPB outbreaks in Alberta was suggested to be an outcome of strong responses with sudden and unanticipated behavior to a small change in climate (Cooke and Carroll, 2017). This was supported by the clustered omission errors and low beetle probability in Alberta using bioclimatic predictors in our previous model (see Chapter III), and the finding of the current study that fire suppression related predictors are more locally-significant. Furthermore, human influences on forest fire activity have become widely recognized in the western United States (Balch et al., 2017; Harvey, 2016; Parisien et al., 2012; Parks et al., 2015). The anthropogenic footprint unavoidably affected other forest disturbances, including beetle outbreaks. Similarly, weak climatic association was found in the forest disturbances with strong influences from forest management (Starrs et al., 2018).

Finally, forest management became unpredictable and complex with rapid changes in the social and ecological dimensions of forest ecosystems (Messier et al., 2016), and adaptive forest management or natural-disturbance-based management was recommended considering its influences on forest disturbances (Drever et al., 2006). Nevertheless, the aggressive fire suppression may have altered some forests that have adapted to frequent and smaller fires and endemic beetle activity, to an alternative state that infrequent and larger fires coexist with intensified beetle outbreaks. This change may have persisted and eventually abruptly shifted the disturbance regime and reorganized the system structure, functions and feedbacks (i.e., a regime shift) in the secondary forest succession from fire-dominant to beetle-dominant. To exemplify, fire suppression interrupts the historic cycle of lodgepole pine renewal through stand-replacing fires, leading to the creation of multi-stories and multiple age cohorts initiated through repeated canopy thinning after various levels of MPB disturbance over time (Axelson et al., 2010, 2009).

4.3. Limitations of the study

The study explored spatial heterogeneity of fire suppression and its relationship with large-scale MPB outbreaks by mapping the defined variables and modeling the relationship globally and locally. To reveal the complexity of fire-insect interactions, we utilized multiple datasets with different spatial and temporal resolutions and data availability, defined cross-scale fire suppression variables, and integrated various statistical methods to examine the robustness of dataset, variables and models. However, two main caveats of the study should be taken into consideration. First, the models violate the assumption that predictors are completely independent, which risks the problem of inseparable effects of variables (Dormann et al., 2013). We incorporated ecological and statistical knowledge to work around the issue. Collinearity among bioclimatic and non-climatic variables was estimated in a correlation matrix and variation inflation factors, to understand collinearity and interpret the model coefficients by grouping of the correlated predictors. Climatic and non-climatic predictors were also selectively applied in simple linear models to examine variance explained and compare with the multiple linear models. With that, we found consistent results on the relative significance of variables in explaining MPB-affected acres on the global level. The primary use of models is to interpolate (i.e., predict new cases within the range of the sampled data), which limits the impact of collinearity (Dormann et al., 2013). We also computed geographically weighted local statistics to understand local covariances and correlations. Moreover, we tested Moran's *I* statistic for the GWR model, and the results ($I = -0.009$, $p = 0.154$) support the null hypothesis of randomness. To exclude the explanation that collinearity has caused locally-insignificant climatic effects, we also used relatively uncorrelated (absolute local correlation < 0.6) variables in GWR to compare the results and reached the same conclusion. Second, the cluster analysis results are sensitive to the fit of GWR model and limited to the current 'best' fit. The results are only to organize the GWR coefficients to show the approximate non-stationarity of climatic and non-climatic effects by combining all predictors and should not be interpreted as a static spatial pattern of local relationships.

5. Conclusions

Although climate change has provided a warmer and drier environment for MPB development at a landscape scale, in the long-term, fire suppression has played a more significant role than climate on MPB outbreaks at a local scale. Using multivariate linear models combined with generalized additive models and bootstrap regression, we evaluated the relationships between MPB-affected acres and four groups of fire suppression variables, that were defined and selected based on the recent fire management, the impacts of fire suppression on forests ecosystems and fire regimes, and forest management. We then applied a geographically weighted regression model to detect the significance of bioclimatic and non-climatic factors locally, followed by a cluster analysis on the GWR coefficients to differentiate which geographic regions are subject to more intensive non-climatic influences. We found a significantly positive relationship between MPB-affected acres and the number of fires suppressed, stand age, tree density, and vegetation condition class. The beetle-affected acreage did not increase or even start to decrease after stand age reached 150 years or the percent of replacement-severity fires was more than 50%. Furthermore, the regions that allow disturbance events have lower MPB-affected acres, while the regions that are subject to intensive management activities have higher MPB-affected acres. We concluded that the suppression of more frequent mix-severity fires had changed vegetation dynamics that eventually contributed to the increased MPB outbreaks by increasing the susceptibility of forests. However, the significance of fire suppression impacts is spatially varied and likely caused by different fire regimes and landscape characteristics. Significant topographic and anthropogenic influences on beetle outbreaks were found in the middle and southern Rockies from the GWR model, while climatic influences were tested not locally-significant in these regions. The strong clustering of less climatically-affected regions from GWR coefficients indicated that non-climatic influences are more locally prominent to MPB outbreaks. Finally, combined with our findings in Chapter III, we argue that human influences increased the nonlinearity and uncertainty of ecosystems and thus the likelihood of shifting disturbance regimes.

CHAPTER V CONCLUSIONS

1. Climate change, fire exclusion and the mountain pine beetle

Humans have been the dominant force in global environmental change in recent decades, since the beginning of Anthropocene-the age of humans or the human-dominated geological epoch-marks the period of 1610-1964 (Lewis and Maslin, 2015). The term "socio-ecological systems" (SES) defines the increasing human impacts on ecosystems, which have become coupled human and natural systems. Climate change has direct, indirect, and interactional effects on forest disturbances (Dale et al., 2001; Seidl et al., 2017), and human-caused climate change is a key driver in large-scale disturbance patterns (Harvey, 2016). Human activities, including fire suppression and ignition, logging, mining, and ex-urban development have been changing forest structure and compositions, and thus landscape disturbances (Balch et al., 2017; Calkin et al., 2015; Naficy et al., 2016). The exploration of human influences on SES is therefore important for natural resource management. As such, this dissertation presented a SES case study on the relative contributions of climate and human factors to the recent large-scale outbreak expansion of the mountain pine beetle in North America.

As the beetle expanded its outbreak range to colder areas, climate change was the primary focus on determining the drivers of MPB expansion in the literature (Bentz et al., 2016, 2010; Carroll et al., 2003; Cudmore et al., 2010; Safranyik et al., 2010; Sambaraju et al., 2012), and MPB-climate relationships are well documented (Aukema et al., 2008; Buotte et al., 2017, 2016; Chapman et al., 2012; Creeden et al., 2014; Fauria and Johnson, 2009; Preisler et al., 2012; Sambaraju et al., 2019; Thomson, 2009; Weed et al., 2015). However, limitations still exist in the understanding of the complexity of climate change effects on MPB eruptions, specifically in relation to the climate space of the continental-scale MPB outbreaks and the relative impacts of climate change versus human activities on the outbreak range expansion. To address the research gaps, the dissertation has 1) investigated MPB climate space, and its dynamics under climate change, to examine whether climate space has remained the same with the changes of geographical space; 2) reconstructed the MPB outbreak range expansion based on climate, spatial, host, and beetle variables, to reveal how climatic factors have contributed to the outbreak expansion; 3) explored the relationship between fire suppression and MPB outbreaks, to understand how human activities have impacted the MPB-affected acres in the American West. To do this, I used various spatial analysis and modeling techniques including spatial overlay, interpolation, aggregation, and regression models (e.g., generalized additive models, generalized linear models, and geographically weighted regression). I also created different visualization methods to understand climate space, MPB spatial patterns and models.

According to the case study, MPB climate space currently remains constrained in the minimum temperatures compared with the host climate space. Although climatic warming has caused MPB migration to northern regions and its climate space has remained stable in the medians, the lower range of MPB climate space has also shifted to colder temperatures. After comparing MPB climate space between the initial state and the expanded state, I found that MPB climate space has expanded its extremes with the recent outbreak expansion in both southern and northern areas. The predicted MPB outbreak probability in the current northern expanded range is also low when only climatic factors are included in the model, while it significantly increases when spatial autocorrelation variables account for beetle pressure. This shows that MPB outbreak expansion is a strong response of MPB to a ‘mild’ climatic change, which is due to many factors including beetle-tree coevolution, host susceptibility, and management. For example, fire exclusion has increased the abundance of host trees with contiguous dense patches, which further facilitated the MPB infestations. I found that anthropogenic factors have a more significant role than climate in driving the MPB outbreak at a local level. Therefore, I concluded that human factors including forest management have amplified the effects of climate change and caused the MPB outbreak expansion. The conceptual models in Figure V-1 summarize the takeaways from the empirical research in Chapters II, III, and IV.

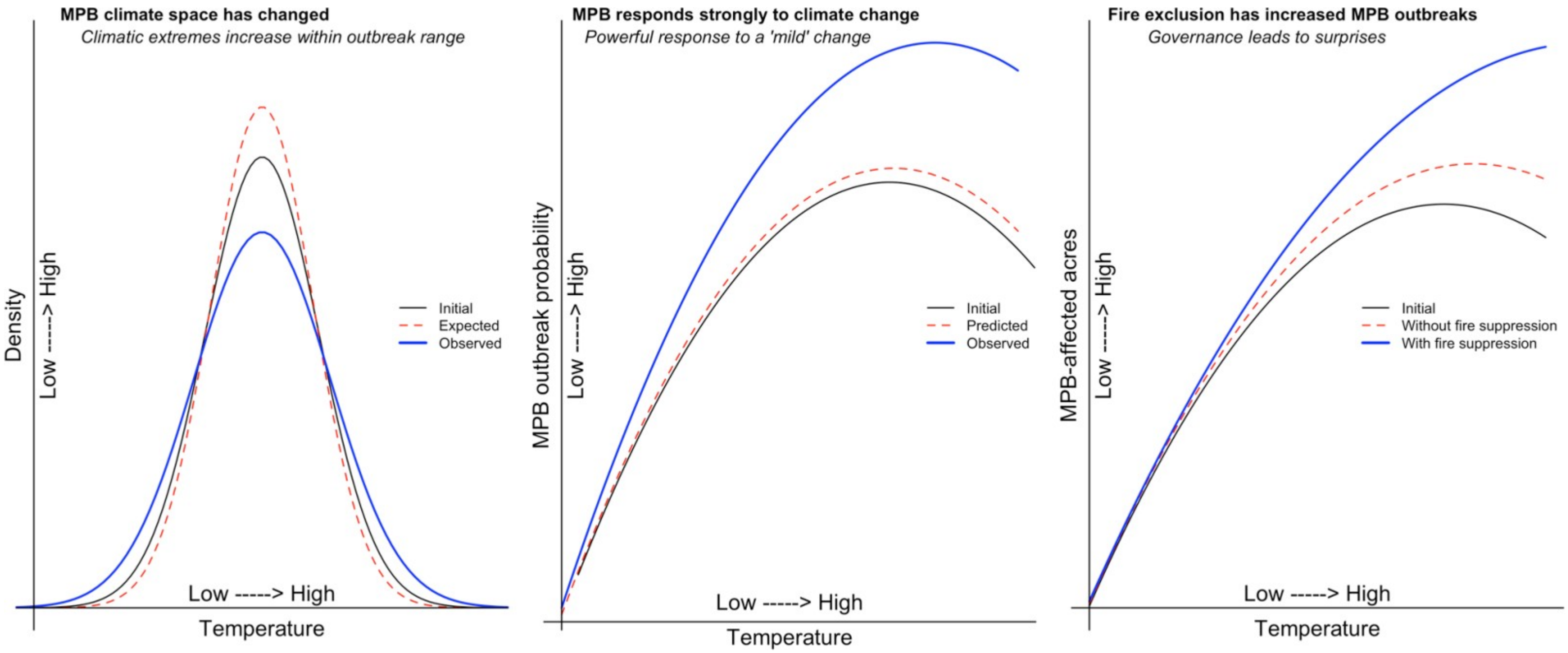
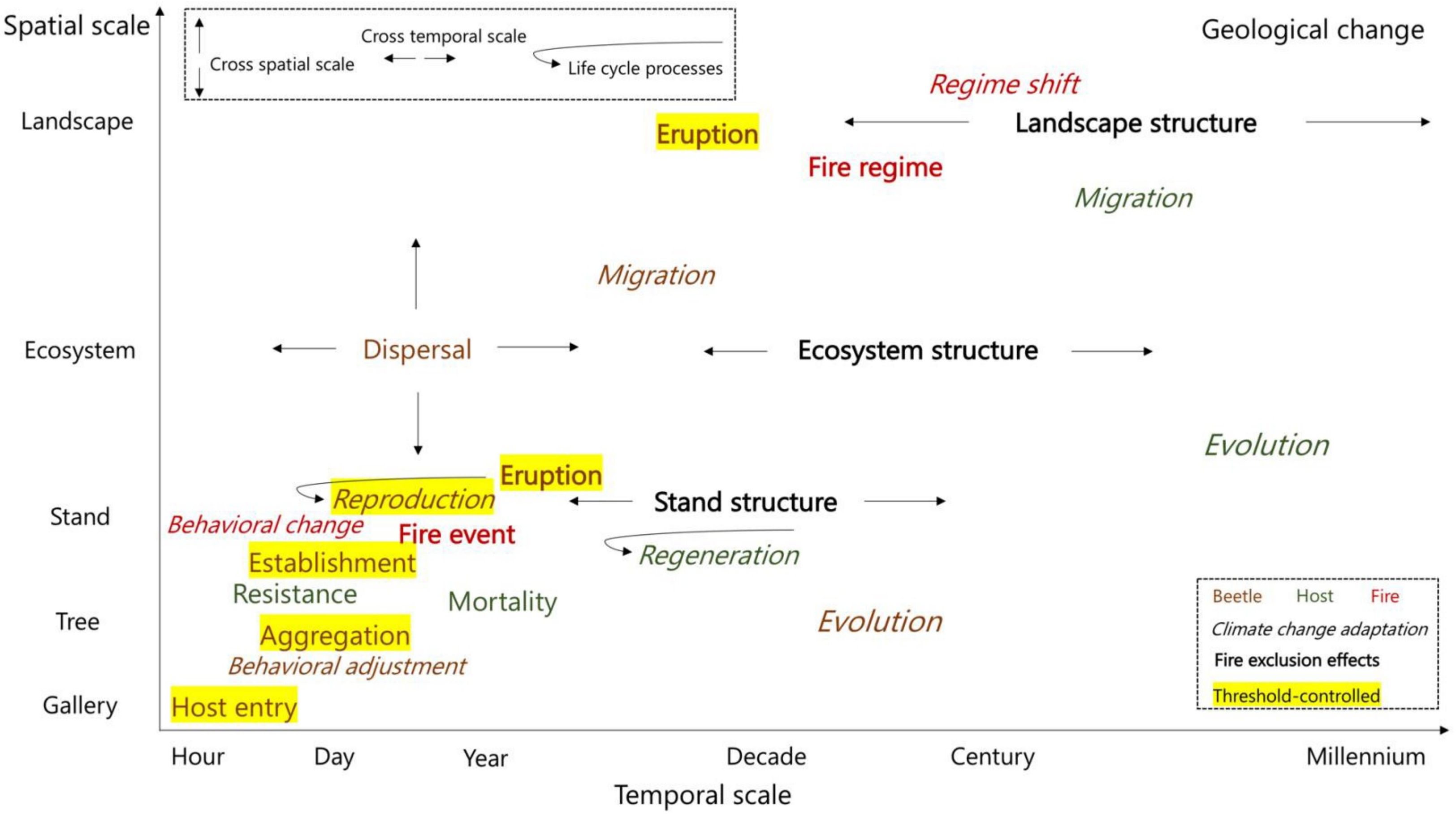


Figure V-1. Conceptual models to summarize the three empirical research chapters II, III, and IV from left to right. The dissertation provides data evidence for previous conceptual models such as Raffa *et al.* (2008) and Cooke and Carroll (2017). The influence of climatic warming on MPB outbreak range expansion was expected to increase the density of warm regions, however, Chapter II concluded that MPB has moved to a colder climate space and MPB climate space has expanded its climatic extremes. Furthermore, the predicted MPB outbreak probability in the recently-expanded geographical space remained low in Chapter III, while the probability increased significantly when spatial autocorrelation and beetle pressure were taken into consideration. Finally, fire suppression as one primary non-climatic factor was predicted to have a positive relationship with MPB-affected acres in Chapter IV.

The conclusions from this study agree with the conceptual model of anthropogenic amplification that was presented in the cross-scale drivers of bark beetle eruptions (Raffa et al., 2008) and the hypothesis that MPB populations may respond very strongly to small changes in climate because of unpredictable complex system behaviors (Cooke and Carroll, 2017). Long-term climate change and fire suppression have synergistically affected the MPB infestations, and the beetle has responded to climatic variations by migrating to suitable environments or adapting to the environment gradually with behavioral or evolutionary changes. Over the last century, beetles and trees have mismatches in their adaptation to climate change because of their differences in life history and dispersal capacities. Beetles may have developed cold-defense mechanisms (Lester and Irwin, 2012; Rosenberger et al., 2017a) with their quick response to the annual climatic oscillation. With a warmer climate and food availability, they moved to colder areas where dense forests resulted from long-term fire suppression, and novel hosts have not co-evolved to resist them (Burke et al., 2017; Raffa et al., 2013). It is also likely that the endemic-level beetle populations in these newly-outbreak-expanded areas erupted to epidemic levels in the susceptible forests when the species surpassed the thermal thresholds of a changing climate. As such, the nonlinear and emergent MPB outbreak patterns were self-organized with thresholds, feedback loops, and time lags. The conceptual model in Figure V-2 illustrates the complex MPB SES, which is based on Raffa *et al.* (2008).

Figure V-2 (next page). Conceptual model for the SES case study of MPB outbreaks. The diagram shows cross-scale events and patterns that affect MPB infestations. From endemic to epidemic level and from host entry to population eruption, MPB populations are threshold-controlled. Both climate change and fire exclusion have gradually changed ecosystems across spatial and temporal scales. Due to different dispersal and reproduction mechanisms, with the long-term climate change, MPB has adapted and evolved more quickly than the evolution of its hosts and moved to colder areas where the host trees have not coevolved to have stronger resistance to MPB. Fire suppression has increased host susceptibility by gradually changing stand, ecosystem and landscape structures. While climate has a global control of the MPB SES, fire suppression and other non-climatic factors have significantly contributed to MPB outbreaks at a local scale. The diagram is based on the conceptual models in Raffa *et al.* (2008), which were revised according to my case study.


Spatial scale
Cross spatial scale
Cross temporal scale
Life cycle processes
Geological change
Regime shift
Landscape
Eruption
Landscape structure
Fire regime
Migration
Migration
Ecosystem
Dispersal
Ecosystem structure
Evolution
Eruption
Reproduction
Stand structure
Stand
Behavioral change
Fire event
Regeneration
Establishment
Resistance
Mortality
Tree
Evolution
Aggregation
Behavioral adjustment
Gallery
Host entry
Beetle
Host
Fire
Climate change adaptation
Fire exclusion effects
Threshold-controlled
Hour
Day
Year
Decade
Century
Millennium
Temporal scale

2. Resilience in the mountain pine beetle socio-ecological systems

The case study presents a typical example for the “tipping points” model (Scheffer et al., 2009) and the MPB SES is subjected to falling into a “landscape trap” (Lindenmayer et al., 2011). The ‘unprecedented’ MPB outbreak patterns in Alberta and increased tree mortality acres in North America in the past two decades increased both spatial autocorrelation and temporal variation, which indicates the early-warning signals for a regime shift, either in the MPB regimes or disturbance regimes, or both. Potential processes and manifestations of regime shift were described in Raffa *et al.* (2008). Although large-scale synchronous outbreaks occurred historically in lodgepole pine forests (Jarvis and Kulakowski, 2015), the outbreak in the 2000s is the most severe in the last 150 years (Hrinkevich and Lewis, 2011), with a sudden northward shift of MPB populations in 1972 (Sambaraju et al., 2019). The pine forest structure and compositions changed with multi-stories and multiple age cohorts, initiated by repeated canopy thinning after MPB infestations, in which MPB is replacing fires as the major disturbance agent in forest succession (Alfaro et al., 2008; Axelson et al., 2009). With the absence of fires, tree mortality in the overstory will be replaced with advance regeneration in the long-term, dominated by subalpine fir, which may increase heterogeneity in forest structure that is expected to make these forests more resistant to MPB attacks (Kayes and Tinker, 2012). To some extent, this landscape trap (without fire disturbances) demonstrates the resilience of SES, in which transformation can be seen as a type of systemic change or regime shift (Reyers et al., 2018). Thus, the understanding of SES resilience can be changed from that of “a loss of resilience can lead to a regime shift” (ecological resilience) to “a regime shift can be a part of resilience, and the loss of transformability can lead to the loss of resilience” (socio-ecological resilience).

3. Management implications

The potential perspective change of resilience in SES raises questions regarding the importance of identifying regime shifts and how to identify them, how to measure the transformability of SES and detect the loss of transformability, how to manage complex adaptive forest ecosystems, etc. The danger of taking the self-repairing capacity of ecosystems for granted (Folke et al., 2004) will lead to unsustainable and undesirable developments. With the speed of global environmental changes, the long-term consequences of regime shift from MPB outbreak cycles have not been fully understood, although the aftermath of the MPB epidemic can be seen in timber supply, forest stand dynamics, and ecosystem resilience (Dhar et al., 2016a). Many surprising challenges will rise from SES, and resilience-building management needs to be flexible and open to learning (Folke et al., 2004). To facilitate management in SES, Folke *et al.* (2004) suggest identifying the crucial slow variables. These variables critically determine the system dynamics and govern the supply of essential ecosystem services, and are often considered to be the variables that have contributed to the most important changes in the system (Ferrara et al., 2016; Folke et al., 2004). Climate change and fire suppression both serve as fast variables in the short term and slow drivers in the long term, however their significance is spatially different as climate change globally and fire suppression locally affect ecosystems. Based on the case study, we need to rethink 'one-size-fits-all' policies (e.g., fire suppression policies and the Healthy Forests Restoration Act) and abandon the 'command and control' forest management approach.

Instead of treating forests as stable sources for a single good or service (e.g., wood, recreation, or water) and managing forests mainly at the stand scale in the timber-based management tradition, the complex adaptive management (CAM) approach can be seen as a holistic multiscale assessment that focuses on a full set of goods and services and promotes adaptability by favoring the capacity of the forests to adapt to uncertain future conditions (Messier et al., 2015). Compared with the ecosystem-based management strategies such as natural-disturbance-based management (Drever et al., 2006), the CAM approach acknowledges non-linearity (i.e., forests may show unexpectedly large or small responses to gradually changing conditions) and uncertainty (i.e., all aspects of forest states and dynamics may never be precisely known) (Messier et al., 2016). The case study also supports the CAM approach by suggesting that a large-scale and long-term assessment is desirable before decision-making, and that forest management should accept variability and unpredictability in space and time with considerations of complexity characteristics, to prevent the negative consequences of scale mismatches

(Cumming et al., 2006). As for beetle management, Raffa *et al.* (2008)
proposed threshold-based strategies.

We also need to consider humans as a prominent force in changing ecosystems, and learn the possible consequences of human actions on SES. Both human-caused climate change and fire exclusion have contributed to the massive MPB-triggered tree mortality, which eventually created positive feedback and worsened the problems so far (or at least in the short term) (Calkin et al., 2015; Kurz et al., 2008; van Mantgem et al., 2009). Also, the unnaturally increased tree density from fire suppression may have decreased the amount of aboveground carbon in western US forests (Fellows and Goulden, 2008). To mitigate carbon emissions, forest management strategies, including reforestation, increasing forest carbon density, replacing fossil-fuel with forest products, and reducing deforestation, were proposed (Millar et al., 2007). Furthermore, fire plays a fundamental role in Earth system processes and has interacted with humans for millions of years (Bowman et al., 2009), yet we are still learning to coexist with fires, and in the past we decoupled human and natural systems by ignoring the human dimensions in fire-prone ecosystems (Moritz et al., 2014). Fires are seen as natural hazards in the human world, and fire suppression will very like continue as path dependence due to climate change and rapid expansion of the wildland urban interface (Masarie et al., 2019). Another interesting paradox is why government agencies around the world have been focusing on firefighting instead of directing their attention to the vulnerable WUI development that could have been less costly (Moritz et al., 2014). Going forward, the understanding of SES and evaluation of human impacts on ecosystems should be emphasized in natural resource management.

4. Limitations and uncertainties in the study

The case study, which examined the MPB outbreaks at a large spatial scale (continental and western Canada and United States), is subject to several methodological limitations in spatial data quality that influenced the decisions on variable and model selection. First, the quality of source data is limited to large-scale research. Beetle presence on a 10km grid identified from the aerial mapping of MPB outbreaks is unable to show the annual spatial pattern of MPB severity. As such, the range map may exaggerate the severity of MPB outbreaks at the landscape level, and the absolute population level of MPB remains unclear. The host presence data, based on the digitized coarse-scale distribution maps of pines from Little (1978), lack temporal and volumetric variation. Fire point data exclude the fire perimeter information, and fires larger than 100 km_2 are constrained. Second, data showing important small-scale interactions that can reflect on large-scale patterns are unavailable, and the interpretation of models requires evidence from small-scale empirical research. Biotic interactions among beetle populations, hosts and fungi associations are not completely clear, particularly in the long-term; they include the coevolution between MPB and host species, competition between MPB populations, and MPB dispersal mechanism. Also, the variation of beetle-climate relationships is ignored at a smaller scale than the resolution examined in this study. Third, errors propagated from spatial data to the final model cannot be excluded or precisely quantified. In light of the limitations of spatial data quality, which are reasonable for large-scale studies, I employed various approaches to increase the robustness and goodness of fit.

In fact, the spatial modeling violated several statistical and ecological assumptions. Predictors are usually expected to be completely independent in regression analysis, which is unrealistic in the case study. Different temperature or water based bioclimatic variables that determine beetle survival and development are correlated, and beetle dispersal is one main reason for spatial autocorrelation of beetle-related variables. I took the risk of collinearity that can inflate or distort coefficients and carefully interpreted the results, in favor of higher accuracy of model predictions with more predictors using cross-validation and regularization to avoid overfit. Multicollinearity does not affect the predictive power and reliability of the models (Midi et al., 2010). I also used methods to account for SAC, such as a block sampling method. Ecological assumptions for species distribution modeling, including the assumptions of ‘equilibrium’, ‘individualism’, ‘niche conservatism’, ‘spatial stationarity’, and ‘isotropic spatial autocorrelation’, are violated as the simplified models cannot address all the complexity of ecosystems. These are considered common misassumptions because they ignore biotic interactions and evolutionary variation over space and time. It is also not clear whether the relevant environmental gradients have been adequately sampled because of a lack of knowledge on the long-term history of large-scale beetle outbreaks.

Finally, the synergistic effects of climate change and fire exclusion cannot be quantified exclusively because ‘everything is connected to everything else’ (Pickett et al., 2005), and the study confirms an abundance of evidence of human-caused ecosystem changes. This is inherent in SES, which shows challenges involving assumptions about ‘excludability’ and ‘the absence of interference’ (Ferraro et al., 2019). The current MPB outbreak range was widely claimed as ‘unprecedented’, and researchers also suggested that MPB ‘recently’ started to attack jack pine (Cullingham et al., 2011; Rice et al., 2007a); however, whether there was historical endemic-level MPB activity in the novel outbreak environment remains unknown. A large body of literature considers this outbreak range expansion as its initial range shift of species distribution (Cudmore et al., 2010; de la Giroday et al., 2012b; Robertson et al., 2009), and claims the causes of range expansion were ‘a strong aerial deposition of epidemic-level beetle populations met with weakly coevolved novel hosts in a habitable environment with a warmer climate and plenty of trees’ (de la Giroday et al., 2012b; Raffa et al., 2013; Safranyik et al., 2010). Although the study did not contradict the previous findings, it also suggested that the current climate in the expanded areas is still colder than its pre-expanded host range, and the outbreak probability remains low in the novel environment without accounting for beetle pressure. As such, the beetle might have adapted to cold climates with climate change, or there may exist a low level of beetle population. In any scenario, the current literature has not provided strong evidence of missing MPB populations in the expanded range in the long-term. We need to be more skeptical when considering the current expansion range in BC and Alberta as the ‘historically unsuitable’ environment.

5. Prospective research

First, empirical research to generate greater understanding of MPB dynamics is still needed. There are twenty-five priority questions suggested for managing beetle impacts on ecosystems and society (Morris et al., 2017). Morris *et al.* (2017) provide a good summary of knowledge gaps in outbreak detection and monitoring, public perceptions and education, and ecosystem services quantification. Here, I specify several interesting and relevant questions that can be developed from this study (Q1~5, 7 and 9 from Morris et al., 2017) to further understand MPB population levels, historical MPB activity, impacts of land-use activities, stand-scale climatic effects, and symbiotic coevolution. Such research depends highly on data availability, including remotely-sensed, palaeoecologically-recorded, dendrological, climatic, and molecule data.

The advance of remote sensing technology will generate high-resolution aerial imagery to support small-scale research, answering questions related to the accuracy of stand-scale tree mortality and tree-level beetle populations. The reconstructions of past MPB outbreaks require more data from lake sediment cores, tree-ring records, and surface pollen, which will help answer questions on whether there was historical MPB activity in the current expanded range. Furthermore, understanding of the temporal and spatial autocorrelation of MPB outbreaks based on high-resolution data will facilitate research on modeling the MPB outbreaks over multi-centennial to millennial time-scales, with the availability of palaeoclimate data. We will then be able to compare the periods before and after the implementation of fire exclusion policies to evaluate the impacts of fire suppression. Moreover, the coevolution among beetles, trees, and the fungi associations revealed through molecular research will provide evolutionary evidence of climatic impacts. This prospective research will eventually detect the MPB regime shifts.

Second, SES research has advanced quickly since the 2000s in terms of the publication volume, yet many questions remain largely unexplored. Firstly, SES, which is originally from different research traditions and has become an emerging interdisciplinary research field, has not been commonly defined (Colding and Barthel, 2019). Researchers used different terms to describe SES (Eakin and Luers, 2006; Liu et al., 2007; Ostrom, 2007; Turner et al., 2003b), and some of them think coupled human and natural systems include human-environment systems and social-ecological systems (Liu et al., 2007). I think these different SES terms reflect a relationship between academic nomenclatures and how SES is perceived (e.g., whether the SES is more a social system or more an ecosystem, the roles of humans in the SES, and so on), which further defines SES research methods. For example, social-ecological was used to emphasize that social and ecological systems are equally important (Berkes, 2017), whereas socio- is a modifier in the term ‘socio-ecological systems’, which emphasize ecosystems and the human impacts on ecosystems.

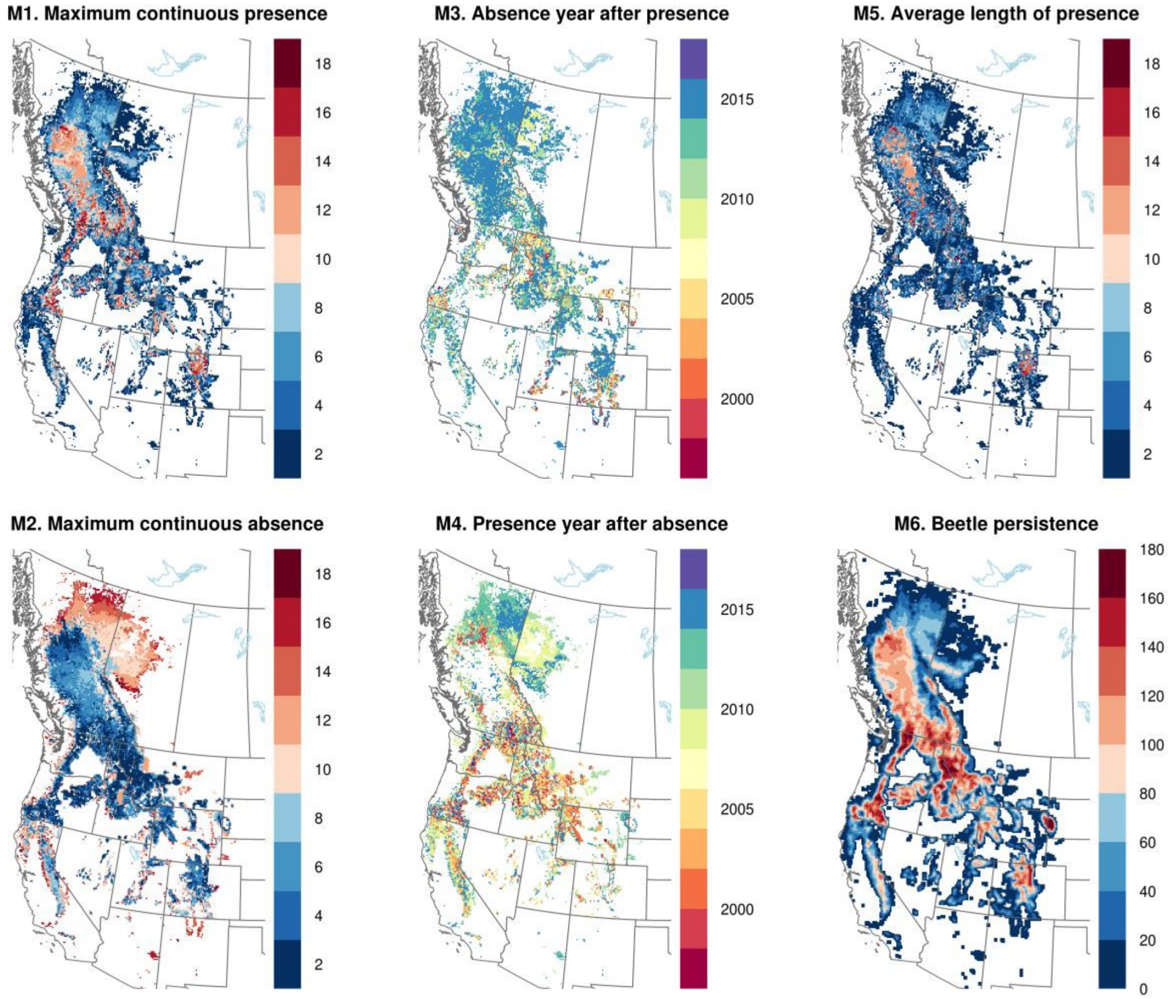
Secondly, the resilience concept has become confusing when the adapted version in SES added ‘transformability’ (i.e., the ability to transform with change), which suggested that regime shifts (Folke et al., 2004) do not mean ‘loss of resilience’ anymore , but refer to ‘large and persistent’ system changes or transformations (Reyers et al., 2018), which are ‘parts of resilience’. This increases the difficulty of measuring resilience since SES may be forever resilient because of the self-repairing capacity of ecosystems or management. Similarly, challenges of expanding the concept to social sciences continue in sustainability science (Olsson et al., 2015), which calls for further SES research to bridge the gaps in the measurability of SES resilience.

Thirdly, many SES frameworks have been proposed (Binder et al., 2013; Pulver et al., 2018), however, the applications of these frameworks are limited to research areas and case studies. The more-widely-used social-ecological systems framework (Ostrom, 2009) has created challenges for synthesis because of the methodological gaps among case studies (Partelow, 2018). To my knowledge, there is no discussion of whether it is important to have a common and comprehensive framework to synthesize SES research or sustainability science, which could integrate the different SES concepts (e.g., complexity, resilience, vulnerability, sustainability), specify possible applications, and identify the research gaps.

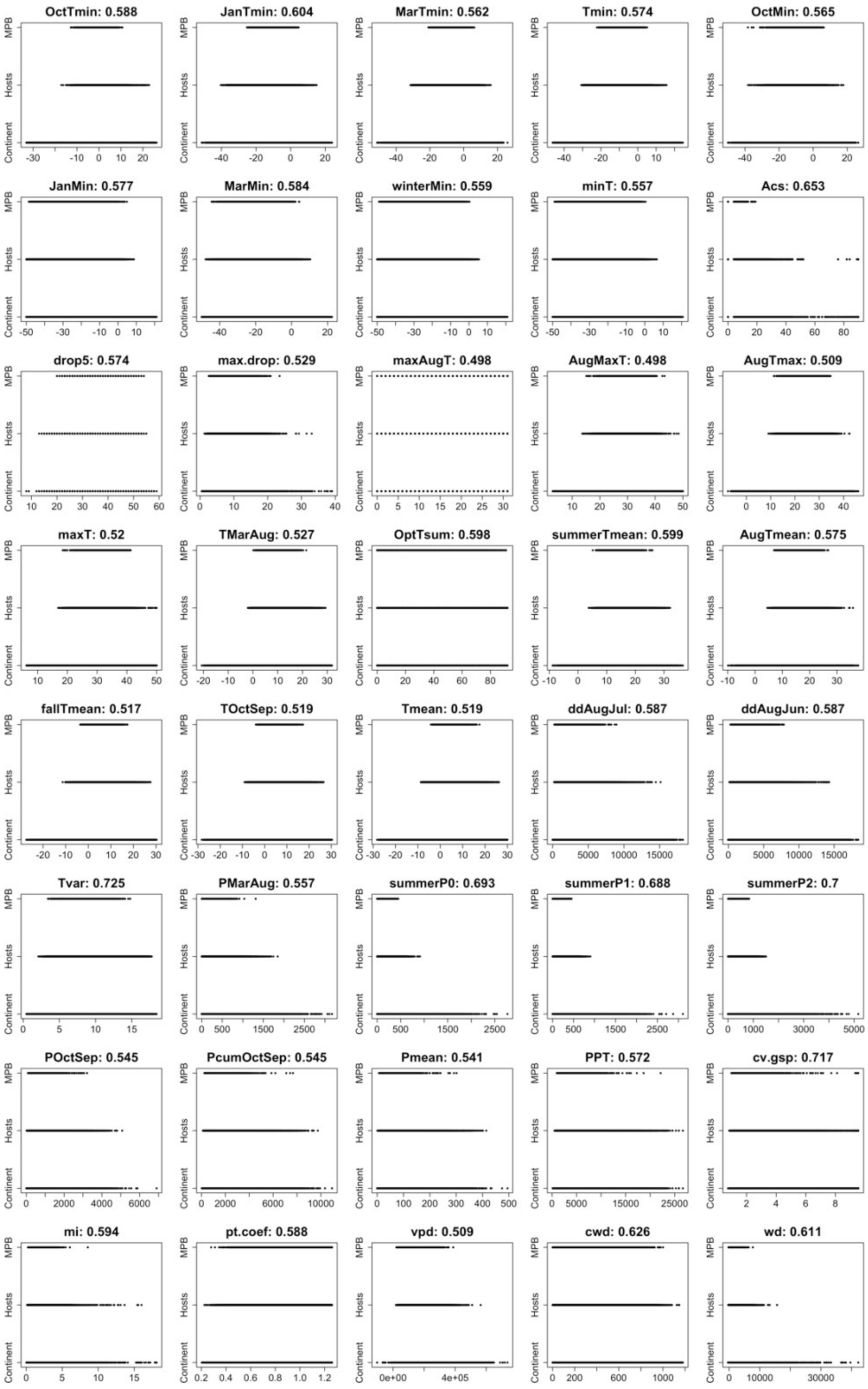
Fourthly, further research on the SES causal inferences (Ferraro et al., 2019) requires development of methods to explore complexity, for example, through integrating spatial statistical analysis with both ecological and sociological research methods, or effective academic-practitioner collaborations. Understanding of the complexity of human behaviors in ecosystems is important to evaluate the human impacts on ecosystems, although some related questions have not been considered as being as pressing (Kramer et al., 2017), which I think is because many ecologists have not examined ecosystems as SES. Investigating SES complexity is prompting calls for new computational methods, advances in artificial intelligence, and modeling techniques that allow for phenomenological emergence (Schoon and van der Leeuw, 2015). For example, agent-based modeling has become a more common tool utilized in this manner (An et al., 2014). The dissertation also provides data and parameters for further exploration of processed-based and agent-based models, which are expected to address more details in the cross-scale interactions and specify the thresholds for regime shifts.

Moreover, methodological developments in SES research for uncertainty analysis are useful for narrowing the science-policy gap (Bradshaw and Borchers, 2000). As shown in this dissertation, narrowing that gap is an essential challenge for the health of the forests of North America. More broadly, the robust implementation of the SES perspectives I have outlined is a critical part in contending with the changes that are reshaping our planet. While, climate change and human impacts are--to a considerable extent--too complex for us to address with simple measures, a more effective engagement with SES is not beyond our reach and can make a significant contribution to mitigating the harmful processes that are already underway.

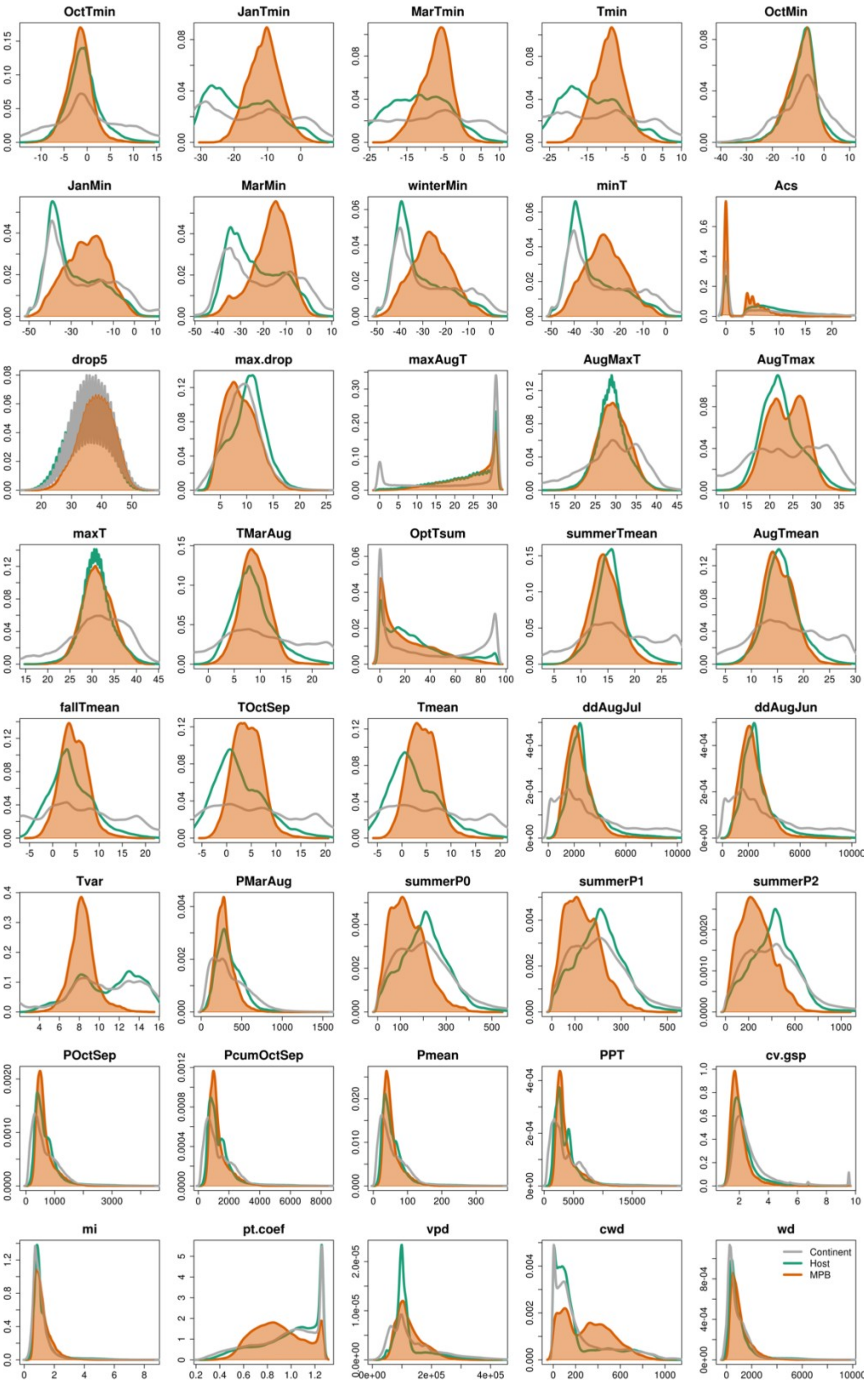
APPENDIX



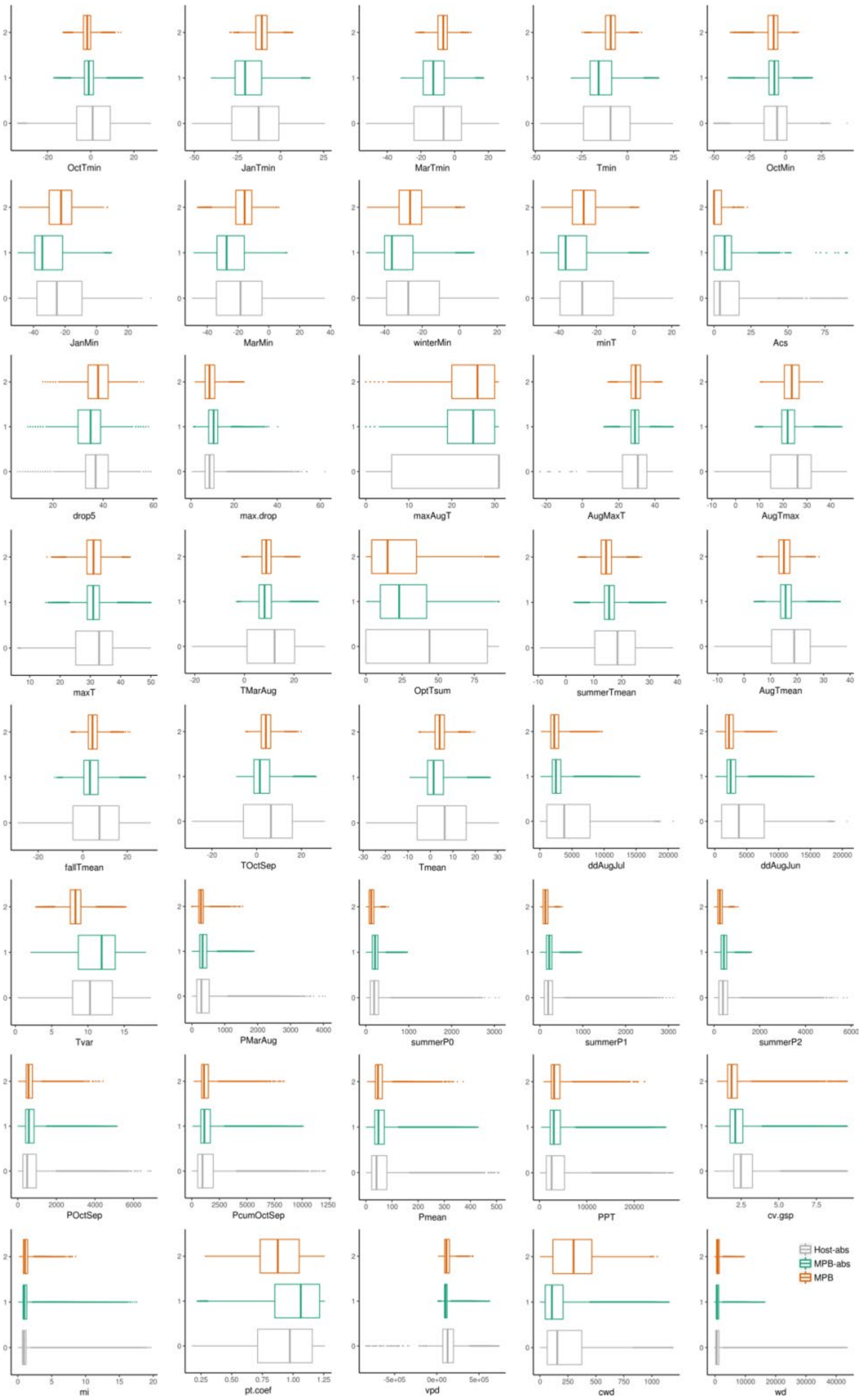
Appendix Figure II-1. Outbreak summary statistics from 1997 to 2016 (M1, the maximum run of consecutive years with outbreak presence; M2, the maximum run of consecutive years with outbreak absence; M3, the first presence year after the longest absence; M4, the absence year after the longest presence; M5, the mean length of continuous presence; M6, the summary of presence in the grid cell and the nearest 8 grid cells).



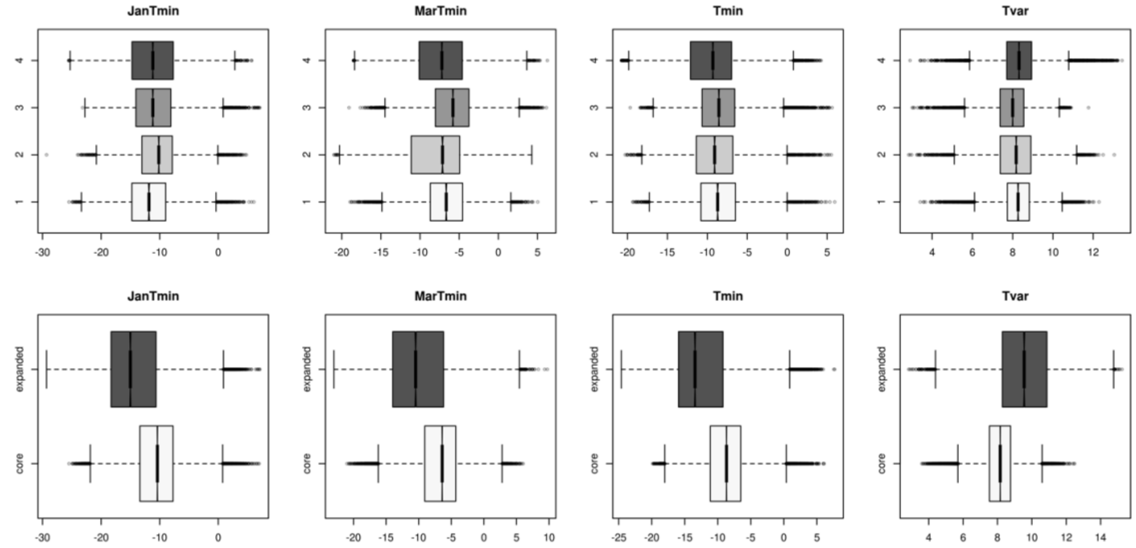
Appendix Figure II-2. Strip charts of bioclimatic variables in the continental, host and beetle climate space with AUC values to differentiate climates in presence and absence. The detailed explanations of variables are shown in Appendix Table II-2.



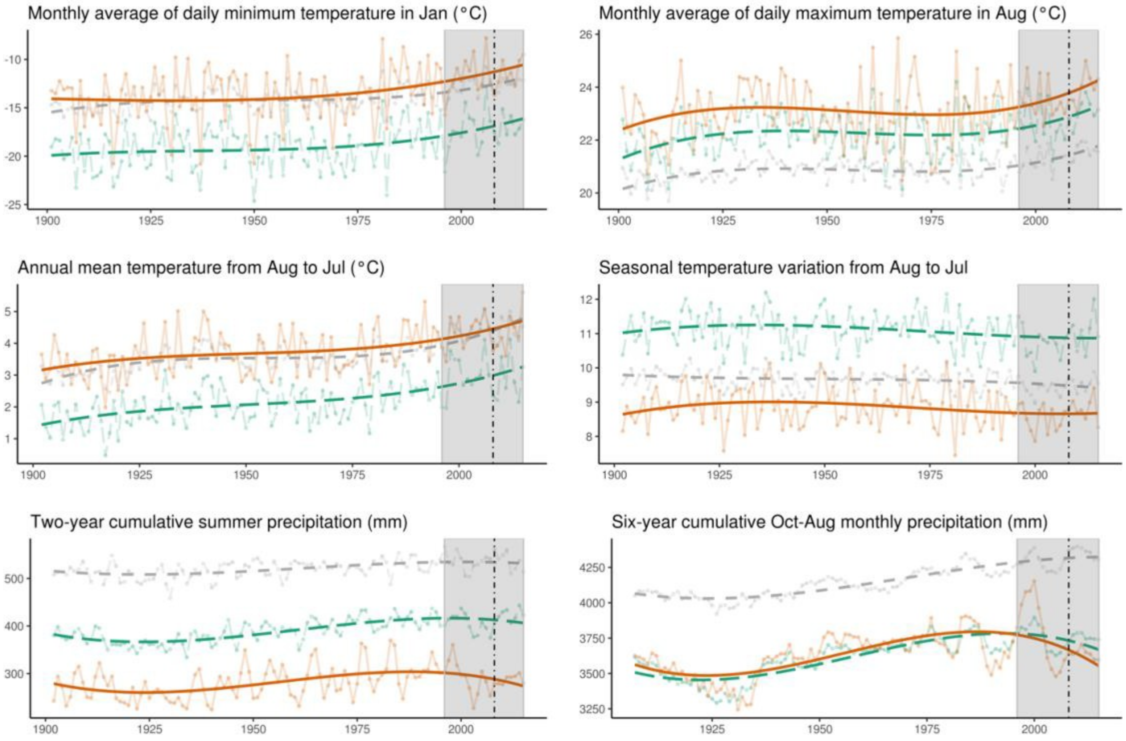
Appendix Figure II-3. Density plots of bioclimatic variables in the continental, host and beetle climate space. The detailed explanations of variables are shown in Appendix Table II-2.



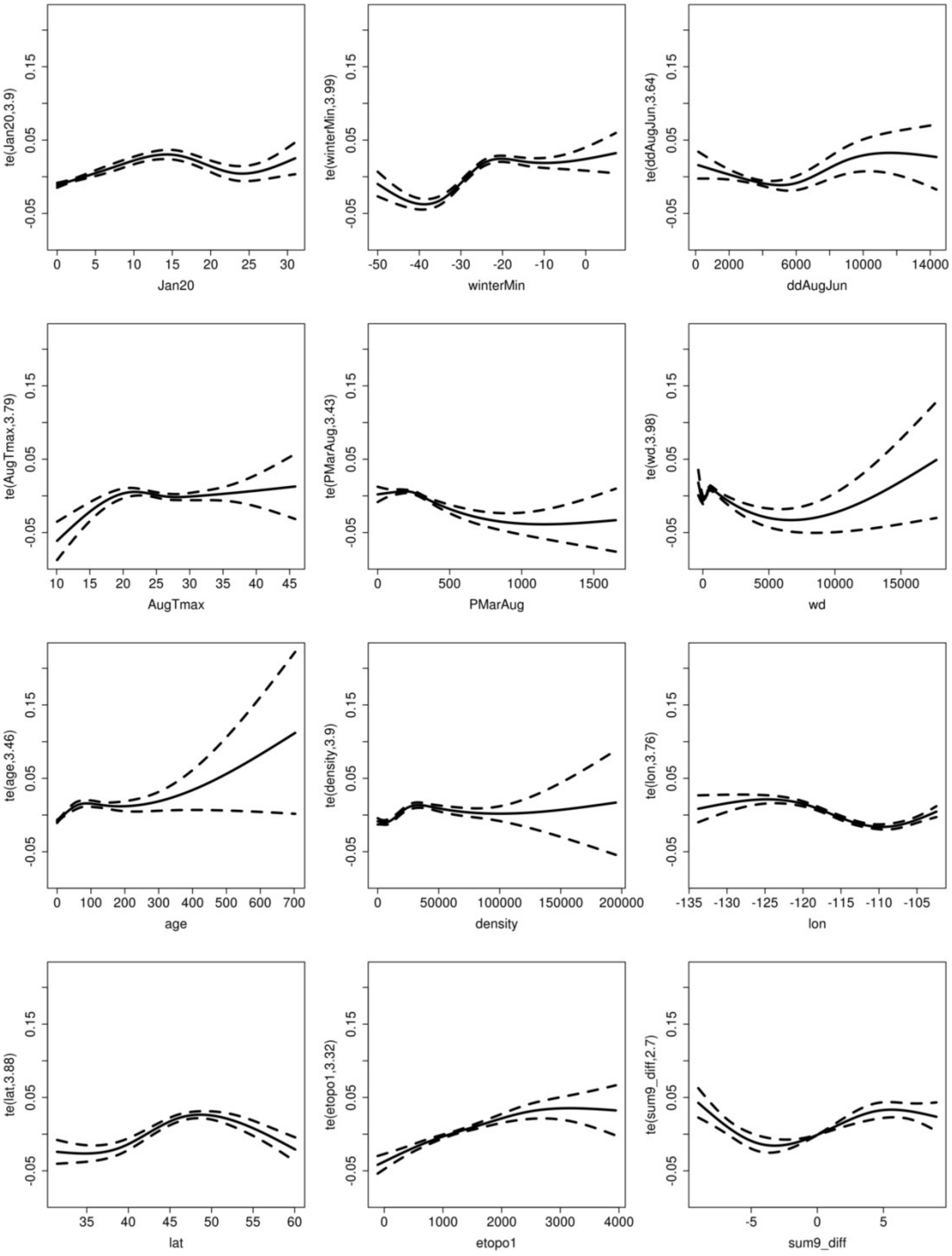
Appendix Figure II-4. Boxplots of beetle outbreak presence, beetle outbreak absence within host climate space, and host absence climate space. The detailed explanations of variables are shown in Appendix Table II-2.



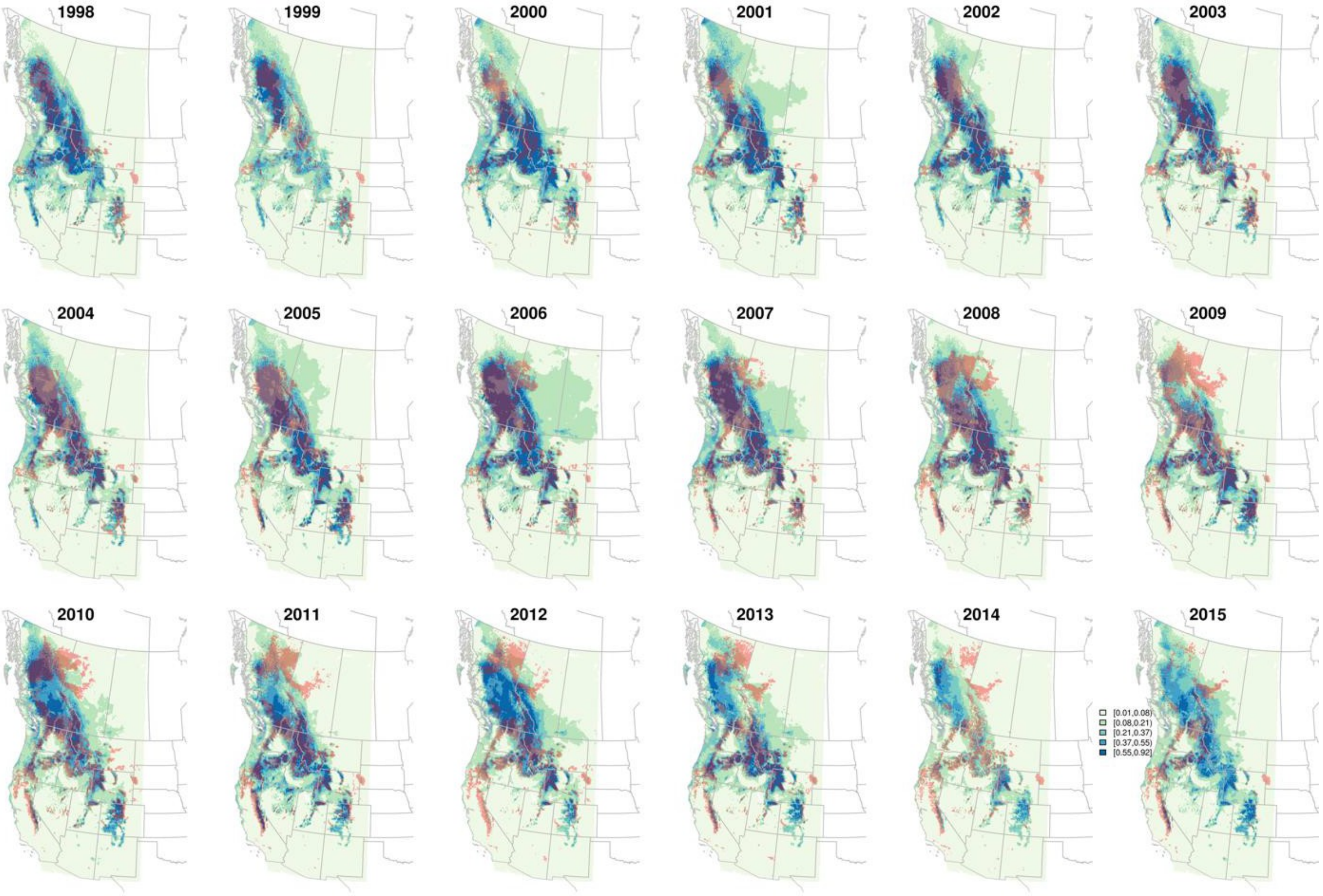
Appendix Figure II-5. Boxplots of the constraint variables during the four expanding periods and between the expanded and core areas. The four periods are 1996-1998, 2000-2002, 2003-2005, and 2006-2008 from 1 to 4 respectively. The constraint variables are average minimum daily temperatures in January, March, and from November to March, and seasonal temperature variation during the beetle life cycle (August to July).



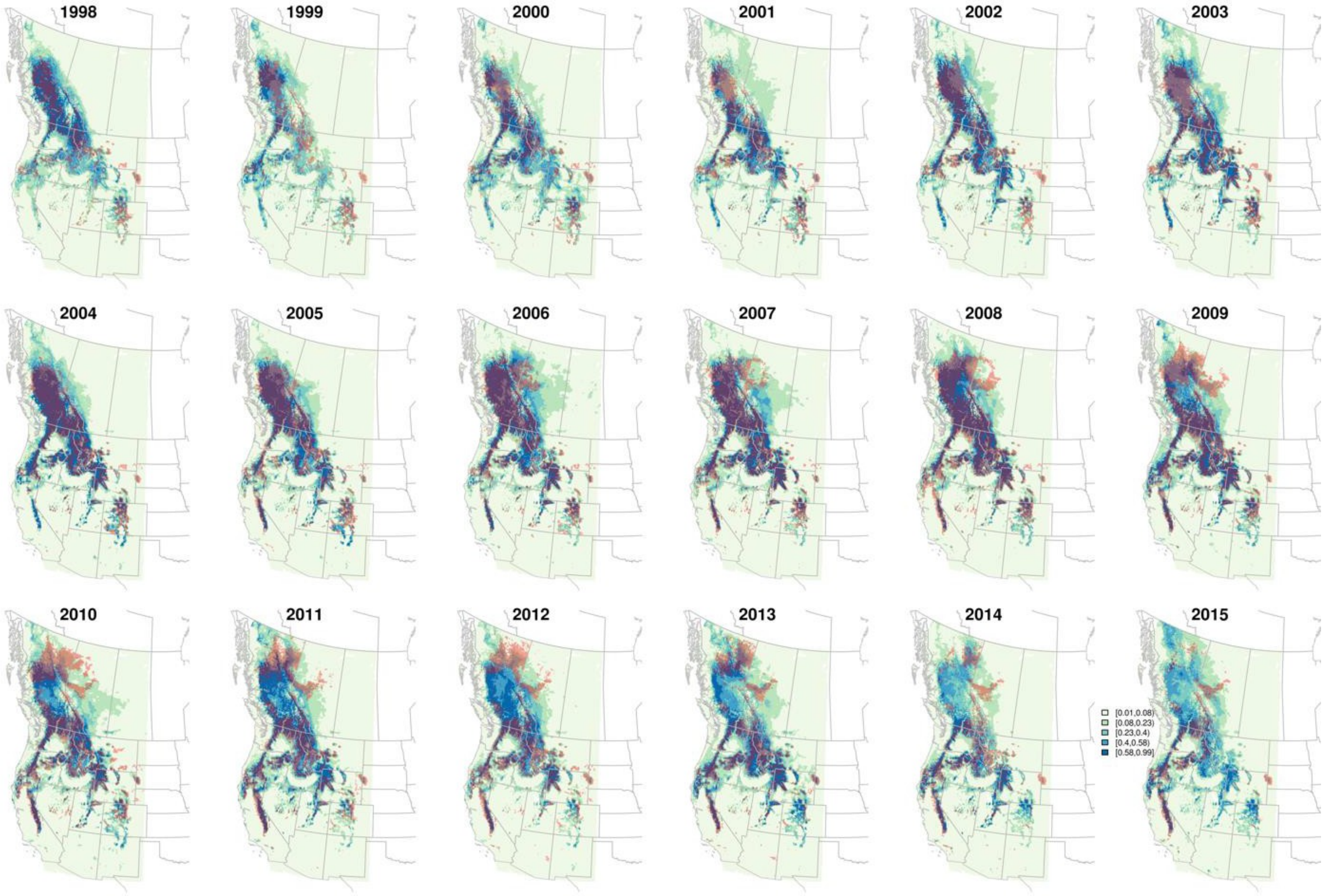
Appendix Figure II-6. Long-term climatic changes using mean values of bioclimates in North America, host range, and current mountain pine beetle range. The dashed gray line, longdashed green line, and solid orange line in a light color indicate the annual mean of bioclimatic values in North America, the core host range, and current beetle outbreak range, respectively. The fitted line in dark color is from a cubic spline basis. The gray shadow highlights the recent years where the dotdashed black line marks the outbreak peak year 2008.



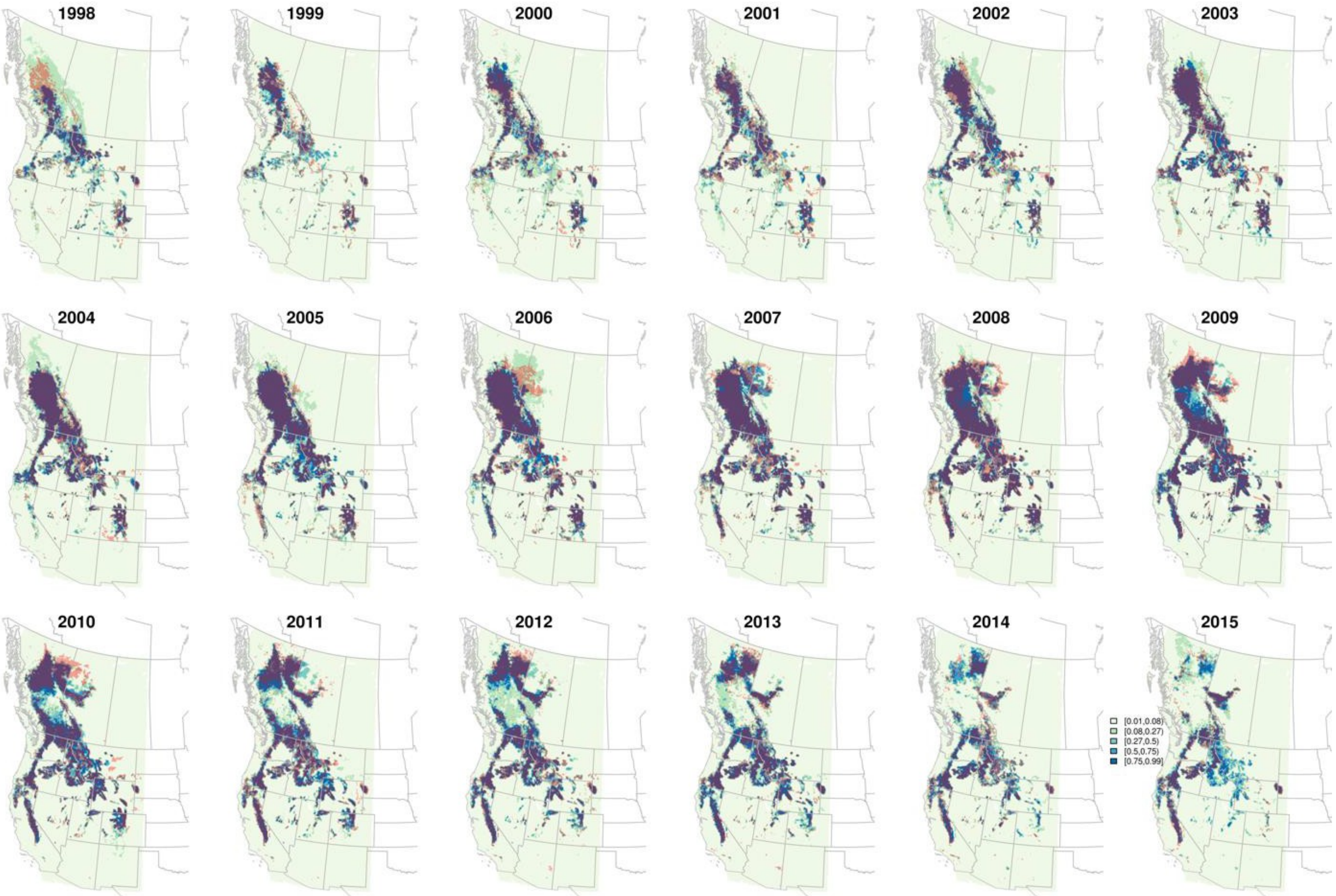
Appendix Figure III-1. Example results from generalized additive models. The names and descriptions of the variables in the x axis can be found in Appendix Table III-1. The probability value shown in a smoothing term in the y axis is the prediction from the additive model. The curves of spline were used to approximate a quadratic or cubic transformation of a particular predictor.



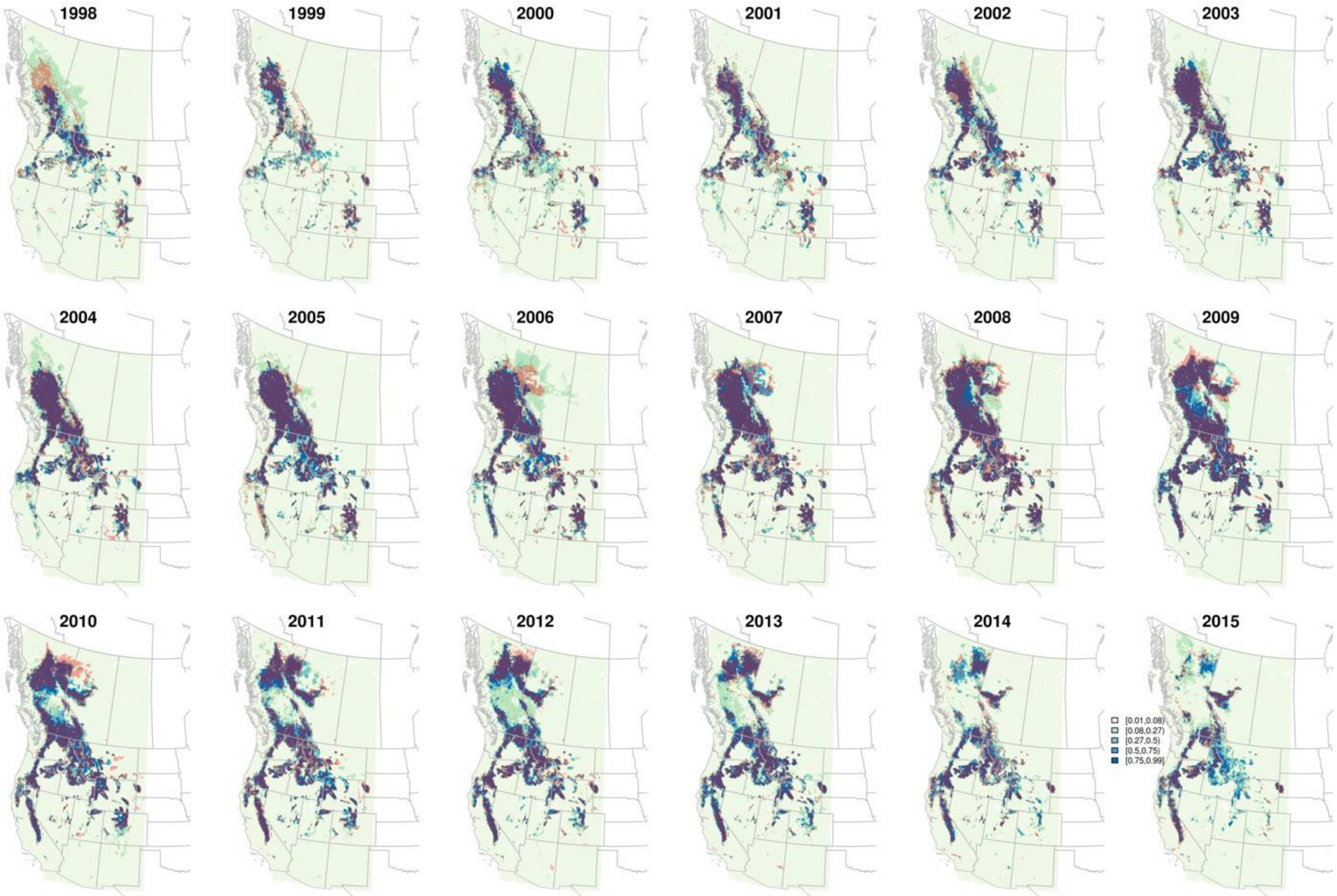
Appendix Figure III-2. Model prediction of MPB outbreak probability with only bioclimatic variables (Model 1). The colors from green to blue indicate the predicted probability, and the red transparent color shows the annual outbreak presence, as in Appendix Figure III-3 – 5.



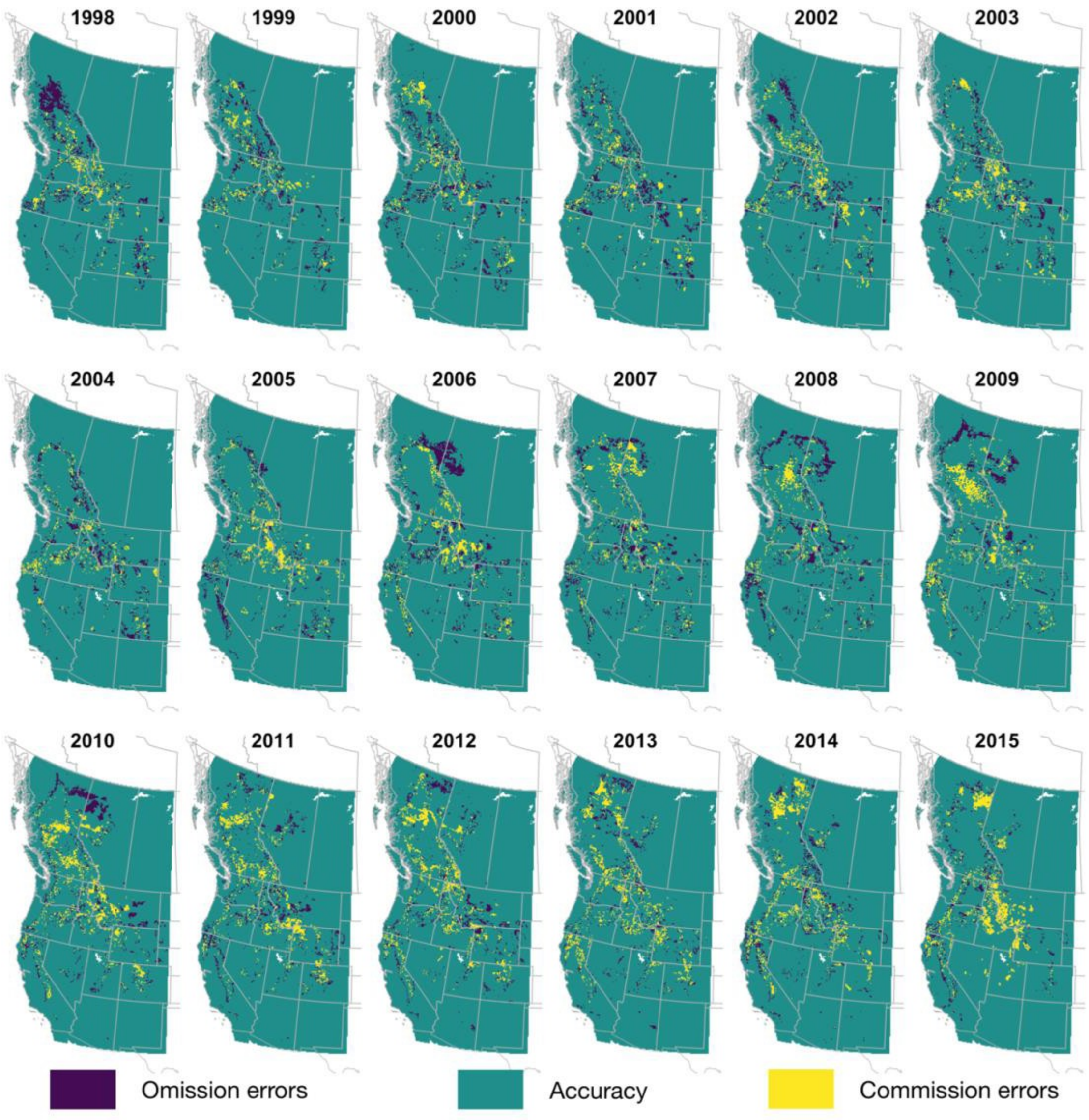
Appendix Figure III-3. Model prediction of MPB outbreak probability with bioclimatic variables, and their transformation and interactions with location variables (Model 2).



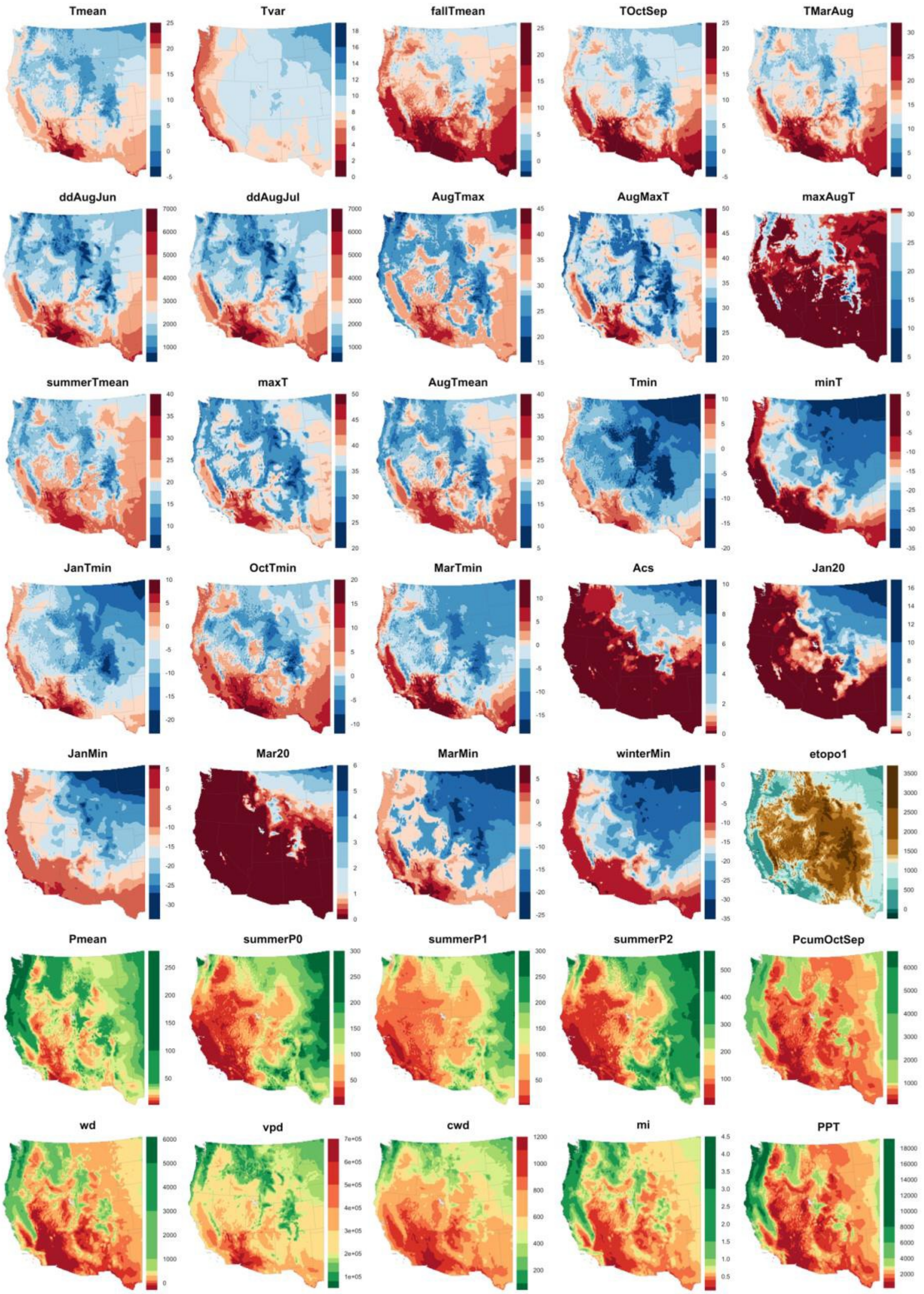
Appendix Figure III-4. Model prediction of MPB outbreak probability with bioclimatic variables, their transformation and interactions with location variables, and beetle-related variables (Model 3).



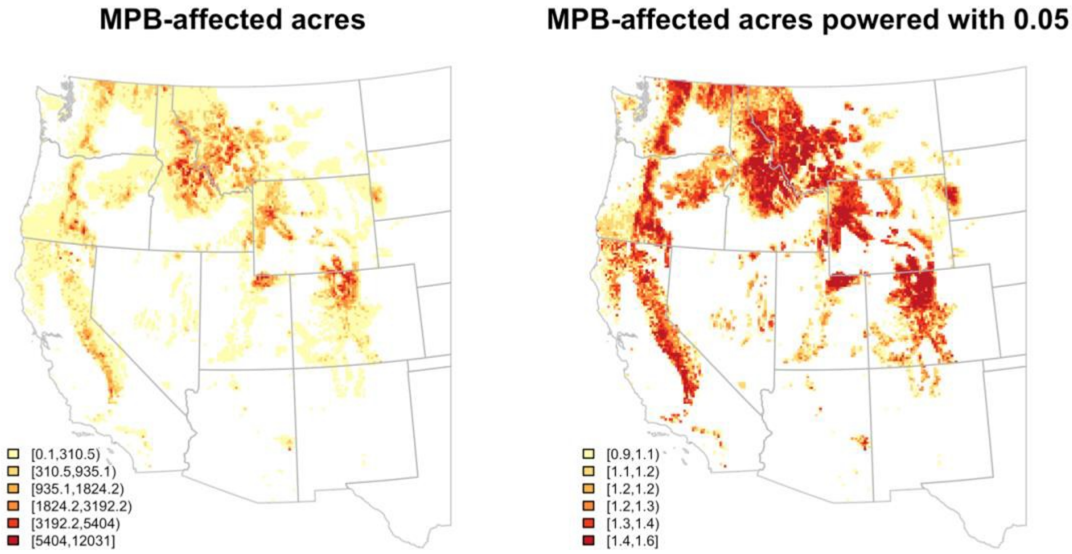
Appendix Figure III-5. Model prediction of MPB outbreak probability with bioclimatic variables, their transformation and interactions with location variables, beetle-related variables, and vegetation-related variables (Model 4).



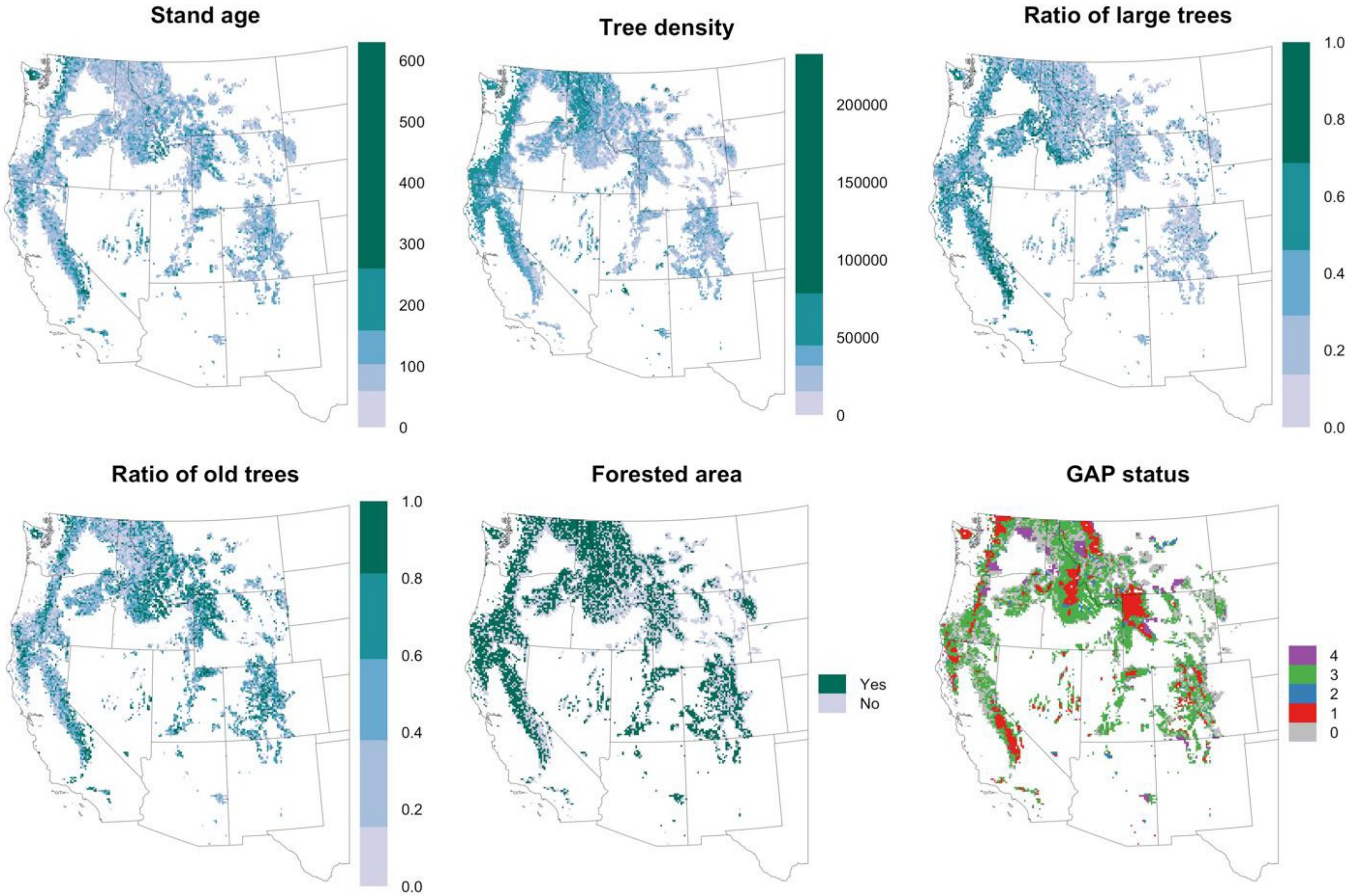
Appendix Figure III-6. Prediction accuracy of MPB outbreak probability from Model 3.



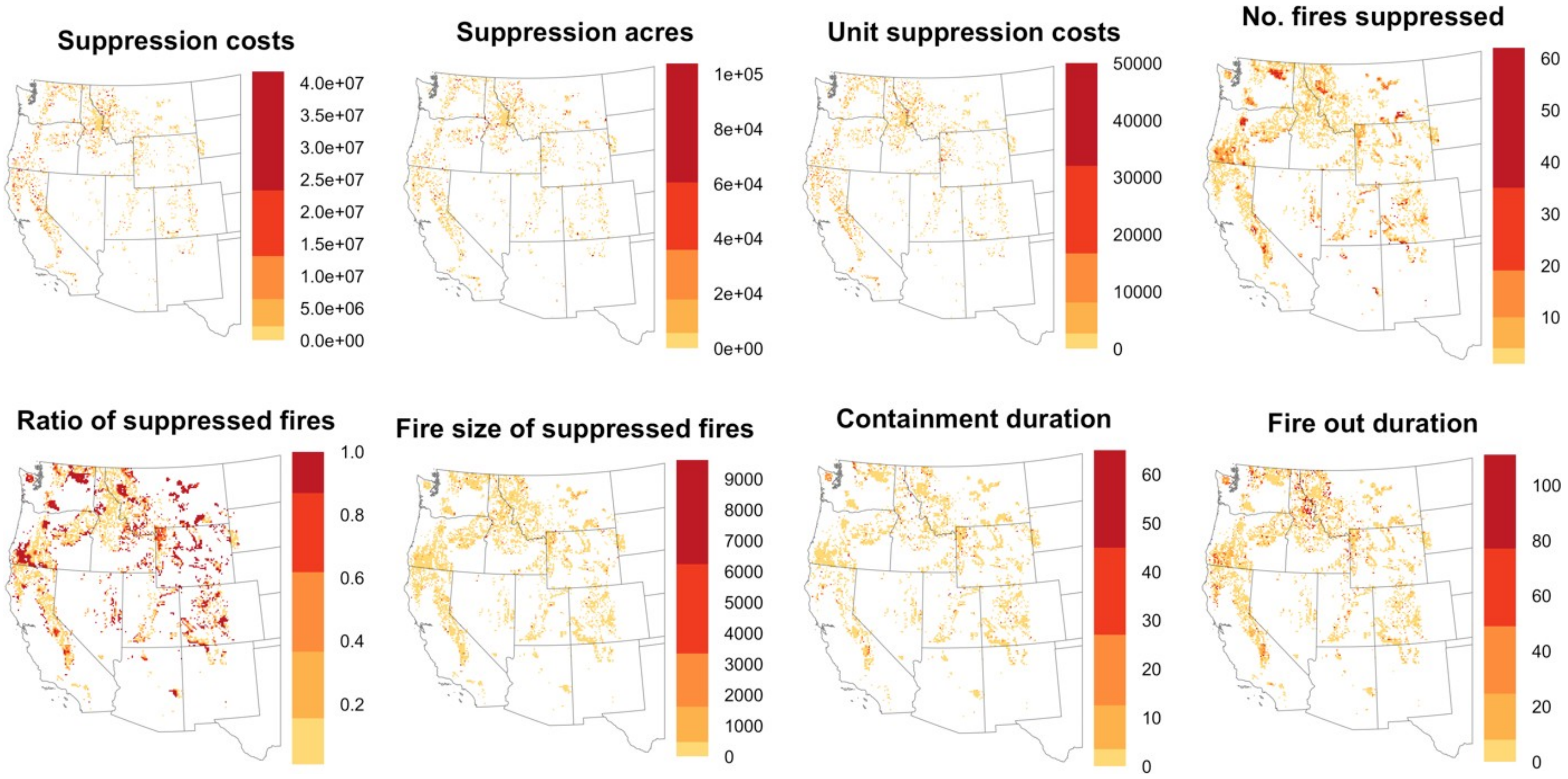
Appendix Figure IV-1. Mean values of bioclimatic variables during 1996 and 2015 and elevation (etopo1) in the America West. The long name and more explanations of bioclimatic variables can be found in Appendix Table IV-2.



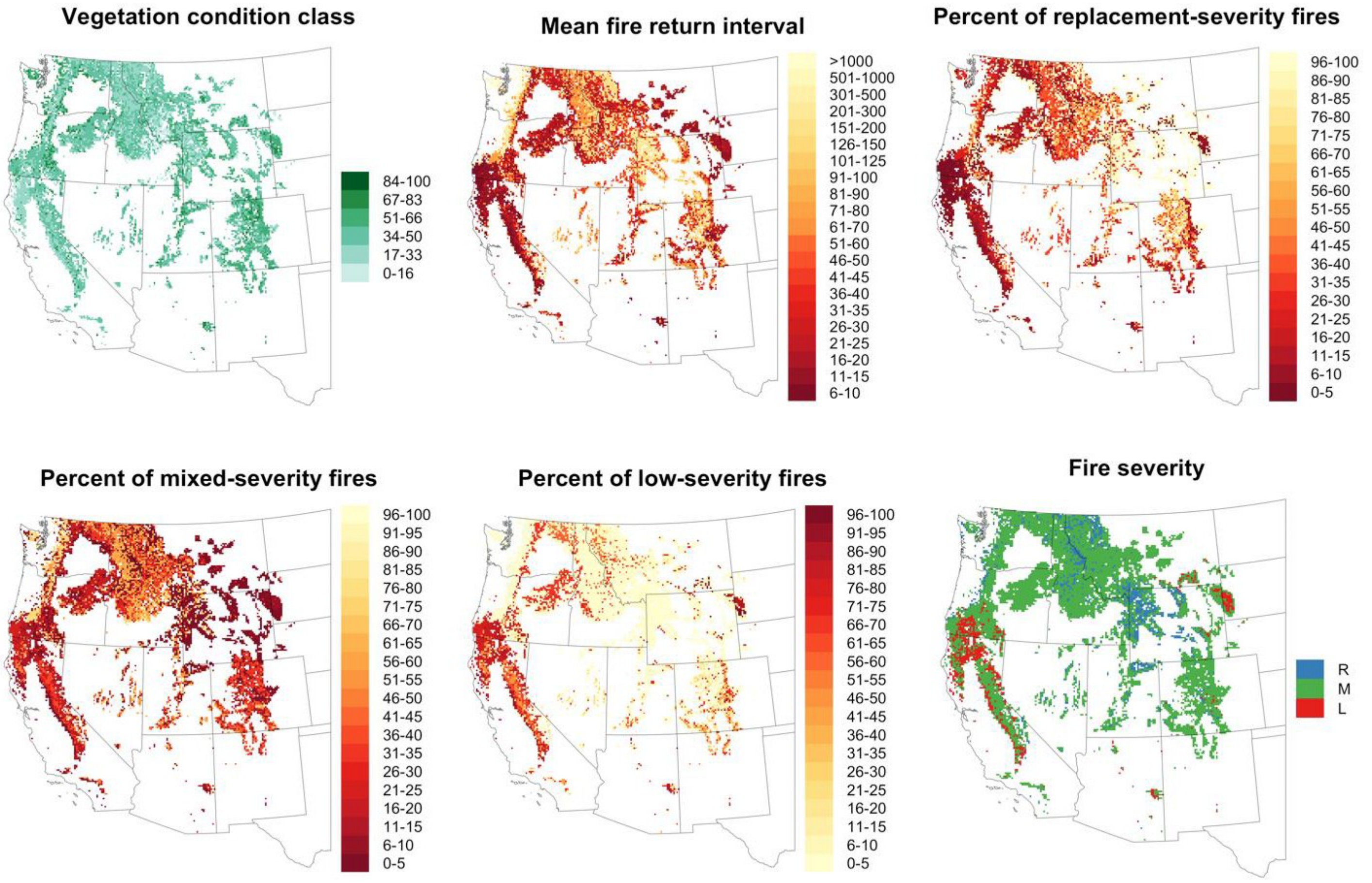
Appendix Figure IV-2. Maps of the mean MPB-affected acres during 1996 and 2015 and the normalized transformation.



Appendix Figure IV-3. Maps of forest stand variables in the MPB-affected area. The GAP status code from 0 to 4 indicates different management for biodiversity, specifically, "unclassified", "disturbance events allowed", "disturbance events suppressed", "subject to extractive or OHV use", and "unknown mandate for protection" respectively. More explanations of variables stand age, tree density, ratio of large trees and ratio of old trees can be found in Table IV-1.

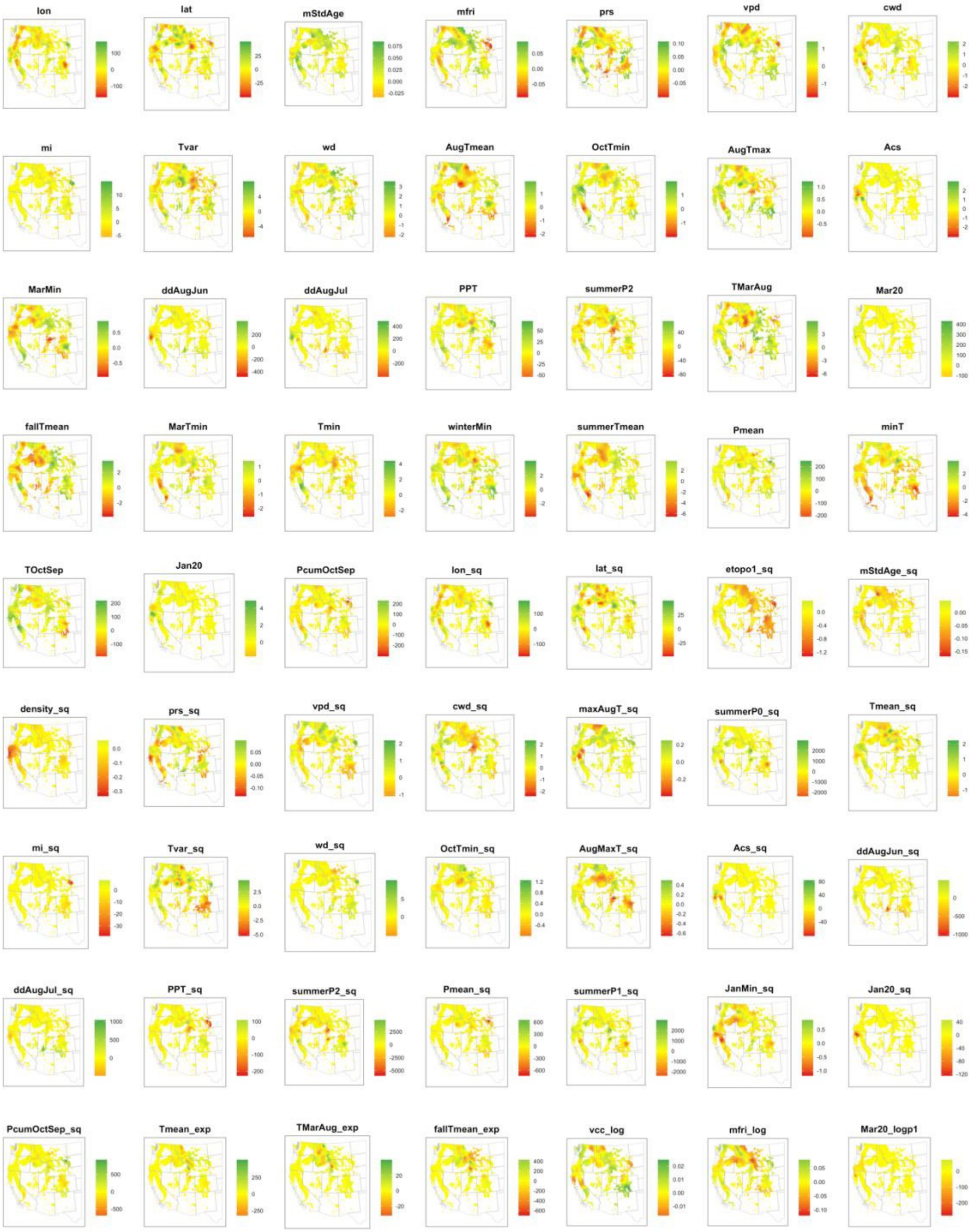


Appendix Figure IV-4. Maps of variables related to the recent fire suppression in the MPB-affected area. More explanations of variables can be found in Table IV-1.

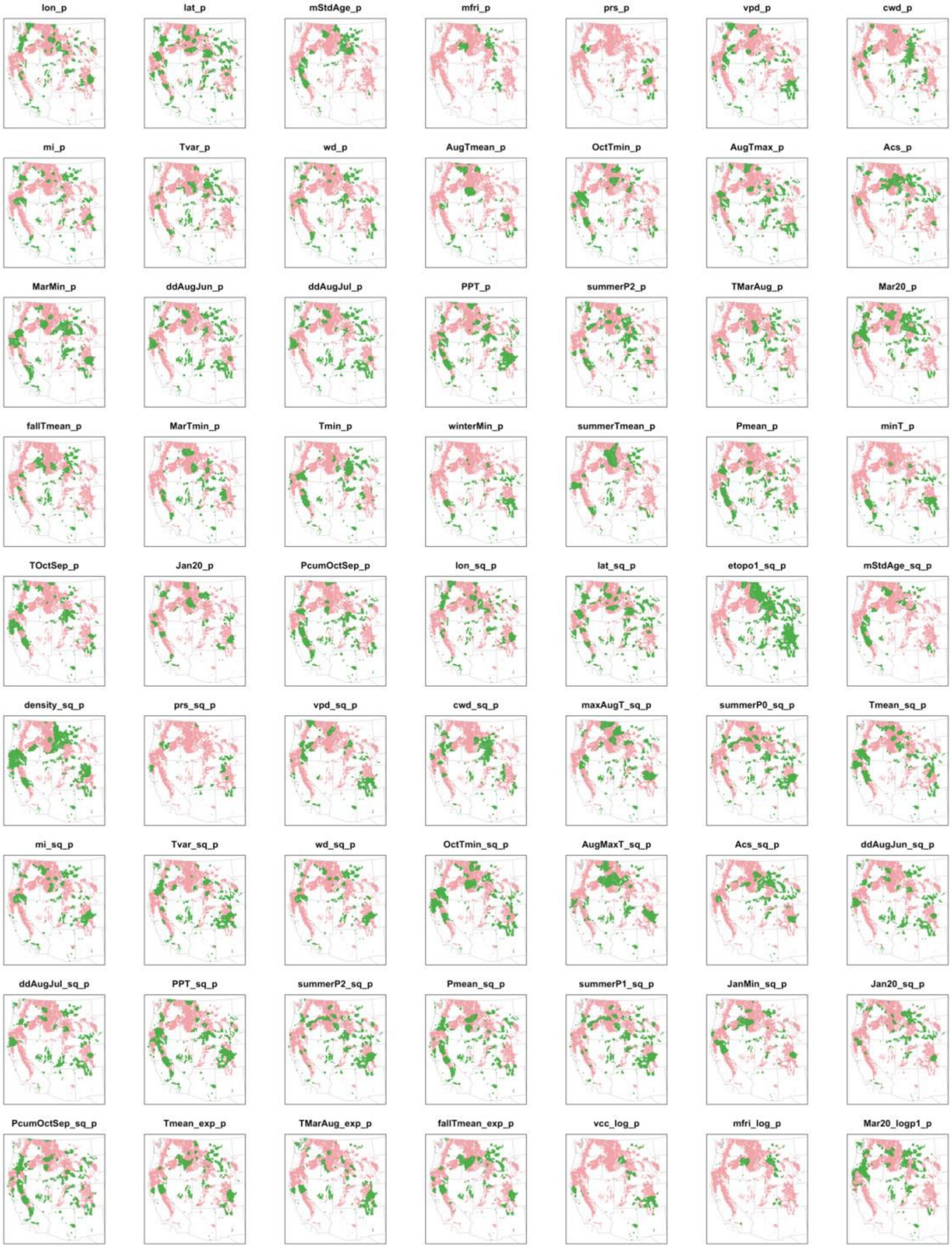


Appendix Figure IV-5. Maps of LANDFIRE variables related to the long-term effects of fire suppression in the MPB-affected area. More explanations of variables except fire severity can be found in Table IV-1. In the map of fire severity, the grid cells with a percent of replacement-severity fires higher than 80% and mean fire return interval higher than 100 years are labeled as replacement severity ("R"), the grid cells with a percent of low-severity fires higher than 80% and mean fire return interval less or equals to 20 years are labeled as low severity ("L"), and the rest grid cells are labeled as mixed severity ("M").

Notes for Appendix Figure IV-6-8 (next pages):
Variables “lon”, “lat”, “ etopo1” are longitude, latitude and elevation respectively. Variable names ended with “_sq” indicate the squared transformation of variable. Variable names ended with “log” indicate the logarithm transformation of variable, while a variable name ended with “_logp1” indicates an adjustment of values by adding one to avoid the logarithm of zeros. Variable names ended with “exp” indicate the exponential transformation of variable. Detailed explanations for bioclimatic and non-climatic variables can be found in Appendix Table IV-2 and Table IV-1.

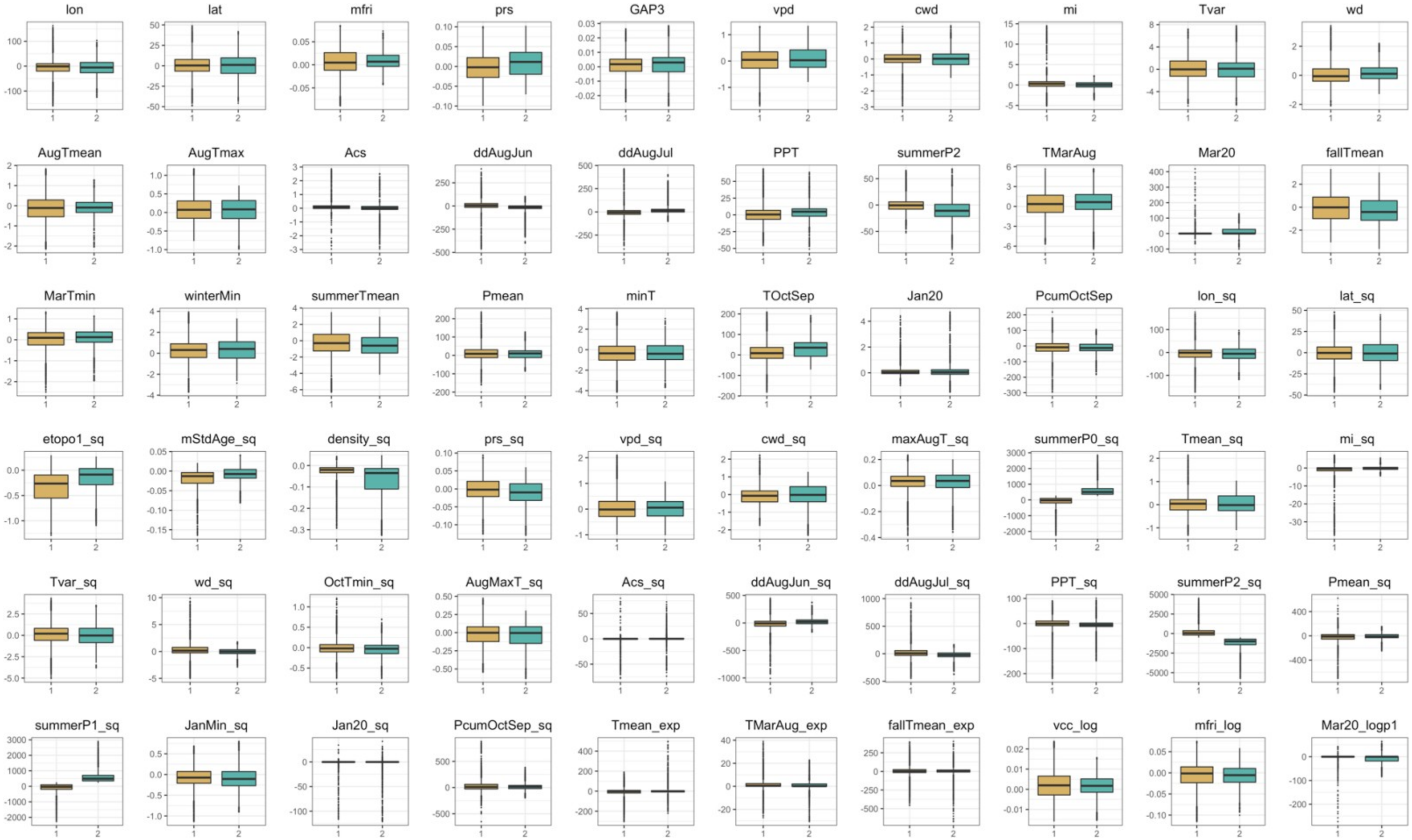


Appendix Figure IV-6. Coefficients of the GWR model.



Appendix Figure IV-7. P values for the coefficients of the GWR model.

Appendix Figure IV-8. Adjusted p values for the coefficients of the GWR mode.



Appendix Figure IV-9. Boxplots of the GWR coefficients (y-axis) in the two clusters (x-axis).

Appendix Table II-1. Data sources.

Dataset	Full name	Raw data type	Spatial coverage	Spatial resolution
CRU TS	Climate Research Unit Time Series	raster	worldwide	0.5-degree
CRU CL	Climate Research Unit Climatology	raster	worldwide	10-minute
Daymet	Daily meteorological observations	raster	North America	1 km
IDS	Insect and Disease Detection Survey	vector, polygon	United States	1:100K quad
HFP	Forest Health Project Aerial Overview Survey	vector, point	British Columbia	1:100K quad?
FHA	Forest Health Aerial Survey	vector, point	Alberta	1:100K quad?
Little Map	Digital Representations of Tree Species Range Maps	vector, polygon	North America	n.a.

Appendix Table II-1 (continued)

Temporal coverage	Temporal resolution	Source
1901-2016	monthly	University of East Anglia
1961-1990	monthly	University of East Anglia
1980-present	daily	Oak Ridge National Laboratory Distributed Active Archive Center
1997-2015	yearly	USDA Forest Service
1999-present	yearly	Ministry of Forests, Lands and Natural Resource Operations
2006-2016	yearly	Alberta Agriculture and Forestry
n.a.	decadal	United States Geological Survey

Appendix Table II-1 (continued)

Link
https://crudata.uea.ac.uk/cru/data/hrg/
https://crudata.uea.ac.uk/cru/data/hrg/
https://daac.ornl.gov/cgi-bin/dataset_lister.pl?p=32
https://foresthealth.fs.usda.gov/portal/Flex/IDS
https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/
http://www.atozmapsdata2.com/downloads/Country/Modern/C-USA-USGSTreeSpecies-index.html

Appendix Table II-2. List of bioclimatic variables.

No.	Process	Rationale	Variable	Variable name
1	cold mortality	unseasonably and/or extremely low temperatures can cause direct mortality of over-wintering insects	Tmin	minimum temperatures from November to March
2			minT	minimum daily temperature
3			JanTmin	average minimum January temperature
4			OctTmin	average minimum October temperature
5			MarTmin	average minimum March temperature
6			Ecs	early cold snap
7			Lcs	late cold snap
8			Ncs	number of cold snaps
9			Acs	average duration of a cold snap
10			drop0	days without temperature drops
11			drop5	days with a 0-5 °C drop
12			drop10	days with a 5-10 °C drop
13			drop15	days with a 10-15 °C drop
14			drop20	days with a 15-20 °C drop
15			drop20plus	days with a > 20 °C drop
16			max.drop	the largest temperature drop
17			Oct20	days with a ≤ -20 °C temperature in October
18			Oct30	days with a ≤ -30 °C temperature in October
19			Oct40	days with a ≤ -40 °C temperature in October
20			OctMin	minimum daily temperature in October
21			Jan20	days with a ≤ -20 °C temperature in January
22			Jan30	days with a ≤ -30 °C temperature in January
23			Jan40	days with a ≤ -40 °C temperature in January
24			JanMin	minimum daily temperature in January
25			Mar20	days with a ≤ -20 °C temperature in March
26			Mar30	days with a ≤ -30 °C temperature in March
27			Mar40	days with a ≤ -40 °C temperature in March
28			MarMin	minimum daily temperature in March
29			winter20	days with a ≤ -20 °C temperature

30			winter30	days with a ≤ -30 °C temperature
31			winter40	days with a ≤ -40 °C temperature
32			winterMin	minimum winter temperature
33	adaptive seasonality	temperature conditions can promote outbreaks by allowing for a one-year life cycle and near-synchronous adult emergence	Tmean	mean temperature during the beetle life cycle
35			Tvar	seasonal temperature variation
36			fallTmean	mean fall temperature
37			TOctSep	mean temperature from October to September
38			TMarAug	mean temperature from March to August
39			ddAugJun	day-degrees above 5.5 from August to June
40			ddAugJul	day-degrees above 5.5 from August to July
41			AugTmax	maximum August temperature
42			AugMaxT	maximum daily August temperature
43			maxAugT	frequency of ≥ 18.3 °C temperature in August
44			OptTsum	number of days with optimum summer temperatures
45			summerTmean	average summer temperature
46			maxT	maximum daily temperature
47			summerT40	number of days with summer temperatures > 40 °C
48			AugTmean	mean August temperature
49	tree resistance	droughts stress trees have lower defensive capabilities than healthy trees	cv.gsp	CV of growing season precipitation
50			Pmean	mean annual precipitation
51			summerP0	summer precipitation in the current year
52			summerP1	summer precipitation in the previous year
53			summerP2	cumulative summer precipitation
54			POctSep	water year precipitation
55			PcumOctSep	cumulative water year precipitation
56			PMarAug	precipitation from March to August
57			wd	water deficit
58			vpd	vapor pressure deficit
59			cwd	cumulative climatic water deficit
60			mi	moisture index
61			pt.coef	Priestley-Taylor coefficient

62	PPT	6-year precipitation

Appendix Table II-2 (continued)

No.	Description
1	mean of monthly average of minimum temperature from November to March
2	minimum of daily minimum temperature from August to July
3	monthly average daily minimum temperature in January
4	monthly average daily minimum temperature in October
5	monthly average daily minimum temperature in March
6	early cold snap occurring mid-October through November
7	late cold snap occurring between March through mid-April
8	total number of cold snaps occurring throughout the winter
9	average duration of a cold snap during winter
10	number of days of positive temperature changes in average daily winter temperatures on any two consecutive days
11	number of days when a 0-5 °C drop on any two consecutive days in temperature is observed during winter
12	number of days when a 5-10 °C drop on any two consecutive days in temperature is observed during winter
13	number of days when a 10-15 °C drop on any two consecutive days in temperature is observed during winter
14	number of days when a 15-20 °C drop on any two consecutive days in temperature is observed during winter
15	number of days when a > 20 °C drop on any two consecutive days in temperature is observed during winter
16	the largest drop in daily average temperature during winter
17	number of days with minimum temperatures at or below -20 °C in October
18	number of days with minimum temperatures at or below -30 °C in October
19	number of days with minimum temperatures at or below -40 °C in October
20	minimum of daily minimum temperature in October
21	number of days with minimum temperatures at or below -20 °C in January
22	number of days with minimum temperatures at or below -30 °C in January
23	number of days with minimum temperatures at or below -40 °C in January
24	minimum of daily minimum temperature in January
25	number of days with minimum temperatures at or below -20 °C in March
26	number of days with minimum temperatures at or below -30 °C in March
27	number of days with minimum temperatures at or below -40 °C in March
28	minimum of daily minimum temperature in March
29	number of days with minimum temperatures at or below -20 °C during winter
30	number of days with minimum temperatures at or below -30 °C during winter

31	number of days with minimum temperatures at or below -40 °C during winter
32	minimum of daily minimum temperature during winter
33	mean of monthly average of daily mean temperature from August to July
35	standard deviation of monthly average of daily mean temperature from August to July
36	mean of monthly average of daily mean temperature from September to November in the previous year
37	mean of monthly average of daily mean temperature from October to September in the current water year
38	mean of monthly average of daily mean temperature from March to August
39	accumulated degree days above 5.5 °C from August to June
40	accumulated degree days above 5.5 °C from August to July
41	monthly average of daily maximum temperature in August
42	maximum of daily maximum temperature in August
43	the frequency of maximum daily temperatures not less than 18.3 °C during August
44	optimum temperature range for mountain pine beetle flight is between 18–30 °C
45	mean of monthly average of daily mean temperature from June to August in the current year
46	maximum daily temperature from August to July
47	number of days with maximum temperatures higher than 40°C during summer
48	monthly average of daily mean temperature in August
49	coefficient of variation of daily precipitation from April to June
50	mean of monthly precipitation from August to July
51	sum of precipitation from June to August in the current year
52	sum of precipitation from June to August in the previous year
53	cumulative precipitation from June to August in the current and previous year
54	sum of precipitation from October and September in the previous year
55	cumulative precipitation from October to September in the current and previous year
56	sum of precipitation from March to August
57	the yearly sum of rainfall minus evapotranspiration in months with mean air temperature > 0 °C
58	average monthly vapor pressure deficit in the current and previous 5 years from May to October
59	cumulative climatic water deficit (i.e., the difference between the potential evapotranspiration and the actual evapotranspiration) in the current and previous 5 years from May to October
60	the ratio of annual precipitation to annual potential evapotranspiration
61	the ratio of actual evapotranspiration to equilibrium evapotranspiration

62 cumulative monthly October-August precipitation in the current and previous 5 years

Appendix Table II-2 (continued)

No.	Year (t as the calendar year of outbreak)	Temporal resolution	Unit	Reference	Dataset
1	Nov [t-1] - Mar [t]	monthly	°C	Fauria & Johnson, 2009	CRU
2	Aug [t-1] - Jul [t]	daily	°C	Aukema et al., 2008	Daymet
3	Jan [t]	monthly	°C	Thomson 2009; Rosenberger et al. 2017b	CRU
4	Oct [t-1]	monthly	°C	Bentz et al. 1991; Chapman et al., 2012	CRU
5	Mar [t]	monthly	°C	Bentz et al. 1991; Chapman et al., 2012	CRU
6	Oct 15th [t-1] - Nov 30th [t-1]	daily	binary	Sambaraju et al., 2012	Daymet
7	Mar 31st [t] - Apr 15th [t]	daily	binary	Sambaraju et al., 2012	Daymet
8	Dec 1st [t-1] - Feb 28/29th [t]	daily	one	Sambaraju et al., 2012	Daymet
9	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
10	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
11	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
12	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
13	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
14	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
15	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
16	Dec 1st [t-1] - Feb 28/29th [t]	daily	°C	Sambaraju et al., 2012	Daymet
17	Oct 1st [t-1] - Oct 31st [t-1]	daily	day	Thomson 2009	Daymet
18	Oct 1st [t-1] - Oct 31st [t-1]	daily	day	Thomson 2009	Daymet
19	Oct 1st [t-1] - Oct 31st [t-1]	daily	day	Thomson 2009	Daymet
20	Oct 1st [t-1] - Oct 31st [t-1]	daily	day	Thomson 2009	Daymet
21	Jan 1st [t] - Jan 31st [t]	daily	day	Thomson 2009	Daymet
22	Jan 1st [t] - Jan 31st [t]	daily	day	Thomson 2009	Daymet
23	Jan 1st [t] - Jan 31st [t]	daily	day	Thomson 2009	Daymet
24	Jan 1st [t] - Jan 31st [t]	daily	day	Thomson 2009	Daymet
25	Mar 1st [t] - Mar 31st [t]	daily	day	Thomson 2009	Daymet
26	Mar 1st [t] - Mar 31st [t]	daily	day	Thomson 2009	Daymet

27	Mar 1st [t] - Mar 31st [t]	daily	day	Thomson 2009	Daymet
28	Mar 1st [t] - Mar 31st [t]	daily	day	Thomson 2009	Daymet
29	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Thomson 2009	Daymet
30	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
31	Dec 1st [t-1] - Feb 28/29th [t]	daily	day	Sambaraju et al., 2012	Daymet
32	Dec [t-1] - Feb [t]/Dec 1st [t-1] - Feb 28/29th [t]	daily	°C	Safranyik et al., 2010; Buotte et al., 2017	Daymet
33	Aug [t-1] - Jul [t]	monthly	°C	Powell et al., 2000; Sambaraju et al., 2012	CRU
35	Aug [t-1] - Jul [t]	monthly	unitless	Powell et al., 2000	CRU
36	Sep [t-1] - Nov [t-1]	monthly	°C	Buotte et al., 2016	CRU
37	Oct [t-1] - Sep [t]	monthly	°C	Preisler et al., 2012	CRU
38	Mar [t] - Aug [t]	monthly	°C	Creeden et al., 2014	CRU
39	Aug 1st [t-1] - Jun 30th [t]	daily	°C	Aukema et al., 2008; Safranyik et al., 2010	Daymet
40	Aug 1st [t-1] - Jul 31st [t]	daily	°C	Aukema et al., 2008; Safranyik et al., 2010	Daymet
41	Aug [t]	monthly	°C	Safranyik et al., 2010	CRU
42	Aug 1st [t-1] - Jul 31st [t]	daily	°C	Aukema et al., 2008	Daymet
43	Aug 1st [t] - Aug 31st [t]	daily	°C	Safranyik et al., 2010	Daymet
44	Aug 1st [t] - Aug 31st [t]	daily	day	Sambaraju et al., 2012	Daymet
45	Jun [t] - Aug [t]	monthly	°C	Sambaraju et al., 2012	CRU
46	Aug 1st [t-1] - Jul 31st [t]	daily	°C	Aukema et al., 2008	Daymet
47	Jun 1st - Aug 31st [t]	daily	day	Sambaraju et al., 2012	Daymet
48	Aug [t]	monthly	°C	Aukema et al., 2008	CRU
49	Apr [t] - Jun [t]	daily	unitless	Safranyik et al., 2010	Daymet
50	Aug [t-1] - Jul [t]	monthly	mm	Chapman et al., 2012	CRU
51	Jun [t] - Aug [t]	monthly	mm	Campbell et al., 2007	CRU
52	Jun [t-1] - Aug [t-1]	monthly	mm	Preisler et al., 2012	CRU
53	Jun [t-1] - Aug [t-1], Jun [t] - Aug [t]	monthly	mm	Preisler et al., 2012	CRU
54	Oct [t-2] - Sep [t-1]	monthly	mm	Preisler et al., 2012	CRU
55	Oct [t-2] - Sep [t]	monthly	mm	Preisler et al., 2012	CRU

56	Mar [t] - Aug [t]	monthly	mm	Creeden et al., 2014	CRU
57	Aug [t-1] - Jul [t]	monthly	mm	Safranyik et al., 2010	CRU
58	May [t-5] - Oct [t-5], May [t-4] - Oct [t-4], May [t-3] - Oct [t-3], May [t-2] - Oct [t-2], May [t-1] - Oct [t-1], May [t] - Oct [t]	monthly	pascal	Buotte et al., 2017	CRU
59	May [t-5] - Oct [t-5], May [t-4] - Oct [t-4], May [t-3] - Oct [t-3], May [t-2] - Oct [t-2], May [t-1] - Oct [t-1], May [t] - Oct [t]	monthly	mm	Buotte et al., 2017	CRU
60	Aug 1st [t-1] - Jul 31st [t]	daily	unitless	Davis et al., 2016	Daymet
61	Aug 1st [t-1] - Jul 31st [t]	daily	unitless	Davis et al., 2016	Daymet
62	Oct [t-6] - Aug [t-5], Oct [t-5] - Aug [t-4], Oct [t-4] - Aug [t-3], Oct [t-3] - Aug [t-2], Oct [t-2] - Aug [t-1], Oct [t-1] - Aug [t]	monthly	mm	Buotte et al., 2017	CRU

Notes: A cold snap is a minimum of four continuous days of average winter temperatures at or below -20 °C.

Appendix Table III-1. Descriptions of predictors applied in this study.

No.	Factor	Variable group	Variable	Description	Reference
1	climate	seasonal temperature	Tmean	mean of monthly average of daily mean temperature from August to July	Powell et al., 2000; Sambaraju et al., 2012
2			Tvar	standard deviation of monthly average of daily mean temperature from August to July	Powell et al., 2000
3			fallTmean	mean of monthly average of daily mean temperature from September to November in the previous year	Buotte et al., 2016
4			TOctSep	mean of monthly average of daily mean temperature from October to September in the current water year	Preisler et al., 2012
5			TMarAug	mean of monthly average of daily mean temperature from March to August	Creeden et al., 2014
6			ddAugJun	accumulated degree days above 5.5 °C from August to June	Aukema et al., 2008; Safranyik et al., 2010
7			ddAugJul	accumulated degree days above 5.5 °C from August to July	Aukema et al., 2008; Safranyik et al., 2010
8		heat	AugTmax	monthly average of daily maximum temperature in August	Safranyik et al., 2010
9			AugMaxT	maximum of daily maximum temperature in August	Aukema et al., 2008
10			maxAugT	the frequency of maximum daily temperatures not less than 18.3 °C during August	Safranyik et al., 2010

11		OptTsum	optimum temperature range for beetle flight is between 18–30 °C	Sambaraju et al., 2012
12		summerTmean	mean of monthly average of daily mean temperature from June to August in the current year	Sambaraju et al., 2012
13		maxT	maximum daily temperature from August to July	Aukema et al., 2008
14		AugTmean	monthly average of daily mean temperature in August	Aukema et al., 2008
15	cold	Tmin	mean of monthly average of minimum temperature from November to March	Fauria & Johnson, 2009
16		minT	minimum of daily minimum temperature from August to July	Aukema et al., 2008
17		JanTmin	monthly average daily minimum temperature in January	Thomson 2009; Rosenberger et al. 2017b
18		OctTmin	monthly average daily minimum temperature in October	Bentz et al. 1991; Chapman et al., 2012
19		MarTmin	monthly average daily minimum temperature in March	Bentz et al. 1991; Chapman et al., 2012
20		Acs	average duration of a cold snap during winter	Sambaraju et al., 2012
21		max.drop	the largest drop in daily average temperature during winter	Sambaraju et al., 2012
22		OctMin	minimum of daily minimum temperature in October	Thomson 2009

23		Jan20	number of days with minimum temperatures at or below -20 °C in January	Thomson 2009
24		JanMin	minimum of daily minimum temperature in January	Thomson 2009
25		Mar20	number of days with minimum temperatures at or below -20 °C in March	Thomson 2009
26		MarMin	minimum of daily minimum temperature in March	Thomson 2009
27		winterMin	minimum of daily minimum temperature during winter	Safranyik et al., 2010; Buotte et al., 2017
28	water deficit	Pmean	mean of monthly precipitation from August to July	Chapman et al., 2012
29		summerP0	sum of precipitation from June to August in the current year	Campbell et al., 2007
30		summerP1	sum of precipitation from June to August in the previous year	Preisler et al., 2012
31		summerP2	cumulative precipitation from June to August in the current and previous year	Preisler et al., 2012
32		POctSep	sum of precipitation from October and September in the previous year	Preisler et al., 2012
33		PcumOctSep	cumulative precipitation from October to September in the current and previous year	Preisler et al., 2012
34		PMarAug	sum of precipitation from March to August	Creeden et al., 2014
35		wd	the yearly sum of rainfall minus evapotranspiration in months with mean air temperature > 0 °C	Safranyik et al., 2010

36			vpd	average monthly vapor pressure deficit in the current and previous 5 years from May to October	Buotte et al., 2017
37			cwd	cumulative climatic water deficit (i.e., the difference between the potential evapotranspiration and the actual evapotranspiration) in the current and previous 5 years from May to October	Buotte et al., 2017
38			mi	the ratio of annual precipitation to annual potential evapotranspiration	Davis et al., 2016
39			PPT	cumulative monthly October-August precipitation in the current and previous 5 years	Buotte et al., 2017
40	vegetation	tree density	density	number of trees per hectare	This study
41		stand age	age	median stand age in years	Buotte et al., 2017
42		host presence	vgt	binary data for the presence or absence of eight core host species	This study
43	beetle	beetle presence in the previous years	btl_t1	binary data for the presence or absence of beetle outbreak in the year before current outbreak year	This study
44			btl_t2	binary data for the presence or absence of beetle outbreak two years before current outbreak year	This study
45		neighboring beetle presence in the previous years	sum9_t1	the summary of beetle presence of the nearest eight grid cells and the center grid cell in the year before the current outbreak year	This study

46	sum9_t2	the summary of beetle presence of the nearest eight grid cells and the center grid cell two years before the current outbreak year	This study
47	sum9_diff	the difference of beetle presence summary of the nearest eight grid cells and the center grid cell in the previous two years (i.e., sum9_t1 - sum9_t2)	This study

Appendix Table III-2. Variable groups applied in the random selection of predictors in generalized additive models.

No.	Variable group	Variables
1	cold0	Jan20, Mar20, Acs, max.drop
2	cold	JanTmin, MarTmin, OctTmin, Tmin, OctMin, JanMin, MarMin, winterMin, minT
3	seasonal	TMarAug, fallTmean, Tmean, Tvar, TOctSep, ddAugJul, ddAugJun
4	heat	summerTmean, AugTmean, AugTmax, maxAugT, OptTsum, AugMaxT, maxT
5	water	PMarAug, summerP0, summerP1, summerP2, Pmean, POctSep, PcumOctSep, PPT
6	water1	wd, vpd, mi, cwd
7	tree	age, density
8	location	lon, lat, etopo1
9	beetle	btl_t1, btl_t2, sum9_t1, sum9_t2, sum9_diff

Appendix Table III-2 (continued)

Rationale
categorical variables related to cold-induced mortality
continuous variables related to cold-induced mortality
seasonal temperatures related to seasonal synchronization
summer temperatures related to adult emergence
water conditions from precipitation related to tree growth and resistance
water conditions from both precipitation and evapotranspiration related to tree growth and resistance
vegetation dynamics related to tree susceptibility and beetle dispersal
spatial variables related to local interactions among different factors
beetle pressure related to population attraction and competition

Appendix Table III-3. A list of performance metrics applied in this study and their comparisons for usage.

Metrics	Description
Accuracy	the number of correct positive and negative results divided by the total number of grid cells
Sensitivity / Precision	the number of true positives divided by the number of true positives and false positives
Specificity	the number of true negatives divided by the number of false negatives and true negatives
Recall	the number of true positives divided by the number of true positives and false negatives
F-score	the harmonic average of the precision and recall
Kappa statistic	a measure of agreement between accuracy and perfectly accurate results
TSS	a measure takes into account both omission and commission errors
AUC	a measure avoids the supposed subjectivity in the threshold selection process
AIC	estimates the relative amount of information lost by a given model
R squared	the proportion of the variance in the dependent variable that is predictable from the independent variable(s)
Adjust R squared	a modified version of R-squared that has been adjusted for the number of predictors in the model

Appendix Table III-3 (continued)

Metrics	Formula
Accuracy	(a+d)/n
Sensitivity / Precision	a/(a+c)
Specificity	d/(b+d)
Recall	a/(a+b)
F-score	2 * precision * recall / (precision + recall)
Kappa statistic	((a+d)/n-((a+b)*(a+c)+(c+d)*(d+b))/n^2)/1-((a+b)*(a+c)+(c+d)*(d+b))/n^2
TSS	sensitivity+specificity-1
AUC	the area under a ROC Curve, which is a plot of 1- specificity against to sensitivity
AIC	2K – 2 * ln (L); K - the number of estimated parameters; L - the maximum value of the likelihood function
R squared	1 - SS_{res}/SS_{tot} ; SS_{res} - residual sum of squares; SS_{tot} - total sum of squares
Adjust R squared	R_2 - (1- R_2)*p/(n-p-1); p - number of parameters, n - number of observations

Appendix Table III- 3 (continued)

Metrics	Advantage	Drawback
Accuracy	quantifies overall accuracy	dependent on threshold and prevalence
Sensitivity / Precision	quantifies omission errors	dependent on threshold and prevalence
Specificity	quantifies commission errors	dependent on threshold and prevalence
Recall	quantifies omission errors	dependent on threshold and prevalence
F-score	balances the use of precision and recall	gives equal importance to precision and recall
Kappa statistic	takes into account the possibility of the agreement occurring by chance	dependent on prevalence
TSS	independent of prevalence	dependent on threshold
AUC	independent of prevalence and threshold	weights omission and commission errors equally
AIC	captures the tradeoff between the model's accuracy and its complexity	not consistent
R squared	simple to apply	risk of overfitting
Adjust R squared	takes into account the penalty for overfitting from extra parameters	not different from R squared in large samples

Notes: The letters a, b, c, d indicate the quantity of different predictions shown as below table.

	Model prediction	
Observation	Presence	Absence
Presence	a	b
Absence	c	d

Appendix Table III-4. Coefficients of z-scored predictors without p values and coefficients of raw predictors with p values in the generalized linear models.

	Model 1				Model 2		
Variable	Coefficient (a)	Coefficient (b)	Pr(>|z|)	Variable	Coefficient (a)	Coefficient (b)	Pr(>|z|)
Tmean	-8.997	-1.58E+00	***	lon:vpd	-5.262	-4.21E-06	***
ddAugJul	5.666	7.70E-03	***	lat_cub	-5.008	-4.37E-04	***
ddAugJun	-5.642	-7.73E-03	***	cwd_sq	-4.869	-2.08E-05	***
AugTmean	-4.560	-8.97E-01	***	etopo1	4.597	3.90E-02	***
TOctSep	4.203	7.45E-01	***	lat:Tvar	3.955	8.88E-02	***
Tmin	3.911	5.53E-01	***	maxAugT	-3.855	-2.22E-01	***
AugTmax	2.858	4.86E-01	***	lat:maxAugT	3.646	1.40E-02	***
vpd	-2.030	-1.81E-05	***	lon:lat:etopo1	3.412	4.41E-06	***
summerTmean	2.025	3.92E-01	***	lat:Tmean	-3.238	-1.24E-01	***
PcumOctSep	1.783	1.86E-03	***	lat:summerP0	2.994	7.89E-04	***
minT	1.597	1.31E-01	***	etopo1:AugTmax	-2.886	-5.52E-04	***
winterMin	-1.543	-1.27E-01	***	lon:OctTmin	-2.880	-2.48E-02	***
mi	-1.011	-9.28E-01	***	wd	2.817	-1.28E-02	***
JanMin	-0.846	-6.92E-02	***	Tvar	-2.770	-1.11E+01	***
Jan20	-0.720	-9.32E-02	***	lon:mi	2.759	2.35E-01	***
summerP1	-0.706	-7.46E-03	***	AugTmean_cub	2.723	9.35E-04	***
POctSep	-0.626	-1.29E-03	***	lat:mi	-2.709	-1.26E-01	***
PPT	-0.559	-1.98E-04	***	lon:Tmean	2.576	3.16E-01	***
OptTsum	-0.461	-1.52E-02	***	lat_sq	-2.418	-5.95E-03	
PMarAug	-0.394	-2.40E-03	***	etopo1:cwd	2.418	1.85E-06	***
Pmean	-0.383	-9.93E-03	***	lon:AugTmean	2.361	6.01E-02	***
Tvar	0.373	1.85E-01	***	Acs	-2.339	-7.04E-01	***
OctTmin	0.371	6.62E-02	***	Tmean	-2.308	4.17E+01	***
MarMin	0.338	2.89E-02	***	mi	2.289	3.15E+01	***
JanTmin	0.311	3.75E-02	***	lon:AugMaxT	-2.270	1.44E-03	*
MarTmin	-0.246	-3.04E-02	***	lat:TMarAug	2.226	-7.04E-03	
summerP0	0.219	2.51E-03	***	ddAugJun	-2.197	-2.11E-02	
maxAugT	0.212	2.96E-02	***	etopo1:ddAugJul	2.189	9.90E-06	***

Mar20	-0.177	-3.50E-02	***	vpd_sq	-2.169	-1.91E-10	***
fallTmean	0.136	2.70E-02	**	lat:Mar20	2.147	2.49E-02	***
Acs	-0.128	-2.66E-02	***	JanTmin_sq	-2.142	-4.23E-03	***
max.drop	-0.080	-2.44E-02	***	lon:wd	2.126	-9.26E-05	***
OctMin	0.079	1.46E-02	***	lat:summerP2	2.100	2.65E-04	***
AugMaxT	-0.050	-1.05E-02	***	etopo1:mi	2.096	1.11E-03	***
maxT	0.042	1.05E-02	***	etopo1_sq	-2.076	-2.09E-06	***
cwd	-0.027	-1.66E-06		ddAugJul	-1.999	1.15E-02	
TMarAug	0.008	8.62E-03		PPT_sq	-1.971	-6.45E-08	***
wd	-0.008	-2.38E-05		lat:MarMin	1.945	1.82E-02	***

Appendix Table III-4 (continued)

	Model 3				Model 4		
Variable	Coefficient (a)	Coefficient (b)	Pr(>|z|)	Variable	Coefficient (a)	Coefficient (b)	Pr(>|z|)
lat:TMarAug	2.192	6.55E-02	***	density:Tmean	-2.433	-3.27E-05	***
AugTmean_cub	1.645	8.46E-04	***	lat:TMarAug	1.976	5.74E-02	***
sum9_diff	-1.563	-1.05E+00	***	AugTmean_cub	1.939	8.86E-04	***
lon:sum9_diff	-1.327	-8.71E-03	***	sum9_diff	-1.515	-9.98E-01	***
lon:lat:etopo1	1.326	2.00E-06	***	lat_cub	-1.433	-4.07E-04	***
Tmean	-1.310	1.68E+01	***	TMarAug_cub	-1.429	-6.53E-04	***
TMarAug_cub	-1.305	-7.35E-04	***	lon:lat:etopo1	1.386	1.76E-06	***
etopo1	1.274	1.54E-02	***	density:TMarAug	1.331	4.99E-06	**
JanTmin_sq	-1.182	-4.45E-03	***	etopo1:vpd	-1.313	-9.77E-09	***
sum9_t2	1.178	5.57E-01	***	JanTmin_sq	-1.274	-4.23E-03	***
etopo1:vpd	-1.177	-9.95E-09	***	lon:sum9_diff	-1.245	-8.07E-03	***
lat:maxAugT	1.173	6.63E-03	***	lon:Jan20	-1.244	2.45E-03	***
lon:Jan20	-1.153	1.99E-03	**	sum9_t2	1.175	5.59E-01	***
etopo1:cwd	1.113	8.52E-07	*	density:TOctSep	1.134	2.67E-05	***
vpd_sq	-1.109	-1.19E-10	***	density:vpd	1.131	1.18E-10	***
minT_cub	1.108	5.88E-05	***	lat:maxAugT	1.108	5.64E-03	***
JanMin_cub	-1.079	-5.10E-05	***	JanMin_cub	-1.100	-4.75E-05	***
lat_cub	-1.072	-5.03E-04	***	Acs	-1.094	-6.88E-01	***
lon:Tmean	1.028	9.24E-02	***	etopo1	1.077	1.28E-02	***
etopo1_sq	-0.974	-1.12E-06	***	etopo1:AugTmean	1.068	5.74E-04	***
lon:JanTmin	0.960	1.65E-02	***	etopo1_sq	-1.061	-9.42E-07	***
lat:fallTmean	0.952	6.54E-02	***	minT_cub	1.054	3.83E-05	***
maxAugT	-0.938	-2.49E-02		lat:AugTmean	-1.049	3.38E-02	***
lon:vpd	-0.920	-2.68E-06	***	lon:JanTmin	1.026	1.79E-02	***
lat:summerTmean	0.909	1.52E-02	*	etopo1:cwd	0.970	7.84E-07	*
lat:AugTmean	-0.909	3.58E-02	***	lat:summerTmean	0.966	1.39E-02	.
Acs	-0.907	-6.88E-01	***	lat_sq	-0.941	3.54E-02	***
etopo1:AugTmean	0.906	5.60E-04	***	maxAugT	-0.907	-1.05E-02	
lat:mi	-0.895	5.06E-02	*	OctMin	-0.900	-3.61E-01	***

OctMin	-0.871	-3.45E-01	***	Tvar	-0.876	-3.12E+00	***
lat:Tmean	-0.835	-1.47E-01	***	lat:OctTmin	-0.851	-8.05E-03	***
Jan20_cub	-0.828	-1.97E-04	***	Jan20_cub	-0.846	-2.07E-04	***
lon:Mar20	-0.822	-7.43E-04		lat:mi	-0.843	8.11E-02	***
PMarAug	0.781	-1.20E-02	*	Tmean	-0.841	1.65E+01	***
lat:OctTmin	-0.770	-1.15E-02	***	lon:Mar20	-0.840	-4.69E-04	
lat:cwd	-0.767	-4.94E-05		lon:OctMin	-0.828	-4.51E-03	***
lat_sq	-0.751	4.71E-02	***	PMarAug	0.817	-1.59E-02	**
Tvar	-0.749	-3.94E+00	***	etopo1:TOctSep	-0.815	-4.11E-04	**

Notes: Variables "lon", "lat", " etopo1" are longitude, latitude and elevation respectively and the rest variables are explained in Table III-1 and Appendix Table III-1. Only the top 38 predictors are listed. The letter "a" notes that the coefficients are from the model with scaled predictors and L1 regularization, and without p values. The letter "b" notes that the coefficients are from the model without scaling predictors and with p values. The semicolon ":" indicates the interactions between variables, the suffix "_sq" indicates the square of variable, and the suffix "_cub" indicates the cube of variable.

Appendix Table III-5. Assumptions in the species distribution modeling of mountain pine beetle outbreaks.

No.	Working assumption	Description
1	climatic determinism	species distributions are determined wholly or partly by aspects of climate
2	equilibrium	species are at equilibrium with their environments (i.e., suitable habitat is fully occupied)
3	dispersal	species are able to disperse to suitable locations and occupy the environmental niche space
4	individualism	each species responds independently to the environmental factors that determine its niche space and thus its habitat occupancy and distribution
5	niche conservatism	the niche envelope is a fixed and immutable characteristic of a species without changing over space and time
6	spatial stationarity	spatial autocorrelation and effects of environmental correlates are constant across the space
7	isotropic spatial autocorrelation	the process that causes the spatial autocorrelation acts in the same way in all directions
8	representativeness	relevant environmental gradients have been adequately sampled

Appendix Table III-5 (continued)

No.	Case study situation	Related to modeling process or output
1	satisfied; beetle development is temperature dependent	relevant climatic variables were included in the models
2	violated; the beetle has expanded to new areas that are colder	northern expansion showed a disequilibrium state
3	satisfied; the beetle has two dispersal mechanisms: short-distance and long-distance	dispersal-related climatic variables and neighboring beetle pressure were included in the models
4	violated; the beetle interacts with hosts, parasites and predators	specific biotic interaction data is not available at the study scale
5	violated; the beetle responds to climate and hosts differently across the space	interactions between location variables, climatic variables and host variables were included in the models
6	violated; variation exists in the effects of climate on beetle outbreaks	climatic variables were weighted by location variables in the interaction terms
7	violated; beetle dispersal impacted by climatic and biological factors are a complex mechanism	relevant information on beetle dispersal is not available at the study scale
8	unknown; the long-term history of large-scale beetle outbreaks were not completely known	currently available multi-year tree mortality data was used

Appendix Table III-5 (continued)

No.	Citations on the assumption	Citations on the case study situation
1	Araújo & Peterson 2012	Bentz et al. 1991; Powell et al. 2000
2	Guisan & Thuiller 2005; Elith & Leathwick 2009; Wiens et al. 2009; Araújo & Peterson 2012	Carroll et al. 2003; Safranyik et al. 2010; Cullingham et al. 2011
3	Wiens et al. 2009; Araújo & Peterson 2012	Chen et al. 2011; Lundquist et al. 2014
4	Wiens et al. 2009; Araújo & Peterson 2012	Safranyik et al. 2006; Walter et al. 2013
5	Wiens et al. 2009; Araújo & Peterson 2012	Weed et al. 2015; Cooke et al. 2017
6	Dormann et al. 2007	Raffa et al. 2013; Rosenberger et al. 2017a
7	Dormann et al. 2007	Robertson et al. 2009; Rosenberger et al. 2017b; de la Giroday et al. 2012
8	Elith & Leathwick 2009	Jarvis & Kulakowski 2015

Appendix Table IV-1. Data sources.

No.	Factor	Dataset	Full name	Version	Raw data type
1	climate	CRU TS	Climate Research Unit Time Series	4.01	raster
2	climate	CRU CL	Climate Research Unit Climatology	2	raster
3	climate	Daymet	Daily meteorological observations	3	raster
4	insect	IDS	Insect and Disease Detection Survey	n.a.	vector, polygon
5	vegetation	FSA	Forest Stand Age	n.a.	raster
6	vegetation	FIA	Forest Inventory and Analysis	8	raster
7	vegetation	GTD	Global Tree Density	n.a.	vector, point
8	fire	FPA FOD	Fire Program Analysis Fire-Occurrence Database	4	vector, point
9	fire	SIT-209	Situation Report	n.a.	tables, point
10	fire	FW FOD	Federal Wildland Fire Occurrence Data	n.a.	vector, point
11	fire	LF-CC	LANDFIRE Vegetation Condition Class	1.4.0	raster
12	fire	LF-MFRI	LANDFIRE Mean Fire Return Interval	1.2.0	raster
13	fire	LF-PRS	LANDFIRE Percent of Replacement Severity Fire	1.2.0	raster
14	fire	LF-PMS	LANDFIRE Percent of Mixed Severity Fire	1.2.0	raster
15	fire	LF-PLS	LANDFIRE Percent of Low Severity Fire	1.2.0	raster
16	land	PAD-US	Protected Areas Database of the United States Data	1.4	vector, polygon

Appendix Table IV-1 (continued)

No.	Relevant variables	Spatial resolution
1	monthly-based bioclimatic variables (see Appendix Table IV-2)	0.5 degree
2	monthly-based bioclimatic variables (see Appendix Table IV-2)	10 minutes
3	daily-based bioclimatic variables (see Appendix Table IV-2)	1 km
4	MPB affected acres (tree mortality acres)	1:100K quad
5	stand age	1 km
6	stand age, ratio of large trees, ratio of old trees	subplot radius is 24 feet
7	tree density	around 1 square kilometers
8	coordinates of SIT-209 data	at least 1-square mile grid
9	suppression costs, suppression acres, unit suppression costs	coordinate-based
10	no. fires suppressed, ratio of suppressed fires, fire size of suppressed fires, containment duration, fire out duration	coordinate-based
11	vegetation condition class	30 meters
12	mean fire return interval	30 meters
13	percent of replacement-severity fires	30 meters
14	percent of mixed-severity fires	30 meters
15	percent of low-severity fires	30 meters
16	disturbance events allowed (GAP status 1), disturbance events suppressed (GAP status 2), subject to human activities (GAP status 3)	< 1:24,000 scale?

Appendix Table IV-1 (continued)

No.	Temporal coverage	Source	Reference
1	1901-2016	University of East Anglia	Harris et al. 2014
2	1961-1990	University of East Anglia	New et al. 2002
3	1980-present	Oak Ridge National Laboratory Distributed Active Archive Center	Thornton et al. 2017
4	1997-2016	USDA Forest Service	USFS 2016
5	present (2000s)	USDA Forest Service	Pan et al. 2011
6	since 2003	USDA Forest Service	USFS 2016
7	present (2010s)	Yale School of Forestry and Environmental Studies	Crowther et al. 2015
8	1992-2015	USDA Forest Service	Short 2017
9	1999-present	National fire and aviation management	n.a.
10	1980-2016	Department of the Interior, Office of Wildland Fire	n.a.
11	present (2010s)	LANDFIRE program	LANDFIRE 2014
12	present (2010s)	LANDFIRE program	LANDFIRE 2010
13	present (2010s)	LANDFIRE program	LANDFIRE 2010
14	present (2010s)	LANDFIRE program	LANDFIRE 2010
15	present (2010s)	LANDFIRE program	LANDFIRE 2010
16	since 1970s?	U.S. Geological Survey	GAP 2016

Appendix Table IV-1 (continued)

No.	Link	Data access date
1	https://crudata.uea.ac.uk/cru/data/hrg/	5/11/18
2	https://crudata.uea.ac.uk/cru/data/hrg/	2/27/16
3	https://daac.ornl.gov/cgi-bin/dataset_lister.pl?p=32	8/22/18
4	https://foresthealth.fs.usda.gov/portal/Flex/IDS	12/10/17
5	https://www.fs.usda.gov/rds/archive/Product/RDS-2014-0025/	7/19/18
6	https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html	3/25/18
7	https://www.nature.com/articles/sdata201669#data-records	7/19/18
8	https://www.fs.usda.gov/rds/archive/Product/RDS-2013-0009.4/	11/6/18
9	https://fam.nwcg.gov/fam-web/	11/20/17
10	https://wildfire.cr.usgs.gov/firehistory/data.html	7/19/18
11	https://www.landfire.gov/version_comparison.php	12/15/18
12	https://www.landfire.gov/version_comparison.php	12/15/18
13	https://www.landfire.gov/version_comparison.php	12/15/18
14	https://www.landfire.gov/version_comparison.php	12/15/18
15	https://www.landfire.gov/version_comparison.php	12/15/18
16	https://gapanalysis.usgs.gov/padus/data/download/	5/25/16

Notes: The letters "n.a." indicate "not applicable".

Appendix Table IV-2. Bioclimatic variables included in the data exploratory analysis of the study.

No.	Rationale	Variable	Variable name	Temporal resolution
1	temperature conditions can promote outbreaks by allowing for a one-year life cycle and near-synchronous adult emergence	Tmean	MPB life cycle mean temperature	monthly
2		Tvar	seasonal temperature variation	monthly
3		fallTmean	fall mean temperature	monthly
4		TOctSep	water year mean temperature	monthly
5		TMarAug	growing season mean temperature	monthly
6		ddAugJun	egg hatch degree days	daily
7		ddAugJul	MPB life cycle degree days	daily
8	heat during summer time is associated with the start of flight and spatial synchronization of beetle outbreaks	AugTmax	August monthly maximum temperature	monthly
9		AugMaxT	August daily maximum temperature	daily
10		maxAugT	frequency of 18.3 °C in August	daily
11		summerTmean	summer mean temperature	monthly
12		maxT	maximum daily temperature	daily
13		AugTmean	August monthly average temperature	monthly
14	unseasonably and/or extremely low temperatures can cause direct mortality of over-wintering insects	Tmin	monthly minimum temperature	monthly
15		minT	daily minimum temperature	daily
16		JanTmin	January minimum temperature	monthly
17		OctTmin	October minimum temperature	monthly
18		MarTmin	March minimum temperature	monthly
19		Acs	average cold snap duration	daily
20		Jan20	no. January cold days	daily
21		JanMin	daily minimum January temperature	daily
22		Mar20	no. March cold days	daily
23		MarMin	daily minimum March temperature	daily
24		winterMin	daily minimum winter temperature	daily
25	droughts stress trees have lower defensive capabilities than healthy trees	Pmean	MPB life cycle mean precipitation	monthly
26		summerP0	current-year summer precipitation	monthly
27		summerP1	previous-year summer precipitation	monthly
28		summerP2	cumulative summer precipitation	monthly
29		PcumOctSep	cumulative water-year precipitation	monthly

30	wd	water deficit	daily
31	vpd	vapor pressure deficit	daily
32	cwd	cumulative climatic water deficit	daily
33	mi	moisture index	daily
34	PPT	cumulative precipitation	monthly

Appendix Table IV-2 (continued)

No.	Description	Reference
1	mean of monthly average of daily mean temperature from August to July	Powell et al., 2000; Sambaraju et al., 2012
2	standard deviation of monthly average of daily mean temperature from August to July	Powell et al., 2000
3	mean of monthly average of daily mean temperature from September to November in the previous year	Buotte et al., 2016
4	mean of monthly average of daily mean temperature from October to September in the current water year	Preisler et al., 2012
5	mean of monthly average of daily mean temperature from March to August	Creeden et al., 2014
6	accumulated degree days above 5.5 °C from August to June	Aukema et al., 2008; Safranyik et al., 2010
7	accumulated degree days above 5.5 °C from August to July	Aukema et al., 2008; Safranyik et al., 2010
8	monthly average of daily maximum temperature in August	Safranyik et al., 2010
9	maximum of daily maximum temperature in August	Aukema et al., 2008
10	the frequency of maximum daily temperatures not less than 18.3 °C during August	Safranyik et al., 2010
11	mean of monthly average of daily mean temperature from June to August in the current year	Sambaraju et al., 2012
12	maximum daily temperature from August to July	Aukema et al., 2008
13	monthly average of daily mean temperature in August	Aukema et al., 2008
14	mean of monthly average of minimum temperature from November to March	Fauria & Johnson, 2009
15	minimum of daily minimum temperature from August to July	Aukema et al., 2008
16	monthly average daily minimum temperature in January	Thomson 2009; Rosenberger et al. 2017
17	monthly average daily minimum temperature in October	Bentz et al. 1991; Chapman et al., 2012
18	monthly average daily minimum temperature in March	Bentz et al. 1991; Chapman et al., 2012
19	average duration of a cold snap (i.e., a minimum of four continuous days of average winter temperatures at or below -20 °C) during winter	Sambaraju et al., 2012

20	number of days with minimum temperatures at or below -20 °C in January	Thomson 2009
21	minimum of daily minimum temperature in January	Thomson 2009
22	number of days with minimum temperatures at or below -20 °C in March	Thomson 2009
23	minimum of daily minimum temperature in March	Thomson 2009
24	minimum of daily minimum temperature during winter	Safranyik et al., 2010; Buotte et al., 2017
25	mean of monthly precipitation from August to July	Chapman et al., 2012
26	sum of precipitation from June to August in the current year	Campbell et al., 2007
27	sum of precipitation from June to August in the previous year	Preisler et al., 2012
28	cumulative precipitation from June to August in the current and previous year	Preisler et al., 2012
29	cumulative precipitation from October to September in the current and previous year	Preisler et al., 2012
30	the yearly sum of rainfall minus evapotranspiration in months with mean air temperature > 0 °C	Safranyik et al., 2010
31	average monthly vapor pressure deficit in the current and previous 5 years from May to October	Buotte et al., 2017
32	the difference between the potential evapotranspiration and the actual evapotranspiration in the current and previous 5 years from May to October	Buotte et al., 2017
33	the ratio of annual precipitation to annual potential evapotranspiration	Davis et al., 2016
34	cumulative monthly October-August precipitation in the current and previous 5 years	Buotte et al., 2017

Appendix Table IV-3. Coefficients of multiple linear models with raw and z-scored predictors.

Model 1	Coefficient	Z-scored	P value	Significance
Tmean	2.41E+00	6.662	1.67E-05	***
TOctSep	-2.22E+00	-6.157	6.48E-05	***
PcumOctSep_sq	1.10E-06	4.020	9.91E-20	***
Pmean_sq	-6.31E-04	-3.964	1.78E-19	***
PcumOctSep	-5.16E-03	-3.820	2.78E-17	***
Pmean	1.13E-01	3.455	4.98E-16	***
Tmean_exp	4.99E-06	2.414	1.64E-03	**
TOctSep_exp	-4.82E-06	-2.339	2.05E-03	**
PPT	1.37E-04	0.299	4.13E-06	***
fallTmean	-9.81E-02	-0.264	1.84E-10	***
lat_sq	-7.85E-04	-0.248	2.18E-07	***
lat	6.23E-02	0.233	5.17E-07	***
summerP2_sq	5.19E-06	0.216	1.21E-04	***
mi	3.44E-01	0.200	2.87E-08	***
TMarAug	-7.69E-02	-0.200	1.00E-02	*
summerP0_sq	-1.83E-05	-0.191	4.58E-04	***
wd	-2.08E-04	-0.168	1.41E-08	***
Tvar	1.27E-01	0.155	9.36E-05	***
AugTmean	-4.77E-02	-0.123	1.32E-03	**
Tmin	-2.50E-02	-0.104	4.71E-07	***
OctTmin	3.35E-02	0.101	6.95E-13	***
Tvar_sq	-4.88E-03	-0.093	2.38E-08	***
maxT_sq	-3.24E-04	-0.071	2.88E-05	***
minT	-9.97E-03	-0.069	2.02E-05	***
vpd	-1.23E-06	-0.060	2.78E-04	***
mi_sq	-2.88E-02	-0.059	1.92E-02	*
AugMaxT_sq	2.61E-04	0.057	7.50E-04	***
AugTmean_sq	6.15E-04	0.056	2.44E-02	*
JanMin	8.40E-03	0.054	9.42E-04	***
Tmean_sq	-1.30E-03	-0.052	5.46E-04	***
Mar20_logp1	1.59E-01	0.052	5.36E-07	***
Mar20	-9.35E-02	-0.051	9.71E-10	***
fallTmean_exp	-4.22E-08	-0.044	4.28E-07	***
AugTmax	1.59E-02	0.043	1.21E-05	***
vpd_sq	2.35E-12	0.043	5.04E-04	***
summerP2	-3.87E-04	-0.037	2.35E-05	***
MarTmin	9.23E-03	0.035	4.77E-02	*
etopo1	4.78E-05	0.032	3.33E-14	***
TMarAug_exp	-1.32E-09	-0.032	5.18E-05	***
wd_sq	1.01E-08	0.031	8.56E-02	.
Jan20_sq	3.44E-03	0.030	4.62E-05	***
lon_sq	2.02E-05	0.027	1.33E-05	***

ddAugJul_sq	1.18E-08	0.024	1.66E-04	***
density	1.38E-06	0.024	6.20E-26	***
Acs_sq	-4.18E-03	-0.022	4.93E-04	***
Jan20	-1.25E-02	-0.021	8.15E-02	.
cwd_sq	-1.23E-07	-0.021	1.83E-03	**
maxAugT_sq	1.22E-04	0.017	6.72E-10	***
Acs	1.16E-02	0.016	6.70E-02	.
OctTmin_sq	9.94E-04	0.015	2.87E-05	***
density_sq	-9.93E-12	-0.013	6.44E-11	***
prs_sq	-7.60E-05	-0.012	7.19E-03	**
prs	1.53E-03	0.011	1.69E-02	*
SprsFires	5.51E-04	0.007	6.81E-13	***
PctSprs	-1.47E-02	-0.006	1.74E-07	***
GAP1	-9.25E-03	-0.003	4.99E-03	**
mStdAge	5.84E-05	0.003	1.22E-01	
mStdAge_sq	-1.58E-07	-0.003	1.47E-01	
SprsAcre	-1.16E-06	-0.003	4.06E-03	**
PctOld	7.08E-03	0.002	2.87E-02	*
OutDays	8.71E-05	0.002	7.03E-02	.

Model results	Model 1	Model 2	Model 3
Multiple R squared	0.529	0.508	0.509
Adjusted R squared	0.518	0.503	0.504
Residual standard error	0.044	0.100	0.101
Degrees of freedom	2756	7104	7565

Appendix Table IV-3 (continued)

Model 2	Coefficient	Z-scored	P value	Significance
summerP2_sq	6.32E-04	24.685	5.60E-04	***
ddAugJul_sq	7.82E-06	16.109	1.87E-02	*
ddAugJun_sq	-7.80E-06	-16.071	1.90E-02	*
Tmean	5.17E+00	14.408	2.61E-09	***
TOctSep	-4.46E+00	-12.445	1.71E-07	***
summerP1_sq	-1.26E-03	-12.358	5.96E-04	***
summerP0_sq	-1.27E-03	-12.343	5.32E-04	***
PcumOctSep	-1.09E-02	-8.628	2.36E-21	***
ddAugJun	1.50E-02	8.481	2.30E-03	**
PcumOctSep_sq	2.27E-06	8.466	4.02E-17	***
ddAugJul	-1.50E-02	-8.433	2.40E-03	**
Pmean_sq	-1.23E-03	-7.873	3.43E-20	***
Pmean	2.31E-01	7.561	6.17E-22	***
PPT	3.92E-04	0.921	4.42E-07	***
fallTmean	-3.26E-01	-0.889	5.66E-29	***
TMarAug	-2.79E-01	-0.715	8.04E-09	***
lat_sq	-1.91E-03	-0.583	5.81E-12	***
Tvar	4.56E-01	0.548	8.19E-09	***
minT	-7.65E-02	-0.541	1.26E-07	***
lat	1.43E-01	0.512	2.26E-10	***
mi	7.53E-01	0.482	1.69E-18	***
summerP0	-1.03E-02	-0.476	9.94E-02	.
PPT_sq	-1.51E-08	-0.472	1.26E-02	*
summerP2	4.94E-03	0.455	1.15E-01	
winterMin	5.86E-02	0.415	5.24E-05	***
lon_sq	3.13E-04	0.403	2.48E-02	*
wd	-4.38E-04	-0.396	2.38E-18	***
lon	5.48E-02	0.309	8.32E-02	.
OctTmin	8.72E-02	0.270	1.87E-35	***
AugTmean	-1.00E-01	-0.252	5.86E-09	***
summerTmean	-9.39E-02	-0.234	2.05E-02	*
Tmin	-5.49E-02	-0.234	3.49E-12	***
maxT	-6.46E-02	-0.219	1.45E-20	***
mi_sq	-7.56E-02	-0.177	1.73E-06	***
etopo1	2.28E-04	0.157	1.76E-34	***
AugMaxT_sq	7.00E-04	0.153	1.91E-10	***
Tvar_sq	-8.01E-03	-0.145	3.94E-09	***
vpd	-2.82E-06	-0.138	2.94E-07	***
AugTmax	4.86E-02	0.130	4.30E-19	***
vpd_sq	6.50E-12	0.117	1.63E-08	***
wd_sq	3.12E-08	0.116	1.24E-05	***
Mar20_logp1	3.39E-01	0.111	5.88E-13	***
Jan20	-6.74E-02	-0.108	9.74E-09	***

Jan20_sq	1.28E-02	0.102	1.43E-20	***
maxAugT_sq	5.87E-04	0.092	1.44E-06	***
MarTmin	2.37E-02	0.092	9.20E-04	***
Acs_sq	-1.82E-02	-0.087	1.18E-21	***
Mar20	-1.59E-01	-0.086	3.89E-11	***
etopo1_sq	-3.33E-08	-0.086	1.38E-14	***
Acs	6.41E-02	0.083	5.27E-12	***
cwd_sq	-3.83E-07	-0.063	3.03E-10	***
JanMin_sq	-2.67E-04	-0.053	3.57E-03	**
Tmean_exp	1.05E-07	0.048	2.72E-02	*
Tmean_sq	-1.16E-03	-0.045	4.16E-03	**
density	2.26E-06	0.038	1.61E-43	***
fallTmean_exp	-3.65E-08	-0.037	4.61E-03	**
OctTmin_sq	1.93E-03	0.031	1.77E-09	***
maxAugT	-9.45E-03	-0.030	7.30E-02	.
prs_sq	-1.59E-04	-0.026	5.94E-04	***
prs	3.08E-03	0.022	5.74E-03	**
TMarAug_exp	-8.33E-10	-0.018	5.64E-02	.
mfri	2.78E-03	0.017	1.02E-03	**
density_sq	-1.05E-11	-0.016	2.18E-12	***
mfri_log	-2.09E-02	-0.016	3.54E-03	**
mStdAge	2.36E-04	0.012	5.15E-05	***
mStdAge_sq	-6.78E-07	-0.011	9.61E-05	***
GAP1	-2.14E-02	-0.008	1.55E-07	***
vcc_log	1.08E-02	0.004	3.38E-03	**
PctLarge	-1.78E-02	-0.004	1.45E-02	*
GAP3	5.00E-03	0.002	8.81E-02	.
PctOld	7.16E-03	0.002	1.46E-01	

Appendix Table IV-3 (continued)

Model 3	Coefficient	Z-scored	P value	Significance
summerP2_sq	4.84E-04	19.177	5.98E-03	**
Tmean	5.57E+00	15.447	2.45E-12	***
TOctSep	-4.84E+00	-13.424	6.08E-10	***
ddAugJul_sq	5.04E-06	10.397	9.14E-02	.
ddAugJun_sq	-5.02E-06	-10.359	9.27E-02	.
summerP1_sq	-9.80E-04	-9.721	5.58E-03	**
summerP0_sq	-9.57E-04	-9.470	6.44E-03	**
PcumOctSep_sq	1.88E-06	6.931	5.48E-13	***
PcumOctSep	-8.37E-03	-6.569	7.12E-15	***
Pmean_sq	-1.03E-03	-6.513	1.69E-15	***
ddAugJun	1.07E-02	6.041	1.37E-02	*
ddAugJul	-1.06E-02	-5.994	1.43E-02	*
Pmean	1.74E-01	5.653	9.23E-15	***
fallTmean	-3.24E-01	-0.879	1.29E-27	***
PPT	3.31E-04	0.769	7.07E-06	***
TMarAug	-2.97E-01	-0.766	1.44E-09	***
lat_sq	-2.26E-03	-0.692	7.83E-16	***
summerP0	-1.37E-02	-0.638	2.72E-02	*
lat	1.74E-01	0.627	9.45E-15	***
summerP2	6.72E-03	0.625	3.01E-02	*
Tvar	4.83E-01	0.587	1.05E-09	***
minT	-7.98E-02	-0.558	2.36E-08	***
mi	7.94E-01	0.507	1.14E-20	***
lon_sq	3.51E-04	0.459	1.08E-02	*
winterMin	6.49E-02	0.454	4.77E-06	***
wd	-4.61E-04	-0.414	9.31E-20	***
lon	6.64E-02	0.381	3.29E-02	*
PPT_sq	-9.55E-09	-0.296	1.02E-01	
summerTmean	-1.07E-01	-0.273	8.27E-03	**
OctTmin	8.32E-02	0.256	5.03E-35	***
AugTmean	-9.47E-02	-0.243	1.28E-08	***
Tmin	-5.71E-02	-0.240	1.82E-13	***
mi_sq	-8.57E-02	-0.199	2.77E-08	***
maxT	-5.77E-02	-0.196	1.84E-17	***
Tvar_sq	-8.48E-03	-0.157	6.46E-11	***
etopo1	2.26E-04	0.154	1.46E-34	***
AugMaxT_sq	6.38E-04	0.138	2.20E-09	***
wd_sq	3.49E-08	0.128	6.78E-07	***
AugTmax	4.72E-02	0.127	1.72E-19	***
vpd	-2.50E-06	-0.124	5.36E-05	***
MarTmin	3.00E-02	0.114	2.12E-05	***
vpd_sq	6.05E-12	0.110	6.84E-06	***
Mar20_logp1	3.21E-01	0.104	2.12E-12	***

Jan20_sq	1.20E-02	0.097	8.98E-20	***
Jan20	-5.74E-02	-0.092	3.89E-07	***
Mar20	-1.60E-01	-0.085	8.51E-12	***
etopo1_sq	-3.28E-08	-0.083	2.01E-14	***
JanMin_sq	-3.95E-04	-0.078	2.52E-05	***
Acs_sq	-1.62E-02	-0.078	1.87E-18	***
Acs	5.89E-02	0.076	4.85E-11	***
maxAugT_sq	3.73E-04	0.058	2.20E-36	***
Tmean_exp	1.02E-07	0.056	1.14E-02	*
Tmean_sq	-1.30E-03	-0.051	1.02E-03	**
cwd	-2.78E-04	-0.046	3.94E-02	*
fallTmean_exp	-3.32E-08	-0.044	2.48E-03	**
density	2.22E-06	0.038	8.13E-46	***
cwd_sq	-2.13E-07	-0.036	6.67E-02	.
MarMin	-6.11E-03	-0.033	2.97E-02	*
OctTmin_sq	2.04E-03	0.032	9.06E-11	***
prs_sq	-1.42E-04	-0.023	1.73E-03	**
TMarAug_exp	-8.89E-10	-0.021	1.58E-02	*
prs	2.58E-03	0.019	1.74E-02	*
density_sq	-1.03E-11	-0.017	3.75E-13	***
mfri	2.40E-03	0.015	3.56E-03	**
mfri_log	-1.83E-02	-0.014	8.86E-03	**
mStdAge	2.32E-04	0.012	1.51E-05	***
mStdAge_sq	-6.39E-07	-0.011	1.30E-04	***
GAP1	-2.04E-02	-0.007	3.84E-07	***
vcc_log	9.93E-03	0.004	4.95E-03	**
GAP3	6.19E-03	0.003	2.93E-02	*

Notes: Variable names ended with "_sq" indicate the squared transformation of variable; variable names ended with "_log" indicate the logarithm transformation of variable, while a variable name ended with "_logp1" indicates an adjustment of values to avoid the logarithm of zeros; variable names ended with "_exp" indicate the exponential transformation of variable; Variables "lon", "lat", " etopo1" are longitude, latitude and elevation respectively and the rest variables are explained in Table IV-1 and Appendix Table IV-2; Model 1 included available FW FOD data, FIA, FSA and GTD; Model 2 removed FW FOD data, and included available FIA, FSA and GTD data; Model 3 removed FW FOD and FIA data, and included available FSA and GTD data.

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