Forest Ecosystem and Avian Niche Modeling: Improving Climate Change Forest Modeling via Interdisciplinary Model Linking

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Authorization to Submit Dissertation

This dissertation of Eric S. Walsh, submitted for the degree of Doctorate of Philosophy with a Major in Natural Resources and titled "Forest Ecosystem and Avian Niche Modeling: Improving Climate Change Forest Modeling via Interdisciplinary Model Linking," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Climate change is impacting forest structure and processes, and more than half of the forested land cover of North America will experience future climates that differ from historical growing conditions. Forest composition and structure are integral to biodiversity, however, climate change induced declines in tree species occurrence, increases in forest mortality events, and increases in burned area will have biodiversity implications. Process-based forest landscape models provide a means to evaluate forest structure, composition, and biogeochemical responses to climate change, while providing data to secondarily model biodiversity responses. This dissertation focuses on integrating forest landscape and avian niche models to evaluate the effects of climate change on the Northern Rockies Ecoregion of Idaho, USA.

Chapter 1 addresses the rational for integrating avian cavity nester niche models with forest landscape models. I introduce the conceptual climate-woodpecker-forest model and conduct a literature review of ongoing and projected responses of woodpeckers to climate change. I found that projections are not always in agreement with observed contemporary trends, and the ecological constraints associated with contemporary woodpecker niches are not being integrated into climate-based projection models. I conclude that the coupling of woodpecker niche models with finer scale process-based vegetation models is a way to better approximate the key ecological constraints of woodpeckers. This coupling will then provide a functional measure of biodiversity in multi-objective ecosystem modeling frameworks.

In Chapter 2, I propose a framework to integrate avifauna niche and forest landscape models. The framework implements a process to 1) aid in selecting available and appropriate niche models for a study region; 2) evaluate the transferability of a niche model when developed in a region outside of the focal study area; 3) derive niche model predictor variable parameterizations from the forest landscape model when the outputs of the forest landscape model cannot directly inform the avian niche model; 4) compare the forest landscape modeled avian niche response to the response derived from the original niche model parameterizations.

Through implementation of this process using two avian cavity nester species and the forest landscape model LANDIS-II, I found model selection and transferability are the primary limiting factors to integration. Secondarily, species that are spatially irruptive because of the dynamics of habitat condition still benefit from this model integration. The spatial extent of core habitat features of these species, which are a product of long term management decisions, can be identified and further evaluated through time using forest landscape model scenarios. Overall, the framework provides a viable process to model integration.

In Chapter 3, I apply LANDIS-II to the Northern Rockies Ecoregion to evaluate the effects of climate change, fire disturbance, and harvest disturbance on the forest composition, structure, and biogeochemical dynamics of the region. I integrate the avifauna niche models from Chapter 2 into the modeling scenarios to provide a measure of biodiversity response. The Northern Rockies Ecoregion is projected to maintain a sink potential to the end of the century. This was primarily caused by harvest management, since harvest interacting with a warming climate resulted in increases in net primary productivity and aboveground biomass. Shifts in species composition with the concurrent aging of forest due to harvest prescriptions increased the niche suitability of the Northern Rockies Ecoregion for the two avian cavity nesting species. This highlighted the importance of the region as a habitat refugia under a warming climate.

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Dedication

This would not be possible without the love, support, and mentoring of my family and friends.

Thank you

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Introduction

As global atmospheric CO_2 has increased, the U.S. has warmed 0.7 – 1.1° C, with most of the warming occurring since 1970 (Walsh et al., 2014). Climate warming and changing precipitation regimes have impacted forest ecosystem structure and function (Anderson-Teixeira et al., 2013). Globally, forests provide many ecosystem services, including sequestration of approximately 30% of global annual anthropogenic CO_2 emissions (Pan et al., 2011) and habitat for 77% of the global avifauna (BirdLife International, 2017). Forest composition and structure are integral to biodiversity (McElhinny, Gibbons, Brack, & Bauhus, 2005). However, climate change induced declines in tree species occurrence (Coops & Waring, 2011a), increases in forest mortality events (Allen et al., 2010; McDowell & Allen, 2015), and increases in burned area (Rogers et al., 2011) will have biodiversity implications (Langdon & Lawler, 2015).

In the next century, the potential ecosystem responses (e.g., fire disturbances, biological outbreaks, harvest, and carbon cycle) to climate change of the Northern Rockies Ecoregion forest ecosystems are complex functions of climate-vegetation-disturbance dynamics. Climatically, this region's yearly mean temperature is projected to increase by 2-3° Celsius (Liu, Goodrick, & Stanturf, 2013). Though precipitation estimates are less certain (National Research Council 2011), projections indicate an increase in fall, winter and spring precipitation (Gutzler & Robbins, 2010; Liu et al., 2013) with most occurring in the form of rain (McCabe & Wolock, 2009). The shifts in precipitation timing and type along with increases in temperature are expected to result in an increase in drought conditions during the summer and fall (Liu et al., 2013). This is projected to shift vegetation distributions (Coops & Waring, 2011b), alter fire dynamics (Rocca et al., 2014), and increase the annual area burned by two-fold (National Research Council 2011). Ecosystem processes and ensuing responses are likely to shift compared to historic conditions.

The effects of climate change on the forests of the Northern Rockies Ecoregion of Idaho has been evaluated conceptually (Rocca et al., 2014; Schoennagel, Veblan, & Romme, 2004), statistically (A. L. Westerling, Hidalgo, Cayan, & Swetnam, 2006; Anthony L. Westerling, Turner, Smithwick, Romme, & Ryan, 2011), and using process-based models at broad spatial scales (Coops & Waring, 2011b, 2011a). However, evaluating the dynamics of fire, effects of harvest, shifts in species composition, and changes in forest structure require finer scaled process-based models, which have not been specifically applied to this study area. Forest landscape models such as the Landscape Disturbance and Successional Model (LANDIS-II) mechanistically simulate complex spatial and temporal forest ecosystem interactions (Scheller et al., 2007). They simulate the interactions of complex stochastic processes such as disturbance events, abiotic factors, and climate resulting in emergent forest ecosystem responses, i.e. stand age and composition, spatial distribution of biomass, and biogeochemical responses (Gustafson, 2013). They can simulate either single or multispatial disturbance processes such as harvest, insect, fire, and wind as a function of management practices (Swanson, 2009) or climate change scenarios (Steenberg, Duinker, & Bush, 2011; Thompson, Foster, Scheller, & Kittredge, 2011). As such, forest landscape models capture the finer-scale dynamics of climate impacts on forest structure and composition providing information at the scale necessary to effect forest management and inform secondary modeling efforts, e.g., species niche models.

The biogeochemical, structure, and composition responses of forest ecosystems to management, climate change, and disturbance processes is the focus of many forest ecosystem modeling efforts. However, the secondary biodiversity responses to those processes is an area of research opportunity. Forest management strategies are currently being developed or implemented to increase suitable wildlife habitat (McComb, 2015) and preserve biodiversity (Braunisch et al., 2014; Onaindia, Fernández de Manuel, Madariaga, & Rodríguez-Loinaz, 2013). Climate change is impacting forest structure and processes and more than half of the forested land cover of North America will experience future climates that differ from historical growing conditions (Charney et al., 2016). Thus, modeling efforts will need the coupled response of vegetation *and* wildlife to climate change to implement realistic management strategies aimed at increasing or preserving wildlife diversity.

Avifauna are an ideal ensemble of wildlife species to function as indicators of forest biodiversity and ecosystem function in an integrated framework of climate, wildlife, and forest dynamics modeling. Specifically, woodpeckers are ideally suited as indicator species of forest ecosystem dynamics (Koch, Drever, & Martin, 2011; Segura, Castaño-Santamaría, Laiolo, & Obeso, 2014), because they are ecologically constrained by landscape scale forest components such as composition, structure (Hannon & Drapeau, 2005), fire and other disturbance regimes (Saab, Dudley, & Thompson, 2004), and management activities (Drever & Martin, 2010). In addition, they are correlated with forest avifauna community diversity (Archaux & Bakkaus, 2007; Diaz, Armesto, Reid, Sieving, & Willson, 2005; Drever, Aitken, Norris, & Martin, 2008; Patton, 1992). However, constructing future niche projections on current climatic conditions associated with contemporary distributions can under-predict the areas that are climatically suitably post climate change (Early & Sax, 2014). By coupling forest landscape and avian niche models under different climate change and management scenarios, the resilience of avian niches to climate impacts can be more finely evaluated compared with climate-avifauna only models (e.g., bioclimatic niche models). Concurrently, the modeled niche responses provide a secondary measure of the effects of climate, disturbance, and management on forest dynamics beyond forest structure, composition, and biogeochemical dynamics. Such integrated modeling underwrites the identification of a suite of adaptive management practices that when implemented in the present will build ecosystem resiliency against future climate impacts.

I focused this research on improving the evaluation of climate change effects on the Northern Rockies Ecoregion of Idaho, USA through the implementation of an integration of forest landscape and avian niche models. First, I present the rational for and benefits of coupling forest landscape models with avian niche models (Chapter 1). Second, I present and discuss a framework for integrating avian niche models with forest landscape models (Chapter 2). Finally, I present the results of model integration under climate change scenarios (Chapter 3).

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Chapter 1: Climate change, woodpeckers, and forests: current trends and future modeling needs

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Abstract

The structure and composition of forest ecosystems are expected to shift with climate-induced changes in precipitation, temperature, fire, carbon mitigation strategies, and biological disturbance. These factors are likely to have biodiversity implications. However, climate-driven forest ecosystem models used to predict changes to forest structure and composition are not coupled to models used to predict changes to biodiversity. We propose integrating woodpecker response (biodiversity indicator) with forest ecosystem models. Woodpeckers are a good indicator species of forest ecosystem dynamics, because they are ecologically constrained by landscape scale forest components such as composition, structure, disturbance regimes, and management activities. In addition, they are correlated with forest avifauna community diversity. In this study, we explore integrating woodpecker and forest ecosystem climate models. We review climate-woodpecker models and compare the predicted responses to observed climate-induced changes. We identify inconsistencies between observed and predicted responses, explore the modeling causes, and identify the models pertinent to integration that address the inconsistencies. We found that predictions in the short-term are not in agreement with observed trends for 7 of 15 evaluated species. Because niche constraints associated with woodpeckers are a result of complex interactions between climate, vegetation, and disturbance, we hypothesize that the lack of adequate representation of these processes in the current broad-scale climate-woodpecker models results in model-data mismatch. As a first step towards improvement, we suggest a new conceptual model of climate-woodpecker-forest modeling for integration. The integration model provides climate-driven forest ecosystem modeling with a measure of biodiversity while retaining the feedback between climate and vegetation in woodpecker climate change modeling.

Introduction

As global atmospheric CO2 has increased, the U.S. has warmed 0.7 – 1.1◦ C, with most of the warming occurring since 1970 (Walsh et al., 2014) impacting forest ecosystems (Anderson-Teixeira et al., 2013). Globally, forests provide many ecosystem services, including sequestration of approximately 30% of global annual anthropogenic CO2 emissions (Pan et al., 2011) and habitat for 77% of the global avifauna (BirdLife International, 2017). Climate warming and changing precipitation regimes have impacted forest ecosystem structure and function (Anderson-Teixeira et al., 2013) including North American avifauna populations (Prince & Zuckerberg, 2015; Tingley, Koo, Moritz, Rush, & Beissinger, 2012). Moreover, predictions indicate that more than half of the forested land cover of North America will experience future climates that differ from historical growing conditions (Charney et al., 2016) with obvious implications for preservation of wildlife biodiversity (Langdon & Lawler, 2015), since forest composition and structure are integral to biodiversity (McElhinny, Gibbons, Brack, & Bauhus, 2005).

The structure and composition of forest ecosystems are expected to shift with climate-induced changes in precipitation, temperature (Lenihan, Bachelet, Neilson, & Drapek, 2008), fire (Abatzoglou & Williams, 2016), carbon mitigation strategies (Hudiburg, Luyssaert, Thornton, & Law, 2013; Law et al., 2018; Law, Hudiburg, & Luyssaert, 2013), and biological disturbances (Weed, Ayres, & Hicke, 2013). Specifically, climate change is expected to cause declines in tree species occurrence (Coops & Waring, 2011a), shifts in carbon stocks (Lenihan et al., 2008), increases in forest mortality events (Allen et al., 2010; McDowell & Allen, 2015), and increases in burned area (Rogers et al., 2011). These changes will affect avifauna habitat. For example, moderate to high severity fires can create open forests, adequate snag density, and minimal mid-story vegetation necessary for some woodpecker habitat (Hoyt & Hannon, 2002; Vierling, Lentile, & Nielsen-Pincus, 2008; Zhu, Srivastava, Smith, & Martin, 2012). But even with increases in area burned or fire intensity, models also predict tree species composition shifts that pose adaptation constraints on woodpeckers (Fogg, Roberts, & Burnett, 2014) and potentially reducing habitat and biodiversity.

We propose the woodpecker guild as an ensemble of wildlife species to function as indicators of forest resiliency and biodiversity in a coupled modeled response of vegetation and wildlife to climate change. Woodpeckers are ideally suited as indicator species of forest ecosystem dynamics (Koch, Drever, & Martin, 2011; Segura, Castaño-Santamaría, Laiolo, & Obeso, 2014), because they are ecologically constrained by landscape scale forest components such as composition, structure, disturbance regimes, and management activities, in addition to being correlated with forest avifauna community diversity (Archaux & Bakkaus, 2007; Diaz, Armesto, Reid, Sieving, & Willson, 2005; Drever, Aitken, Norris, & Martin, 2008; Patton, 1992). Woodpeckers are also strongly associated with old-growth/structurally complex forests (Hannon and Drapeau 2005, Drever et al. 2008, Segura et al. 2014), which sustain greater biodiversity (Mazziotta et al., 2016) and are key habitat characteristics that modulate woodpecker population responses. These include snag density (Saab, Russell, & Dudley, 2009), tree density and diameter (Dudley, Saab, & Hollenbeck, 2012), time since last burn (Covert-Bratland, Block, & Theimer, 2006; Hannon & Drapeau, 2005; Hobson & Schieck, 1999; Saab & Dudley, 1998; Saab, Russell, & Dudley, 2007), burn severity (Covert-Bratland et al., 2006; Saab & Vierling, 2001; Vierling et al., 2008), and beetle outbreak (K. Martin, Norris, & Drever, 2006; Saab et al., 2014). Because these forest components will be impacted by climate change (Allen et al., 2010; Anderson-Teixeira et al., 2013; Parks et al., 2016; Rocca et al., 2014; Weed et al., 2013), the change will have cascading effects on woodpecker responses rendering them viable indicators in modeling future changes to biodiversity.

We reviewed the current and predicted trends associated with climate change impacts on woodpecker responses to identify ways to integrate woodpecker and forest ecosystem models. In addition, our intent is to provide a collective baseline of woodpecker responses to current and future climate change for integrated modeling efforts to be evaluated against. To identify ways to integrate woodpecker models, we identify inconsistencies between current (observed) and predicted responses, explore the modeling causes, and identify the models pertinent to integration that will address inconsistencies. We acknowledge there is vast syntheses possible when studying the response of woodpeckers to climate change. However, the focus of this review is to seek the information to facilitate identification of the model attributes that can best serve an integrated framework of climate-woodpecker-forest modeling. Having this framework will facilitate including other biodiversity measures (e.g., other species) in future climate modeling efforts.

Methods and Reviewed Literature

We conducted a systematic literature review of the observed and predicted responses to climate change of 22 North American woodpecker species. We refer to woodpecker response models as any of the following: species distribution, occupancy, abundance, and demographic models. Search terms using Google Scholar and Web of Science included "avian cavity nesters climate change", "woodpeckers climate change", "birds climate change", and "birds breeding climate change". The search spanned all literature through June 2018. We included all papers that modeled the effects of climate change on woodpecker responses. Models that based predictions on alternative analyses to evaluated datasets (Distler, Schuetz, Velásquez-Tibatá, & Langham, 2015; Rodenhouse et al., 2008; Schuetz et al., 2015) or reported woodpecker responses aggregated at the community level (Diana Stralberg et al., 2009) were excluded, because they did not provide individual species responses or were redundant data.

There were a limited number of woodpecker models (studies n=7; Table 1.1) that predicted future responses to climate change. These were mostly bioclimatic niche models (Table 1.1) and predicted changes to the breeding and/or winter geographic range, abundance, demographic and dispersal responses, niche temperature gradients, secondary responses inferred from range projections (species richness and niche flexibility), and species climate vulnerability (sensitivity, exposure, adaptive capacity) (Table A.1.1). These projections all used one or more climate variables (temperature, precipitation, bioclimatic) and several included non-climate variables (tree species occurrence, elevation, latitude, plant functional types, land use, biological traits, and survey effort) (Table A.1.2). Because the studies used a range of climate models and/or green-house gas (GHG) emission scenarios, we attempted to compare across similar GHG emission scenarios, acknowledging the range of responses, and when possible providing the average response.

Observed woodpecker responses to climate change (studies, n=14; Table 1.2) were largely statistically based and included a variety of dependent variables to characterize a suite of woodpecker species responses in the breeding and non-breeding seasons (Table A.1.3). These responses included range shifts (elevation, latitude, longitude), niche tracking, migration timing, community composition, energetic demand, and reproductive timing/performance. A few studies implicitly evaluated climate effects on avian responses via overall range shifts. Among the explicit climate effect models, the explanatory variables included climate variables (temperature, precipitation, and extremes (seasonal and annual minimums and maximums), their aggregates (e.g., bioclimatic variables), and physiography variables (e.g., snow depth). Some studies included non-climate explanatory variables such as habitat (land use), home range, population trends, and individual characteristics (body condition, age, breeding experience, inbreeding status, mean clutch size, diet breadth, and territory type) (Table A.1.4).

Predicted Woodpecker Responses to Climate Change

Generally, geographic forecasts indicate a north-northeast shift of eastern U.S. avifauna species by 2100 (Matthews, Iverson, Prasad, & Peters, 2011), and a concurrent change in community composition (Langham, Schuetz, Distler, Soykan, & Wilsey, 2015; Diana Stralberg et al., 2009). By 2080, breeding bird assemblages of northern Canada and Alaska may gain as many as 80 species while the greatest species loss is predicted along the Canadian-U.S. border and through the Rocky Mountains (Langham et al., 2015). Model results show that the resulting dissimilarity to contemporary species composition will be greatest throughout Canada and the Rockies. These trends will downscale to regional extents; for example, upwards of 57% of California may have novel breeding bird species assemblages by 2070 with no current analogs (Diana Stralberg et al., 2009). In addition, central and southern California are areas of peak losses of species in the non-breeding season (Langham et al., 2015).

Among the models reviewed, Langham et al. (2015) is the most comprehensive in relation to the greatest number of species and spatial extents modeled. The authors predict distributional changes to 2100 and compare these to species distributions in 2000 using bioclimatic modeling under a range of climate change scenarios for North American avifauna, including 20 North American woodpecker species. They used 13 combinations of emission scenarios and general circulation models over three time periods to produce 39 different climate futures. All woodpeckers' contemporary breeding and winter geographic ranges are predicted to contract due to climate change (Figure 1 and 2), and 13 of the 20 woodpecker species evaluated are predicted to be climate endangered or threatened due to loss of breeding and/or wintering range by the end of the century (Table A.1.1). Some of the range losses will be mitigated by climatically suitable range expansions. This results in an overall 53% and 23% of the woodpecker species breeding and non-breeding ranges to exhibit net contractions by 2080, respectively (Figure 1 and 2). Overall, all woodpecker species will lose climatically suitable habitat by the end of the century, and even with net gains, a majority are labeled as climate threatened or endangered based on climatic range changes (Table A.1.1).

In comparison, a trait-based assessment of climate change vulnerability via assessment of sensitivity, exposure, and adaptability found a mixed response among woodpeckers to those metrics. Most North American woodpecker species are sensitive to climate change. However, all are ranked as low vulnerability because of exposure ("the extent of the species' environment that will change") and/or high adaptive capacity ("the species' ability to avoid the negative impacts of climate change through dispersal and/or micro-evolutionary change") (Table A.1.1) (Foden et al., 2013). This discrepancy between the bioclimatic niche predictions (Langham et al., 2015) and climate vulnerability assessments (trait-based assessment) (Foden et al., 2013) may be explained by the inclusion of measures of sensitivity and adaptability in the trait-based evaluation. Though a qualitative assessment, the trait-based vulnerability metric exposure to climate change (the quantified metric in bioclimatic niche models) is further modulated by the species' sensitivity and adaptability to derive vulnerability. Bioclimatic niche models quantitatively assess the exposure of a species with minimal inclusion of the other measures of climate vulnerability (i.e., sensitivity and adaptability).

Hence, a species may be exposed to shifts in climatically suitable habitat but may have adaptability potential via phenotypic plasticity or not be sensitive to the degree of climate change represented in the bioclimatic niche model.

Spatially, there is an emergent pattern of predictions among woodpeckers relative to their contemporary distributions. The climatically suitable ranges of species with contemporary northern or western distribution centroids (i.e., those associated with conifer/boreal forests) are projected to contract (Langham et al., 2015). This is in concordance with other model results of climate induced declines in avifauna abundance and species richness in conifer/boreal habitats of North America (D. Stralberg et al., 2015) and Europe (Virkkala, Heikkinen, Leikola, & Luoto, 2008). Most avian species with breeding range distributions that are associated with eastern deciduous woodlands/forests and southern mixed-pine forest are predicted to be climate stable. This includes projections of the Red-Headed Woodpecker (*Melanerpes erythrocephalus*), Red-Bellied Woodpecker (*Melanerpes carolinus*), Downy Woodpecker (*Picoides pubescens*), and Pileated Woodpecker (*Hylatomus pileatus*) (Langham et al., 2015; Matthews et al., 2011; Rodenhouse et al., 2008) . Though, species at the southern edge of their range within this region (e.g., American Three-toed Woodpecker (*Picoides dorsalis*) and Black-backed Woodpecker (*Picoides arcticus*)) may diminish because of the encroachment of hardwoods from lower elevations into their primary habitat (spruce-fir) (Rodenhouse et al., 2008). Nevertheless, coastal and southern regions of the United States are predicted to provide climates amendable to many wintering species (Schuetz et al., 2015).

Observed Woodpecker Responses to Climate Change

Generally, avian species across the globe are exhibiting behavioral and phenological shifts in response to climate change via an advancement in migration timing (Ahola et al., 2004; Hüppop & Winkel, 2006; Jenni & Kéry, 2003; Miller-Rushing, Lloyd-Evans, Primack, & Satzinger, 2008; Vegvari, Bokony, Barta, & Kovacs, 2010) and breeding date (Crick & Sparks, 1999; P. Dunn, 2004; P. O. Dunn & Møller, 2014; Visser, Holleman, & Gienapp, 2006; Winkel & Hudde, 1997). The lack of adaptation to current climate change is causing some avian population declines, possibly due to the mistiming between resource availability (e.g., prey) and migration timing (Møller, Rubolini, & Lehikoinen, 2008). Although the functional pathways of these mechanisms (i.e., phenotypic plasticity and microevolution) are not fully understood, some individuals and populations do appear to be responding to climate change, and phenotypic plasticity appears to mitigate fitness loss due to these changes (Gienapp, Teplitsky, Alho, Mills, & Merilä, 2008).

Laying date advancement and increase in reproductive productivity of Northern Flickers (Colaptes auratus) was observed along the U.S. Pacific coast (Wiebe & Gerstmar, 2010). The authors showed that the response is spatially explicit; it correlates with increases in local ambient temperatures instead of broad regional climate indices or range wide temperature gradients. Moreover, differing climatic conditions is producing similar phenology responses within the same species. Red-cockaded Woodpeckers (Leuconotopicus borealis) are laying earlier, and those that do are more productive (Schiegg, Pasinelli, Walters, & Daniels, 2002). The climate factors that correlate to these responses differ between populations; one population is responding to increases in temperature and the other increases in precipitation (Schiegg et al., 2002). Mechanistically, this may be occurring via genetic diversity and age based experience, which increases plasticity (Schiegg et al., 2002). Woodpecker phenology may be shifting in response to changing climatic conditions, however behavioral plasticity may not always mitigate climate vulnerability.

Climate change effects manifested via habitat suitability change are not producing behavioral plasticity responses among some woodpeckers. In the southwest U.S., lack of behavioral plasticity caused Northern Flicker, Red-naped Sapsucker (Sphyrapicus nuchalis), Williamson’s Sapsucker (Sphyrapicus thyroideus), Hairy Woodpecker (Leuconotopicus villosus), Downy Woodpecker, and Acorn Woodpecker (Melanerpes formicivorus) populations to decline significantly, correlating with the climate change induced density decline of quaking aspen (Populus tremuloides) (Di Orio, Callas, & Schaefer, 2005; Worrall et al., 2008, 2013), their preferred nesting tree (T. E. Martin, 2015). This is rendering some species more vulnerable because of sensitivity to changes in nesting tree availability and lack of exhibited adaptability. Martin (2015) noted that resource specialization and scale dependent habitat selection will be important factors in species population responses to climate-induced habitat change. This means that accounting for such ecological niche shifts (i.e., loss of nesting trees) and subsequent habitat selection in models is important to capture the vulnerability of species and biodiversity dynamics of an ecosystem.

In response to changing climatic conditions, avifauna geographic distributions are shifting in the breeding (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hitch & Leberg, 2007; Hovick et al., 2016; Matthews, O'Connor, Iverson, & Prasad, 2004; Parmesan & Yohe, 2003; Thomas & Lennon, 1999; Tingley et al., 2012) and non-breeding seasons (La Sorte & Jetz, 2012; La Sorte & Thompson III, 2007). Though most woodpecker populations are increasing, distribution shifts in relation to ongoing climate change are heterogeneous and differ across spatial and temporal scales (Table A.1.3) (Bateman et al., 2016; Hitch & Leberg, 2007; Huang, Sauer, & Dubayah, 2017; La Sorte & Thompson III, 2007; Tingley et al., 2012; Tingley, Monahan, Beissinger, & Moritz, 2009; Zuckerberg, Woods, & Porter, 2009). Among the North American woodpecker species, these heterogeneous shifts are likely confounded by abundance changes, because based on Breeding Bird Survey and Christmas Bird Count data, most woodpecker populations have been increasing in the last four decades during the breeding and non-breeding seasons (Figure A.1.1 and A.1.2) (Sauer et al., 2017; Soykan et al., 2016).

Studies that have specifically evaluated woodpeckers (n=8) have found geographic and elevational shifts (Table A.1.3), and most woodpecker range extents are either expanding or not changing with the exception of the contracting Ladder-backed Woodpecker (Dryobates scalaris), Williamson's Sapsucker, and Red-headed Woodpecker (Bateman et al., 2016). Stephens et al., (2016) found that 13 of the 20 woodpecker species included in their comprehensive avifauna study have been advantaged by climate change across most of the evaluated states, i.e., the probability of occurrence was positively associated with climatic trends and was independent of abundance trends (Table A.1.3). It has been hypothesized that as yearly mean temperatures rise, breeding and non-breeding ranges in North America will likely continue to track climatically suitable habitat north and only be constrained by terrestrial habitat features (La Sorte & Jetz, 2010). Though over the last four decades, avifauna have not always tracked their climatic niches; there has been a lag effect in some North American species (La Sorte & Jetz, 2012). In some instances, species that have colonized human dominated systems do not fully track their climatic niche shifts (Tingley et al., 2009).

The complexity of woodpecker range responses can be appreciated by comparing several species. Only the Red-headed Woodpecker (decreased distribution at southern range edge) and Red-bellied Woodpecker (expansion at northern range edge and northwest range centroid shift) had the same directional response among the breeding and non-breeding seasons, respectively (Table A.1.1) (Bateman et al., 2016; Huang et al., 2017; La Sorte & Thompson III, 2007; Zuckerberg et al., 2009). The distribution contraction of the Red-headed Woodpecker and expansion of the Red-bellied Woodpecker are consistent with them being climate disadvantaged and advantaged, respectively (Table A.1.3) (Stephens et al., 2016). In contrast, the Yellow-bellied Sapsucker (Sphyrapicus varius) shifted south (Hitch & Leberg, 2007; Zuckerberg et al., 2009) and east during the breeding season (Bateman et al., 2016), but tracked the mean winter temperature increases northward during the non-breeding season (La Sorte & Thompson III, 2007). The increase in Yellow-bellied Sapsucker breeding season abundance between 2005 and 2015 within the United States (Sauer et al., 2017) is concurrent with a southern and eastern range shift but appears independent of climatic shifts. Based on the breeding distribution of the Yellow-bellied Sapsucker between 1980 to 2010 and independent of abundance trends, it is considered disadvantaged by climate change in a majority of the states evaluated (Table A.1.3) (Stephens et al., 2016). In addition, the northward winter range shift is occurring without a concurrent population abundance change (Table A.1.1) (Soykan et al., 2016). The Yellow-bellied Sapsucker, in contrast to Red-headed Woodpecker and Red-bellied Woodpecker range changes explained by climate, highlights the complexity of climate-based range changes; climate is expected to increase the vulnerability of this species even though it is not inducing observed range and population dynamics.

Generally, North American winter avifauna species richness and the average body mass of community assemblages are increasing (Table A.1.3) (La Sorte, Lee, Wilman, & Jetz, 2009). In eastern North America, winter bird occupancy is being climatically constrained (Zuckerberg et al., 2011) and community assemblages are becoming dominated by warm-adapted species as mean winter temperature increases (Prince & Zuckerberg, 2015). The northward winter range shift of the Pileated Woodpecker, Red-bellied Woodpecker, Northern Flicker (larger bodied woodpeckers), and Yellow-bellied Sapsucker are strongly contributing to these winter community composition changes (Prince & Zuckerberg, 2015). However, only the Pileated and Red-bellied Woodpecker populations, both resident migrants, exhibited a concurrent increase in abundance during the winter season (Table A.1.1) (Soykan et al., 2016). In the context of modeling, associated climate change induced community scale dynamics over time are not necessarily in agreement with spatial climatic trends, i.e., under the auspice of climate change, observed spatial gradients relating to climate may not accurately predict temporal trends of species assemblages at the community scale (La Sorte et al., 2009).

Montane environments of the western U.S. are losing breeding season avifauna diversity at all elevational gradients (Tingley & Beissinger, 2013) and latitude and elevation range shifts have been idiosyncratic (Auer & King, 2014). Among the studies reporting elevation climate space tracking (Tingley et al., 2012; Zuckerberg et al., 2009), woodpeckers responded heterogeneously (Table A.1.3). In the Sierra Nevada of California, avifauna with low and high elevation range centroids tend to track favorable precipitation and temperature conditions (Tingley et al., 2012, 2009) shifting species upslope and downslope, respectively (Tingley et al., 2012). Comparing 1911-1929 to 2003-2009, Tingley and Beissinger (2013) found avian populations decreased across all elevational gradients, species richness was lower, and compositions changed. However, woodpecker responses differed slightly from the community response with more than half not declining. The adaptive capacity of these woodpeckers is considered high (Table A.1.1) (Foden et al., 2013), so climate change alone may not drive responses and community dynamics may not scale to the species level. Thus, accounting for two-dimensional climate space interactions (Tingley et al., 2012) and subsequent niche constraints in models is important for montane populations.

The described range shifts and behavioral responses likely reflect complex interactions between climate, habitat changes, and anthropogenic influences (La Sorte & Thompson III, 2007) that will affect future population dynamics. For example, the Red-bellied Woodpecker's range expansion north between 1966-2009 (Bled, Sauer, Pardieck, Doherty, & Royle, 2013) was attributed to maturing forest, backyard bird feeders, (Jackson & Davis Jr, 1998; Meade, 1988), and planted trees in the Great Plains (Shackelford et al., 2000). Although, climate is likely influencing these broad-scale range changes and expansions, it is difficult to ascribe change to climate, if it can be explained by other spatially explicit variables, e.g., habitat patterns (Bled et al., 2013). Currie & Venne (2017) found that among some passerines their realized niche temperatures have changed in the last three decades and that represents changes in ambient temperature and not necessarily species movements. That is, species did not maintain more constant thermal niches through time or exhibit strong poleward shifts especially at the higher latitudes, therefore climate change, more specifically temperature, is not always the major driver of continental species' range shifts (Currie & Venne, 2017). Moreover, observed lag responses to contemporary climate change are likely to occur in the future resulting in miss-estimations of range change based on climatic condition only models (Hovick et al., 2016; La Sorte & Jetz, 2012; La Sorte et al., 2009). Factors other than broad-scale climate are confounding distribution and habitat use responses. The mechanisms underlying observed shifts are numerous (Currie & Venne, 2017; Hitch & Leberg, 2007; Hovick et al., 2016; La Sorte & Thompson III, 2007; Tingley et al., 2009) and require further consideration, especially within modeling frameworks, if climate induced distribution changes are to be accurately predicted.

Comparing Climate Induced and Predicted Trends

We found that 7 of 15 species short-term breeding geographic range predictions under one or both emission scenarios are not in agreement with observed trends (Table 1.3). The contemporary breeding ranges of the Williamson's Sapsucker, Ladder-backed Woodpecker, and Red-headed Woodpecker are contracting, and the Golden-fronted Woodpecker, Lewis's Woodpecker, Red-breasted Sapsucker, and White-headed Woodpecker (*Picoides albolarvatus*) ranges are stable. In addition, the American Three-toed Woodpecker climatically suitable range is predicted to contract substantially in the short-term (Table 1.3), however observed trends from 2005-2015 indicate an increasing population (Sauer et al., 2017). The disagreements between short-term predictions and observed trends highlight the potential incongruencies between future potential climatic niches and realized niches based on climate-woodpecker bioclimatic niche models.

We hypothesize that woodpecker responses derived from climate-woodpecker models are likely not in agreement with observed trends because additional niche characteristics (e.g., forest composition) are responding differently to climate change, and these changes are not represented in the models being used. Therefore, mismatches in observed and future trajectories will continue to arise as actual vegetation cover (i.e., habitat) differs from theoretical because of climate conditions interacting with landscape scale processes (e.g., fire, seed dispersal) (Hampe & Jump, 2011). A comparison between climate-woodpecker model projections and habitat responses of such species in climate-forest models emphasizes the potential for such inconsistencies.

For example, western montane and boreal woodpecker species such as the American Three-toed Woodpecker, Red-naped Sapsucker, Williamson's Sapsucker, and White-headed Woodpecker are predicted to lose climatically suitable habitat by the bioclimatic niche models (Figure 1.1 and 1.2) (Table A.1.1). Climate-forest models associated with these woodpeckers' habitats project shifts in species distribution and composition (McKenney, Pedlar, Lawrance, Campbell, & Hutchinson, 2007). In other words, Climate-woodpecker models indicate a range loss due to climate change, but climate-forest models report a mixed response of the underlying habitat. Assuming tree species of this region (associated with woodpeckers' suitable habitat) track their climate niches (i.e., the climatically suitable range of woodpeckers is more closely associated with a congruent shift in vegetation); forest composition change projections are mixed leading to the potential for habitat persistence. Lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*) and aspen geographic ranges will likely decline (Coops & Waring, 2011b, 2011a; McKenney et al., 2007; Rehfeldt, Ferguson, & Crookston, 2009), ponderosa pine (*Pinus ponderosa*) range projections show mixed results (Coops & Waring, 2011b; McKenney et al., 2007), and Douglas fir (*Pseudotsuga menziesii*) range is predicted to increase (Coops & Waring, 2011b; McKenney et al., 2007). However, tree species will exhibit some level of delayed climate niche tracking (McKenney et al., 2007) because tree species migration will likely not keep pace with projected climate changes (L. R. Iverson, Schwartz, & Prasad, 2004). This will result in a lag effect between changing climatically suitable geographic range and subsequent woodpecker species colonization because contemporary vegetation patterns will not perfectly track climatic shifts. This will increase the likelihood of the persistence of suitable habitat or refugia (Beever et al., 2016) through the 21st century, which are undetectable with bioclimatic niche models (Wiens & Bachelet, 2010).

Using climatic conditions associated with contemporary distributions can under-predict the areas that are climatically suitably post climatic change (Early & Sax, 2014) because landscape scale processes can cause a lag in vegetation (Wu et al., 2015) or animal (Menéndez et al., 2006) responses. Processes that create a mismatch between expected and actual vegetation could result in the persistence of suitable habitat patches that mitigate short term climate change pressures on some populations (Kellermann & van Riper, 2015). For example, fire potential and frequency are predicted to increase across most of the U.S. and more specifically the Rocky Mountains (Liu, Goodrick, & Stanturf, 2013; Rocca et al., 2014). This is proposed to fundamentally change the western U.S. fire regime to dynamics not observed in the historical and paleoecological record, i.e., a novel fire-climate-vegetation relationship is predicted (Anthony L. Westerling, Turner, Smithwick, Romme, & Ryan, 2011). Bioclimatic range projections can track climate change assuming processes occurring under current climatic conditions persist. However, bioclimatic niche models do not fully capture the shifting woodpecker niche constraints resulting from novel climate-vegetation-disturbance interactions. It is possible that increases in fire severity and or frequency may be beneficial to some woodpecker species in the western U.S. (Hutto & Patterson, 2016), and that climatic changes that do not pose direct physiological constraints on woodpeckers may result in suitable habitat via forest composition and structure changes. Therefore, accounting for vegetation and the ecosystem processes underlying vegetation dynamics is important in the climate-woodpecker-forest integration framework.

There are instances where climate-woodpecker models agree with observed trends, and future predictions are supported by climate-forest projections of the underlying habitat vegetation composition. However, the mechanisms underlying these observed and predicted trends are nuanced and identifying them will improve model integration. For example, the Yellow-bellied Sapsucker has short-term predictions that are in agreement with observed trends (Table 1.3) and long-term predictions indicate range contractions (Langham et al., 2015; Matthews et al., 2011). The Yellow-bellied Sapsucker has been increasing in abundance at its southern range extent since 1966 (Sauer et al., 2017), shifting south, expanding east, and increasing in geographic range (Bateman et al., 2016; Hitch & Leberg, 2007; Zuckerberg et al., 2009), though this is despite climatic factors (Table A.1.3) (Stephens et al., 2016). They favor early-successional forests and are currently increasing because of the reversion of post-European settlement agricultural land use to forests (Walters, Miller, & Lowther, 2002). The contemporary geographic breeding range is projected to decrease by 2080 and shift north under the highest emissions scenario (A2 model; Figure 1); this will result in an overall geographic range reduction of 31% (Langham et al., 2015) and a breeding range almost entirely in Canada (National Audubon Society, 2017). Further, the predicted decline (Table A.1.1) is in agreement with results from a climate-woodpecker-forest model for the eastern and northeastern regions of the U.S. (Matthews et al., 2011; Rodenhouse et al., 2008), which represents the southern portion of the breeding range.

This predicted decline of the Yellow-bellied Sapsucker climatically suitable range appears to be supported by climate-forest projections. The tree species most associated with their mixed-forest breeding habitat (quaking aspen (*Populus tremuloides),* red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and paper birch (*Betula papyrifera*)) (Walters et al., 2002) will shift north with concurrent contractions in climatically suitable ranges (except: red maple range will increase) according to bioclimatic tree models (McKenney et al., 2007). Southern limited species (e.g., sugar maple (*Acer saccharum*), American basswood (*Tillia americana*), and bitternut hickory (*Carya cordiformis*)) (McKenney et al., 2007; Terrier, Girardin, Perie, Legendre, & Bergeron, 2013) will expand north, causing a tree composition change towards more deciduous dominance (Terrier et al., 2013).

Although these climate-forest bioclimatic niche tree models may suffer from under prediction errors (Early & Sax, 2014), a process-based model of these forest ecosystems indicates a seral stage shift (Thompson, Foster, Scheller, & Kittredge, 2011), which will affect Yellow-bellied Sapsucker habitat suitability. The contemporary early-successional forests of the northeast U.S. will change by mid-century; at the southern edge of the Sapsucker's breeding range, a shift towards late successional species is expected and possibly accelerated as climate change has a net positive impact on growth (Thompson et al., 2011). In addition, the contemporary Sapsucker population is likely above historical size because of the large scale changes in land use post-European colonization (Walters et al., 2002). It is likely, the current population size and range extents are not sustainable because of antecedent land use change and forest succession; however, climate change will synergistically interact with successional trajectories.

The predicted declines of climatically suitable range of the Yellow-bellied Sapsucker appear to be consistent with shifts in climate induced tree species composition and forest successional dynamics. Although short term climate-woodpecker predictions agree with observed trends, climate is not underlying this trend. Thus, climate-woodpecker predictions may not fully capture future dynamics. Contemporary range distributions are likely a function of forest vegetation shifts, due to historic land use. Future distributions will likely be a function of vegetation shifts resulting from climate change interactions with forest succession. Capturing the effects of climate and forest successional dynamics in the integrated framework of climate-woodpeckers-forest modeling will help account for more nuanced distribution responses.

As the niche constraints (e.g., forest composition, structure) associated with woodpeckers respond to climate change (Ganey & Vojta, 2012; A. L. Westerling, Hidalgo, Cayan, & Swetnam, 2006), climate variables may poorly approximate woodpecker species responses compared to measures of ecosystem dynamics, e.g., forest net primary productivity (Tingley et al., 2009) or forest composition. Therefore, ecosystems predicted to be climatically unsuitable (per bioclimatic niche models) but predicted to maintain or increase key habitat species or functions (per process-based climate-forest models) may still be suitable habitat for woodpeckers because of resource persistence. Accounting for associated niche constraints in a climate-woodpecker-forest modeling framework will produce more informative responses.

Framework Integration

Development of forest management strategies aimed at increasing or preserving wildlife species in a changing climate requires modeling efforts that include the coupled response of vegetation *and* wildlife to climate change. We suggested woodpeckers as an indicator species of forest resiliency and biodiversity in an integrated forest-wildlife modelling framework, because they are ecologically constrained by forest structure, composition, and processes that affect a diversity of other organisms. Based on our comparison of predicted and observed woodpecker responses to climate change, we propose a framework for integration of climate, woodpecker, and forest modeling (Figure 1.3).

Models used to project future abundances and distributions of North American woodpecker species have largely been developed independently of process-based models of forest vegetation responses to climate change (Table 1.1) (Figure 1.3). The available bioclimatic niche models that predominate the predictions about woodpeckers (Figure 1.3-B) provide potential broad-scale range distribution trends (Pearson & Dawson, 2003), however they lack the finer scale habitat details (e.g., forest structure, composition, and habitat characteristics) that affect localized woodpecker population responses and may strongly interact with climate change. Habitat use and population persistence in a changing climate are difficult to ascertain without vegetation responses. For example, the inclusion of vegetation indices in distribution forecasts of boreal and mixed conifer forests avifauna is important for improved modeling results (Cumming et al., 2014). The complexities of climate, vegetation, and disturbance interactions that modulate woodpecker habitat use underscores the need for coupled modeling that accounts for these ecological details (La Sorte & Jetz, 2010).

While the inclusion of vegetation (dynamic global vegetation model: DGVM (Figure 1.3-A); for a review of the spectrum of climate-forest models see: Scheller & Mladenoff, 2007)) have improved avian distribution models (Conlisk, Syphard, Franklin, & Regan, 2015; Matthews et al., 2011), plant functional types (outputs of DGVMs) still do not adequately account for future habitat distributions of woodpeckers (i.e., the type of climate-forest model (Figure 1.3-A)). This is because plant functional groupings may be of a scale too course to model woodpecker responses to forest characteristics. For example, Bancroft et al. (2016) found no impact of climate change on Red-cockaded Woodpecker habitat loss. They modeled climate as a direct (i.e., precipitation effects on reproduction) and indirect (i.e., plant functional group responses to temperature and precipitation) effect. However, the resilience of the Red-cockaded Woodpecker population is related to the structural components of a stand (tree density and size class distributions) and ground cover composition (James et al. 2011), which are indistinguishable at the scale of plant functional groups. Therefore, even with the persistence of the needle-leaved evergreen biome or long-leaf pine successional stages within this region (Costanza, Terando, McKerrow, & Collazo, 2015), finer scale niche attributes are important (Schiegg et al., 2002) and should be included in model integration.

Dynamic-community process-based forest landscape models (Scheller & Mladenoff, 2007) such as the LANDIS models (LANDIS-II and LANDIS PRO) (Figure 1.3-A) that incorporate finer scale climate-vegetation-disturbance interactions compared to bioclimatic DGVMs are promising (Di Febbraro et al., 2015; Louis R. Iverson, Prasad, Matthews, & Peters, 2011; LeBrun et al., 2016; Tremblay, Boulanger, Cyr, Taylor, & Price, 2018). These models could improve woodpecker distribution modeling, especially within the context of multi-objective management scenarios (K. L. Martin, Hurteau, Hungate, Koch, & North, 2014). Many of the key habitat characteristics and processes (e.g., forest composition and structure; disturbance type, intensity, and temporal trends) that modulate woodpecker population responses are already output variables of forest landscape models, allowing for points of integration between the two modeling disciplines (Figure 1.3-A and C). In addition, these models can be modulated by climate data, which is the integration point in the climate-woodpecker-forest framework (Figure 1.3-D).

Integration examples support this proposed framework. LANDIS-II model projections by K. L. Martin et al. (2014), found that managing long-leaf pine habitat for carbon storage decreases biodiversity and Red-cockaded Woodpecker habitat at the expense of increased carbon sequestration. Similarly, the Black-backed Woodpecker in boreal forest of Canada are predicted to decline under climate change or business as usual harvest practices (Tremblay et al., 2018). The LANDIS models (Figure 1.3-A) allow for climate data integration, simulate ecosystem processes that produce emergent vegetation dynamics that constrain woodpecker distributions, and output variables that can inform woodpecker-forest models (Figure 1.3-C).

In summary, after evaluating the predicted and observed woodpecker trends associated with climate change, we found there are inconsistencies between climate-woodpecker predictions and observed woodpecker responses, highlighting the uncertainty of future woodpecker distribution and population predicted responses. We conclude that implementation of climate-smart management strategies aimed at increasing or preserving wildlife species, will require modeling efforts to include the coupled response of climate-wildlife-forest (Figure 1.3). The use of an indicator species of climate effects on forest biodiversity and resiliency is an improvement to ecosystem modeling. The general principle of coupled modeling frameworks is not a new proposal with regards to climate change (Root & Schneider, 1993). However, to date, we are aware of no model (Figure 1.3-D) that has managed to actually fully combine wildlife niche modeling into a climate-forest model; meaning modeling activities have utilized multiple models in tandem with data handoffs rather than have the models interact with feedbacks to processes. Our review suggests that fully integrating climate-woodpecker-forest models will address the limitations of climate-woodpecker models, while providing a biodiversity measure for climate-forest modeling efforts. Selection of the proper models within the framework will improve the resolution of fine-scale woodpecker population responses to climate change and support multi-objective management through integration of a biodiversity metric.

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Table 1.1. The reviewed studies of woodpecker predictions to climate change. BBS: Breeding Bird Survey; CBC: Christmas Bird Count; Collected: data from study; GBIF: Global Biodiversity Information Facility.

Studies	Geographic Location	Prediction Period (out to)	Study Season	Training/Informing Data Source	Spatial Grain of Prediction	Climate Models	Emission Scenarios	Number of Woodpecker Species	Conceptual Model Intersection (Figure 3)
Bancroft et al. 2016	Fort Benning, Georgia USA	2100	Breeding	Collected	2500 m^2	CCSM3, CGCM3.1, UKMO-HadleyCM3	B1, A1B, and A2	1	D
Foden et al. 2013	Global	NA	NA	Expert Opinion	NA	NA	NA	22	NA
Langham et al. 2015	United States and Canada	2100	Breeding/Non-Breeding	BBS and CBC	100 km^2	CCCMA-CGCM3.1T47, CSIRO-Mk3.0, IPSL-CM4, MPI-ECHAM5, NCAR-CCSM3.0, UKMO-HadleyCM3, UKMO-HadleyGEM1, NIES	B2, A1B, and A2	22	B
Matthews et al. 2011	Eastern United States (east of the 100th meridian)	2100	Breeding	BBS	400 km^2	HadleyCM3, GFDL CM2.1, PCM	B1 and A1 fi	5	D
Rodenhouse et al. 2008	Northeast United States	2100	Breeding	BBS	400 km^2	HadleyCM3, GFDL CM2.1, PCM	B2 and A1 fi	5	B
Ralston & Kirchman, 2013	New York, Vermont, and New Hampshire USA	2080	Breeding	ORNIS and GBIF	NR	HadleyCM3	B2 and A2	2	B
Tremblay et al. 2018	eastern Canada	2100	Breeding	Previous Research	250 m^2	CanESM2	RCP 2.6, 4.5, and 8.5	1	D

Table 1.2. The reviewed studies of observed woodpecker responses to climate change. BBS: Breeding Bird Survey; CBC: Christmas Bird Count; PFW: Project Feeder Watch; BBA: Breeding Bird Atlas; Collected: data from study.

Study	Study Period	Study Season	Data Source	Geographic Location	Number of Woodpecker Species
Bateman et al. 2016	1950-2011	Breeding	BBS	Contiguous United States	15
Hitch and Lebrg 2007	1967-1971 and 1998-2002	Breeding	BBS	BBS Central and East regions	2
Huang et al. 2017	1969-2012	Breeding	BBS	Contiguous United States and southern Canada	7
La Sorte and Jetz 2012	1975-2009	Non-Breeding	CBC	Between 25° and 49° N latitude	4
La Sorte and Thompson III 2007	1975-2004	Non-Breeding	CBC	Contiguous United States, Canada, and Mexico	13
La Sorte et al. 2009	1975-2001	Non-Breeding	CBC	Contiguous United States and southern Canada	18
Prince and Zuckerberg 2015	1989-2011	Non-Breeding	PFW	Eastern North America (below 50° N latitude E of the 100th meridian)	5
Schiegg et al. 2002	1986-1998	Breeding	Collected	South-central North Carolina, USA	1
Stephens et al. 2016	1980-2010	Breeding	BBS	Contiguous United States	20
Tingley et al. 2009	1911-1929 and 2003-2008	Breeding	Collected	Sierra Nevada of California	6
Tingley et al. 2012	1911-1929 and 2006-2009	Breeding	Grinnell Resurvey Project	Sierra Nevada of California	9
Wiebe and Gerstmar 2010	1998-2009	Breeding	Collected	Riske Creek, British Columbia	1
Zuckerberg et al. 2009	1980-1985 and 2000-2005	Breeding	New York State BBA	New York State	6
Zuckerberg et al. 2011	2007-2008	Non-Breeding	PFW	North-eastern United States and adjacent Canadian provinces	4

Table 1.3. The predicted 2020 breeding range size relative to the 2000 range (Langham et al., 2015) and observed contemporary breeding range changes (Bateman et al., 2016). Breeding predictions that disagree (>10% from 1) are highlighted. Emission scenarios are the A2 (high) and B2 (low) IPCC SRES.

Species	Predicted Breeding		Observed Breeding
	High Emissions	Low Emissions	
Acorn Woodpecker	1.37	1.25	expanding
American Three-toed Woodpecker	0.30	0.27	
Arizona Woodpecker	NA	NA	
Black-backed Woodpecker	NA	NA	
Downy woodpecker	1.15	1.18	expanding
Gila Woodpecker	3.29	3.64	expanding
Gilded Flicker	3.12	2.83	
Golden-fronted Woodpecker	0.71	0.95	no change
Hairy Woodpecker	0.92	0.97	no change
Ladder-backed Woodpecker	1.49	1.56	contracting
Lewis's Woodpecker	0.84	0.89	no change
Northern Flicker	0.96	0.83	
Nuttall's Woodpecker	0.97	0.93	no change
Pileated woodpecker	1.25	1.27	expanding
Red-bellied Woodpecker	1.15	1.15	expanding
Red-breasted Sapsucker	0.95	0.82	no change
Red-cockaded Woodpecker	NA	NA	
Red-headed Woodpecker	1.07	1.08	contracting
Red-naped Sapsucker	1.08	0.83	
White-headed Woodpecker	0.73	0.67	no change
Williamson's Sapsucker	1.55	0.92	contracting
Yellowbellied sapsucker	1.44	1.62	expanding

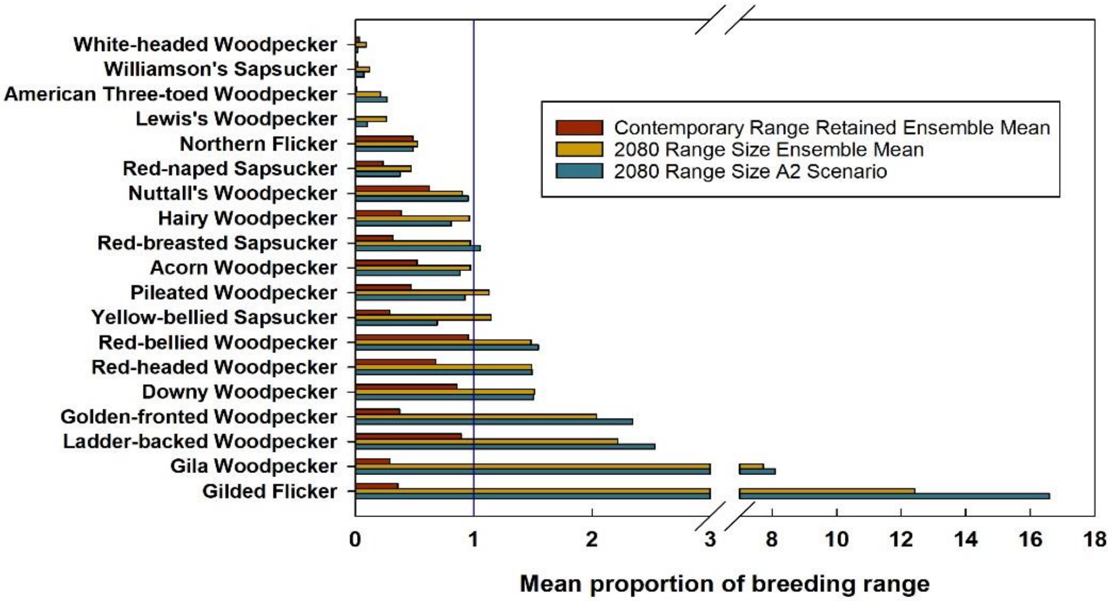

Figure 1.1. The mean proportion of North American contemporary woodpecker breeding range retained by the end of the century based on the ensamble global climate model emission scenarios (B2, A1B, and A2: listed from low to high emissions). The overall proportional change of the breeding range by 2080 compared to 2000 based on the high emissions climate model scenario (A2) and emission scenario ensamble means (B2, A1B, and A2). Values <1 represent a decline. Data from Langham et al. (2015).

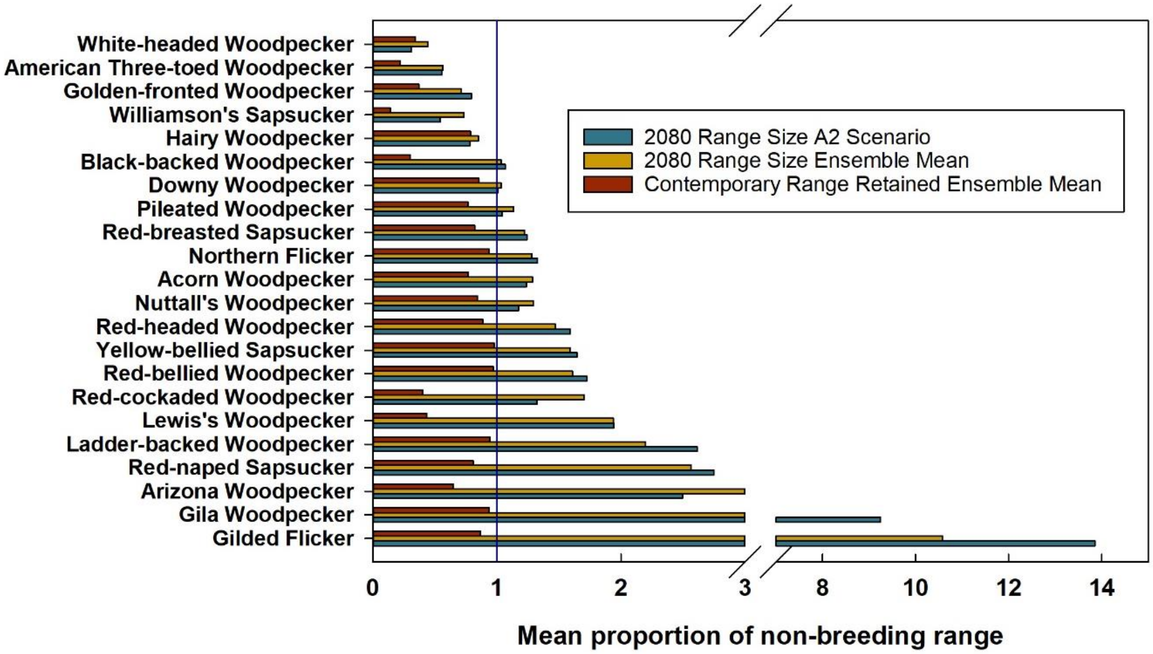

Figure 1.2. The mean proportion of North American contemporary woodpecker non-breeding range retained by the end of the century based on the ensamble global climate model emission scenarios (B2, A1B, and A2: listed from low to high emissions). The overall proportional change of the wintering range by 2080 compared to 2000 based on the high emissions climate model scenario (A2) and emission scenario ensamble means (B2, A1B, and A2). Values <1 represent a decline. Data from Langham et al. (2015).

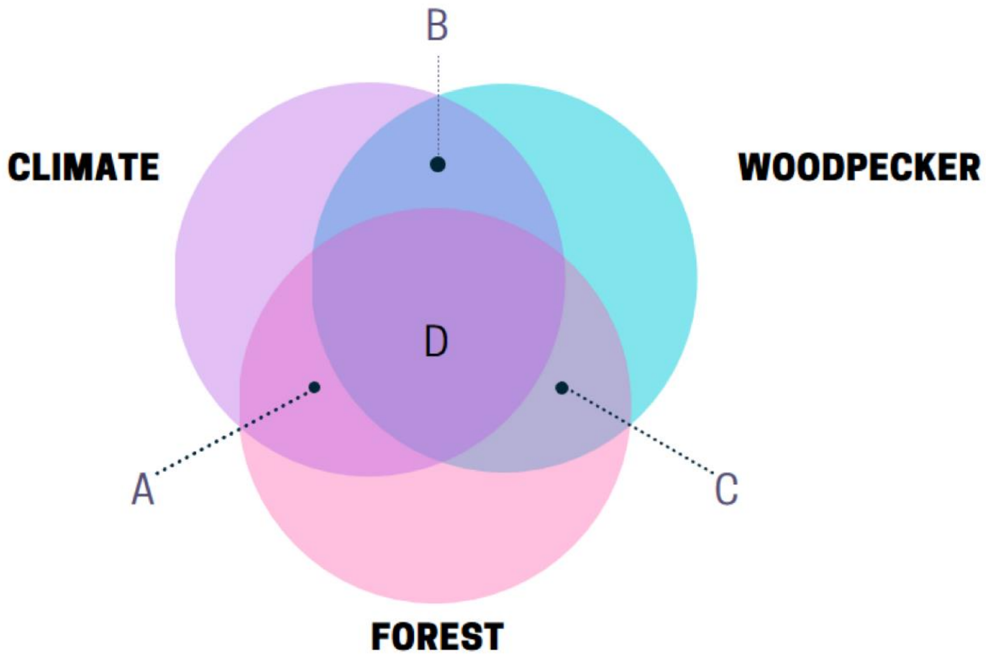

Figure 1.3. The integrated framework of climate-woodpecker-forest modeling (D) resulting from the linking of separate model types (A-C). A) Climate-Forest prediction models include a spectrum of model types: dynamic global vegetation Models (DGVM) to GAP models to dynamic community process-based forest landscape models (i.e., dynamic communities, spatial interactions, and ecosystem processes); B) Climate-Woodpecker prediction models include bioclimatic envelope models; C) Woodpecker-Forest models include realized niche models (e.g., occupancy), potential niche models (e.g., habitat suitability), and demographic models.

Chapter 2: An integration framework for linking avian cavity nesting species niche models with forest landscape models.

Under consideration in *PLoS One*

Abstract

Avian cavity nesters (ACN) are viable indicators of forest structure, composition, and diversity. Utilizing these species responses in multi-disciplinary climate-avian-forest modeling can improve climate adaptive management. We propose a framework for integrating and evaluating climate-avian-forest models by linking two ACN niche models (Flammulated Owl (*Psiloscops flammeolus*) and American Three-toed Woodpecker (*Picoides dorsalis*) with LANDIS-II (a forest landscape simulation model). The framework facilitates the selection of available ACN models for integration, evaluation of model transferability, and evaluation of successful integration of ACN models with LANDIS-II at landscape scales. We found selecting a model for integration depended on its transferability to the study area (Northern Rockies Ecoregion of Idaho in the United States), which limited the species and model types available for transfer. However, transfer evaluation of the tested ACN models indicated a good fit for the study area. Several niche model variables (canopy cover, snag density, and forest cover type) were not directly informed by the LANDIS-II model, which required secondary modeling (Random Forest) to derive values from LANDIS-II outputs. In instances where the Random Forest models performed with a moderate classification accuracy, the overall effect on niche predictions was negligible. Predictions based on LANDIS-II simulations performed similarly to predictions based on the niche model's original training data types. This supported the conclusion that the proposed framework of informing niche models with LANDIS-II data is viable. Even models that poorly approximate habitat suitability, due to the inherent constraints of predicting spatial niche use of irruptive species produced informative results by identifying areas of management focus. This is primarily because LANDIS-II estimates spatially explicit data that were unavailable over large spatial extents from alternative datasets. Thus, without integration, the ACN niche model was not applicable to the study area. The framework will be useful for integrating

avifauna niche and forest ecosystem models, which can inform management of contemporary and future landscapes under differing management and climate scenarios.

Introduction

The structure and composition of forest ecosystems are expected to shift with climate-induced changes in precipitation, temperature (1), fire (2), carbon mitigation strategies (3,4), and biological disturbances (5). Specifically, climate change induced declines in tree species occurrence (6), shifts in forest carbon stocks (1), increases in forest mortality events (7), and increases in forest burn area (8) have been predicted. Forest composition and structure are integral to biodiversity (9), and the climate induced changes are likely to have biodiversity implications (10) especially for avifauna (11). For example, moderate to high severity fires can create open forest habitat, adequate snag density, and minimal mid-story vegetation for avian cavity nesters such as woodpeckers (12). Though climate models predict increases in area burned or fire intensity, which may increase habitat suitability for woodpeckers (13), tree species composition shifts via climate change may pose adaptation constraints on them (14). Integrating the feedbacks between avian biodiversity and forest processes in a modeling framework could improve our understanding of climate induced biodiversity changes and subsequent climate-forest adaptive management.

We use avian cavity nesters (ACN), both primary excavators and secondary cavity users, to test our framework, because they are an ideal ensemble of wildlife species to function as indicators of forest biodiversity and ecosystem function by combining climate, wildlife, and forest ecosystem modeling. ACN are ideally suited as indicator species of forest ecosystem dynamics (15–18), because they are ecologically constrained by landscape scale forest components such as composition, structure, disturbance regimes, and management activities. Primary cavity excavators are also correlated with forest avifauna community diversity (15) and cavity nesting webs (19,20). Some woodpecker and owl species are associated with the characteristics of mature and structurally complex forests (15,21,22), which sustain greater biodiversity (23) and modulate their population responses. The forest characteristics that influence woodpecker and owl occupancy include include snag density (24,25), tree density and diameter (26), burn severity (12,27), and beetle outbreak (28). These forest ecosystem components will be impacted by climate change (5,29,30), likely having cascading effects on some ACN responses rendering them viable indicators in modeling future changes to biodiversity under a range of climate and management scenarios.

An interdisciplinary approach that links future forest structure and composition (from mechanistic based forest ecosystem models) with ACN ecological niche models would account for the intrinsic feedbacks between climate, disturbance, vegetation, and biodiversity (Figure 2.1). This approach would have two primary outcomes. First, the inclusion of vegetation and other ecological constraints can further improve climate change based avian distribution models (31,32). Second, the derived avifauna response after integration provides an additional metric beyond biogeochemical to assess differing future scenario effects (e.g., climate, management, and natural disturbance) on forest ecosystems.

The integration of vegetation into an avifauna distribution model framework via dynamic global vegetation models (DGVM: models that project vegetation type shifts) has been shown to be effective (33) benefitting range-restricted species, which are more likely constrained by non-climatic factors. Moreover, fine-scale vegetation modeling of specific environments (e.g., montane and boreal environments) may be necessary to evaluate the feasibility of avifauna distributional changes (34,35). Process-based forest landscape models such as the LANDIS models (LANDIS-II and LANDIS PRO) that incorporate finer scale climate-vegetation-disturbance interactions are promising (36–39). Many of the key habitat characteristics and processes (e.g., forest composition and structure; disturbance type, intensity, and temporal trends) that modulate ACN habitat use responses are output variables of forest landscape models, allowing for points of integration between the two modeling disciplines. Studies that have used this integration approach (Figure 2.1) found that managing for forest carbon storage decreased biodiversity (39) and populations would decline under climate change or business as usual timber harvest practices (38).

Despite these previous efforts, cross-discipline model linking has been limited to a few study areas and is hampered by lack of framework for transferring, especially quantitative niche models. We present a framework to integrate ACN ecological niche models with LANDIS-II and formalize the process. First, our focus is on using existing models and readily available data to achieve model integration. Since this results in models that are not applied in situ, we address transferability. Second, because forest landscape model outputs do not always function as direct inputs into ACN ecological niche model (e.g. percent forest cover versus age or leaf area index), we explore the methods necessary to translate landscape model outputs to the inputs required. Finally, we address the process of verifying that LANDIS-II outputs will adequately inform the ecological niche model when compared to the model's original inputs (i.e., the data types used to originally train the niche model). We use the standardized terminology of ecological niche model, realized niche model, potential niche model, and habitat suitability map proposed by (40).

Materials and Methods

Study Area

The study area was the Environmental Protection Agency Level III Northern Rockies Ecoregion of northern Idaho (41). This area covers 3.1 million hectares and is 88% forested. The region is 61% publicly held with 76% of the public land managed by the U.S. Forest Service. It is comprised of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), western white pine (*Pinus monticola*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophylla*). The climate varies across topographic gradients from cooler-wet to warmer-dry affecting forest productivity and fuel loads. Historically, the region had a mixed-severity fire regime with low/moderate severity fire rotations of < 20 years in the low to mid-elevation forests (42) to high severity fires occurring every 150-500 years across elevation gradients (43,44).

Model Integration Framework

Taxonomically, bird species distribution models transfer better to other regions compared to invertebrate and plant models (46). However, the transferability of a model both spatially and temporally requires an evaluation of environmental equilibrium of the species' niche, environmental similarity between model training and projection regions, and maintenance of the correlation matrix among predictors between study regions (47). These constraints and others related to model development methods (48) limit the number of models available for integration, because models that pertain to a specific focal species, region, temporal period, transferability potential, and accommodate the level of inference desired are not readily available. Thus, the availability of models was limited because of: 1) transferability issues due to the inability to apply a model to a novel landscape (e.g., machine learning models) do not produce parametric equations for publication easily, hampering model application beyond the training region) (Figure 2.2-A) or; 2) the lack of parameter concordance between the avian model inputs and LANDIS-II outputs or its derivatives (Figure 2.2-B). Models that were available for integration were then scrutinized for transferability.

Model Types

We selected two avian niche models to demonstrate the process of model integration with LANDIS-II. The first was a Flammulated Owl (*Psiloscops flammeolus*) realized niche model that predicts potential distribution and was originally informed by presence-absence data while accounting for imperfect detection (49). The second was an American Three-toed Woodpecker (*Picoides dorsalis*) potential niche model that predicts the extent of suitable habitat without considering potential distributions (50). Both applications resulted in habitat suitability maps of the study region. We selected these models to demonstrate the application of realized and potential niche models within the framework and for pragmatic reasons. The Flammulated Owl model was trained in an ecological region similar to our study area, which allowed for transferability. The American Three-toed Woodpecker model is considered broadly applicable across the woodpecker's distribution (50), thus rendering it readily available and transferable.

Transferability Assessment

The transferability assessment (Figure 2.2-A) was implemented following the suggestions of (47). The first assumption of transferability is that the species is in equilibrium with the environment or current climate suggesting that the species occupies all climatically suitable habitat. This can be evaluated by comparing the observed distributions to modeled distributions based on climate envelope modeling or through analysis of co-variation between species assemblages and climate (51). The latter analysis indicates birds have a high co-variation with climate and can be assumed to be at equilibrium, which is likely because of dispersal ability (51). Thus, we accepted the assumption of equilibrium.

The second assumption of transferability is the application and training region have similar environmental characteristics. We tested for similarity by comparing the distribution of each model's predictors between the training and application regions using the multivariate environmental similarity surface (MESS) methods outlined in (52)(53). In our study, the MESS calculates how similar a grid cell in the application area is to the set of grid cells in the training area based on the set of predictors of the respective model being evaluated. As the similarity value of a grid cell approaches 1, the grid cell is less novel, which at 1 the application predictor values are all equal to the median value in the training area. A negative cell value indicates a predictor in the application area that is outside the range of the training area, i.e., the cell represents a novel environment (see MAXENT Novel tutorial at http://www.cs.princeton.edu/~schapire/maxent/). The third assumption of transferability is the co-variation structure of the predictor variables remains spatially and temporally constant. We tested for changes in the correlation matrix using a Pearson correlation.

Cross-model Processing

Flammulated Owl Model

The Flammulated Owl model was originally parametrized (hereafter referred to as the *base model*) and trained using data from the Boise National Forest in southern Idaho. The input variables (Table 1) were processed for our study area at the appropriate spatial scales reported for the original study. An initial probability of occupancy was calculated for the study area using the same methods described in (49). This initial distribution was used to evaluate the efficacy of using LANDIS-II to inform the Flammulated Owl model (Figure 2.2).

The parameters for the Flammulated Owl model were not all directly transferable from the LANDIS-II outputs, canopy cover and land cover required secondary modeling (Table 1) (Figure 2.2-B). The *base model* uses the LANDFIRE Forest Canopy Cover dataset (54) aggregated into four canopy cover classes (1 = 0-10%, 2 = 11-40%, 3 = 41-70%, and 4 = 71-100%) with the category's midpoint value assigned to a grid cell. To calculate canopy cover from LANDIS-II outputs, we used Random Forest (RF) (55) to predict the canopy cover classes of the study area from the LANDIS-II biomass estimates (Appendix B.1.1). For model validation, we first used the RF error estimate of classification (Out-of-Bag (OOB)) to approximate the models internal performance. Second, we evaluated the sufficiency of the RF canopy cover predictions to inform the realized niche model when compared to the niche model informed with LANDFIRE canopy data at simulation time step 0 (Figure 2.2-C). We compared the two habitat suitability maps using an ArcGIS 10.5 Band Collection Statistic correlation matrix.

Land cover types and diversity (Shannon Diversity Index) metrics of the Flammulated Owl *base model* are based on the land cover classes of the LANDFIRE Existing Vegetation Type (EVT) within differing buffers around each grid cell at multiple scales. The *base model* is parameterized using 11 EVT classes (49). Our LANDIS-II estimated cover types resulted in a much more spatial heterogeneity of plant functional types than the LANDFIRE classifications for our study region. This required an aggregation of the LANDIS-II output into the 11 LANDFIRE classifications. We accomplished this by training a RF model to spatially predict the LANDFIRE cover types of the initial landscape from the LANDIS-II species composition-biomass spin-up values (Appendix B.1.1).

We generated habitat suitability maps (Figs 1D and 1E) based on the probability of occupancy without aggregating into discrete suitability levels, as this tends to diminish the available information (56). We compared the habitat suitability map informed by the *base model* datasets to the LANDIS-II informed habitat suitability map (Figure 2.2-F) using ArcGIS 10.5 Band Collection Statistic correlation matrix. Observed Flammulated Owl location data from the Idaho Department of Fish and Game (IDFG) (57) and an associated 400 m buffer representing a home-range (49) were also compared to the occupancy predictions (Figure 2.2-G). The location data (n=47) were incidental/causal (n=36) and targeted survey (n=9) field sightings across the study area and spanned the period 1980-2012.

American Three-toed Woodpecker Model

The American Three-toed Woodpecker potential niche model applied here was developed by the Utah Division of Wildlife Resources and The Nature Conservancy using an Ecological Integrity Table (EIT) format (50). EITs identify the key ecological attributes or conceptual factors (e.g., environmental regimes and constraints) that sustain a target's (here: a species) composition, natural dynamics, and long-term persistence (50,58). Associated with the conceptual factors are real indicators that can be quantified or qualified to assess ecological integrity. The transferability assessment was not relevant to this model (Figure 2.2-A), because it is a trait based potential niche model based on threshold assessments of environmental parameters to produce ordinal levels of suitability. The model is explicitly intended to be broadly applicable across the woodpecker's range (i.e., transferable); the exception being the elevation indicator which is applicable specifically to Utah (50). Unlike the Flammulated Owl model, which could be informed by the original model development datasets and LANDIS-II outputs, these model characteristics precluded the development of a comparative habitat suitability map for model verification. We therefore assumed the model informed from LANDIS-II outputs was an accurate representation of suitable habitat elements.

The American Three-toed Woodpecker model has 12 indictors of which eight are considered most important (50). We included six important indicators and one of the alternative indicators (Table 2) omitting the important indicators *larvae of bark beetles* and *forest management*. This was necessary, because we did not model biological disturbances in the LANDIS-II modeling, and there was no process to identify areas of *none* management activity associated with the EIT's *forest management: very good* suitability level. However, the *forest management* indicator is indirectly included among the other indicators such as *stand age* (50). Further, it was not possible to explicitly identify non-harvested areas of the previous 100 years to properly inform the *timber harvest* indicator. We used *stand age* as a proxy to identify areas with rotation ages >100 years and meet the criteria of the *timber harvest* indicator (Table 2).

The *plant associations'* spruce-fir cover extent was derived using the same land cover RF dataset as the Flammulated Owl model. The *elevation* parameterizations were not applicable outside of Utah and were assigned new threshold values based on the study area (59) (Table 2). The *stand age and snag and decadent trees* indicators are qualitative ordinal variables in the EIT. To improve spatial modeling in a GIS of these variables, we assigned quantitative thresholds from other published sources (59,60) (Table 2). *Stand age* was informed from the LANDIS-II spin-up initial landscape maps. S*nag and decadent trees* indicator could not be directly informed by LANDIS-II outputs (Figure 2.2-B). We implemented a RF classification (Appendix B.1.1) model using Forest Inventory Analysis data (FIA) (61) to predict a binary (present/absent) response for the appropriate snag density of each grid cell of the study area, because predicting a quantitative snag density response would be uninformative due to FIA methodology. The FIA methods for plot level estimates result in a minimum scaled snag density of ~14 snags/ha for each recorded dead tree on a plot, which is significantly above the optimal 1.2 snags/ha associated with the American Three-Toed Woodpecker. For RF model training, we filtered the response variable to only include dead standing trees meeting specific criteria (dbh > 26 cm, height > 21 m, and decay code > 2). By accounting for only snags meeting these criteria, we indirectly accounted for the EIT indicators *dbh of snags* and *height of snags* in our modeling.

The habitat suitability map was produced by assigning each indicator layer a one through seven-digit value with each initial digit being unique to the layer (e.g., layer 1 = 1, layer 2 = 20, layer 3 = 300, etc.) (Figure 2.2-E). This created a continuum of potential suitability depending on the number of suitable layers intersecting at a grid cell. Areas that lacked the inclusion of one or more layers were explicitly identified along with a suitability index value indicating the number of intersecting layers present. For example, if a grid cell was coded as 7654320, the layer 1 conditions were not present in the grid cell and the suitability index value would be six.

Like the Flammulated Owl assessment, IDFG known locations of American Three-toed Woodpecker (57) were compared to the potential habitat suitability maps (Figure 2.2-G). The location data (n=113) were incidental/causal (n=46), traveling count (n=16), targeted survey (n=49), and other (n=2) field sightings across the study area and spanned the period 1979-2013. To account for the potential territorial habitat around an observation point, we quantified the suitable habitat using a 147 ha buffer. The buffer was based on the median value of the reported highly variable territory sizes (59).

Results

Flammulated Owl Model

The transferability assessment of the Flammulated Owl realized niche model suggest that it is an acceptable fit for the Northern Rockies Ecoregion of Idaho. The MESS analysis indicated the application area did not have many novel locations compared to the training area; almost all predictor values within the Northern Rockies Ecoregion are within the range found in the training region (Figure B.2.1). The correlation structure between predictors was mostly consistent between areas; several variable pairs only differed in degree of correlation (Figure B.2.2). However, the ponderosa pine density variable differed in direction and degree with respect to non-forest land cover density and canopy cover (Figure B.2.2).

The RF model (Appendix B.1.1) that predicted canopy cover classes from the LANDIS-II outputs was adequate (OOB accuracy: 54.9%). The model overestimated the grid cells that were considered medium, underestimating the high and low canopy classes (Table B.1.2.3). However, the overall performance of the RF did not appear to affect the predicted Flammulated Owl distribution; the two distributions (LANDFIRE and RF canopy cover models) were 99.6% correlated. This is plausible since the effect of canopy cover is minimal (Table 1).

The RF model (Appendix B.1.1) that predicted land cover classes from the LANDIS-II outputs performed well (OOB accuracy: 90.6%). The land cover classes with sparse representation across the application area were predicted poorly and of the three land cover parameters that informed the Flammulated Owl model (Douglas-fir, non-forest, and ponderosa pine), ponderosa pine had the highest prediction error rate (43%) (Table B.1.2.4). Douglas-fir had the lowest prediction error (3%) (Table B.1.2.4) and is a strong predictor of Flammulated Owl habitat occupancy (Table 1). The predicted realized niche using the RF predicted land cover was 94.8% correlated with the *base model* predictions. Differences >10% in occupancy probability were negligible, being mostly relegated to the edges of the study area and non-forested areas (Figure 2.3). The probability of occupancy was similar between models (Table B.2.1) (Figure B.2.3) and among the known Flammulated Owl locations (Table B.2.2). Among the known owl locations, the probability of occupancy was low (Table B.2.2), however the habitat buffers of the known locations did contain older forest stands (mean = 93 years old).

American Three-toed Woodpecker

The EIT was not fully informed because the study area lacked contiguous blocks of mature or old-growth forest that met the *tracts of old-growth forest* indicator threshold (Table B.2.3). Most of the potential niche was associated with public lands, specifically the U.S. Forest Service. Both levels of suitability were limited by the area of appropriate stand age, timber rotation, and snag presence (Table B.2.3). The snag RF model (Appendix B.1.1) was moderately sufficient (OOB accuracy: 74.3%) to predict presence across the landscape. Less than 2% (*very good*) and 4% (*good*) of the region was associated with four or more of the EIT indicators (Table B.2.4 and B.2.5) with 1476 ha of *very good* and 5544 ha of *good* suitable habitat associated with six indicators.

Areas with at least three indicators present comprised major contiguous tracts of potential suitability. Areas with more than three indicators present were disjunct and sparsely distributed across the landscape (Figure 2.4). There was a slight increase in area of suitability level *good* because of the inclusion of mixed-conifer and Douglas-fir cover in the *plant associations* indicator. However, this had minimal impact on increasing the area of suitable habitat based on the total number of indicators present (Table B.2.4). At the *very good* and *good* suitability level, the observed American Three-toed Woodpecker point habitat buffers were mostly associated with areas relegated to no indicators and one indicator present, respectively (Table B.2.6). Some buffers contained areas with up to five EIT indicators Table B.2.7). The known Woodpecker locations had a mean elevation of 1060 m, majority mixed-conifer landcover, median stand age of 52, and were subjected to a simulated burn. A comparison of FIA plots meeting the *very good* and *good* suitability level to the predictions indicated spatial agreement (Figure B.2.4). The FIA plots were not located outside the areas predicted to have one or more EIT indicators.

Discussion

Ecological modeling focused on the effects of climate change and management scenarios (e.g., fire, carbon mitigation, harvest) on forest resiliency will need to account for the effects of these dynamics on biodiversity and specific species management interests. Thus, to implement climate adaptive management strategies aimed at increasing or preserving wildlife species, modeling efforts will need to include the coupled response of vegetation *and* wildlife to climate change. We evaluated a framework for integrating ACN ecological niche and forest landscape models to improve ACN climate change niche modeling and provide ecological modelers with a means to account for wildlife habitat measures in biogeochemical forest modeling.

Transferability assessment

Ecological niche models developed independent of forest landscape models will often require a transfer from the model's trained to implementation region, increasing the uncertainty of model applicability to a potentially novel region. Generally, models that more readily capture the foundations of the ecological niche (62) and with predictors that encompass a wider environmental range in the development region, especially among confounding variables (e.g., elevation and temperature), are more readily transferable (63). To maximize transferability potential, a candidate set of models should be constructed based on the environmental similarity between the training and application regions, the methods used to evaluate model fit within the training region, the ecological rational and association between predictor variables and niche response, and the type of model (inference focused or machine learning).

Ideally, mechanistic models, which are more robust at capturing the processes that limit species distributions (64) would be implemented within this framework. It will not always be feasible to implement a process-based niche model, since a significant proportion of ecological niche models are correlative models (65) and are readily available for implementation. Therefore, the primary limiting factor of applying the framework is identifying niche models that are trained in geographic and environmental space similar to the application region to ensure correlative models that are transferred are applied to environments with similar covariance structures. Meeting this criterion is important because geographical orientation, anthropogenic land use, and ecological memory (the persistence of adaptations and individuals post disturbance that shape responses) affect species distributions and are difficult to standardize across regions (63). This factor limited the implementation of models (66), because the models were developed in regions too dissimilar to the study area.

Transferability is also limited by the niche model algorithm. A Black-backed Woodpecker (*Picoides arcticus*) niche model developed in the same ecoregion but outside the study area (67) met the geographic constraint criterion. However, the model was developed from a machine learning algorithm (MAXENT), which limits transferability. Models that use predictor variables based on sound ecological relationships with close causal links to response variables increase transferability (68). Ideally then, statistical models are more readily transferable, because they are focused on inference and ascertaining the causal relationships between predictor and response variables that have biological interpretations within clear conceptual frameworks (69). Alternatively, machine learning processes are more readily used for prediction through identification of patterns in often complex datasets. Ecological interpretations of such models is challenging, because relationships are not readily related to biological knowledge (69). This makes transferability difficult because though machine learning algorithms like RF are immune to random noise overfitting (55), they are not immune to overfitting due to heterogeneity of predictor-response relationships (70,71). This overfitting and failure to make general predictions to novel geographic extents has been observed in machine learning processes applied to avifauna distributions (72). Without a sound ecological basis for modeled predictor-response variable relationships, regardless of the model's *in situ* prediction success, it is best to avoid transferring these models to a novel region.

The integration framework is intended to support modeling efforts that focus on climate change scenarios and evaluating the temporal changes in avifauna niches. Ensuring the feasibility of a cross-temporal transfer of the niche model is also important; it is best to select models that have been evaluated for parsimony and not just correlative fit. Parsimonious models, those with moderate complexity as determined using for example Akaike's Information Criterion, exhibit better cross-temporal transferability than models with higher correlative fit to training conditions as determined using Area Under the Curve (71). Models like the Black-backed Woodpecker niche model with many predictor variables are also limited in transferability because parsimony limits cross-temporal applications.

The Flammulated Owl model applied within this study meets the criteria described. It was developed within a geographic region similar to our study area (Figs 2 and 3). The model's predictor variables are based on *a priori* biological knowledge; they approximate known key habitat-use variables and at scales appropriate to capture dynamics of different ecological processes (e.g., juvenile dispersal, predator interactions, and foraging range) (49). In addition, the training selection criteria to produce a parsimonious model and prevent over-fitting (49) supports its use in a cross-temporal modeling application.

Assessing the transferability of a qualitative potential niche model like the American Three-toed Woodpecker model, which is based on ecological integrity assessments, takes a different approach than a realized niche model (Flammulated Owl). The EITs are the tools of an ecological integrity assessment, which evaluate ecosystems for a 'a species composition, diversity, and functional organization comparable to that of similar, undisturbed ecosystems in the region' (73). The individual assessments (i.e., EITs) determine the viability of a species within an ecosystem by evaluating the composition, structure, function, and processes occurring within a natural range of variation important for resiliency and adaptation to most natural and anthropogenic perturbations (58). They are intended among other things to provide a baseline and trend assessment when applied at broad spatial and temporal scales and are inherently transferable (50). However, differing ecologies across a species' range and introduced biases because of model development region (i.e., the American Three-toed Woodpecker model was originally developed in Utah and with a western U.S. focus, making transferability to eastern sections of its range questionable) will influence transferability. Unlike the Flammulated Owl model, assessment of transferability required evaluation of which indicators to include, adjusting thresholds to reflect the study region, and transforming indicators to a quantitative form to improve spatial modeling.

The EIT model meets the criteria for selecting a model for inclusion and transferability assessment. First, though originally applicable across the species' geographic range, the Woodpecker model was developed for a western U.S. state (50); focusing the model's indicators to environmental conditions similar to Idaho. Second, the indicators have a close association with the response variable (potential suitable habitat) and are founded on ecological associations, which are inherent features of an EIT (58). Even with the inherent applicability, model caveats were addressed to improve transferability.

The EIT is constrained by ecological variation across different geographies, correlated indicators, and reliance on taxonomically similar species for ecological information (50). We addressed these constraints to improve the model's application to the study area. Environmental variation within the *plant associations* and *elevation* indicators across geographic regions are noted in the EIT. We used the *plant associations* variations in spruce-fir and lodgepole pine/mixed-conifer forest cover to inform suitability levels of *very good* and *good*; thereby expand the model's applicability to the study area. In addition, the *elevation* indicator was parameterized based on literature values as this was explicitly noted as being applicable to Utah. Addressing the variations in these indicators improved model transferability to the study area.

We used the correlation among indicators to minimize variable redundancy and account for variables that could not be directly informed. The *stand age, timber harvest,* and important but excluded indicator *forest management* were considered correlated (for this study) based on their descriptions in the EIT. We lacked temporally relevant information for *timber harvest and forest management,* which would have affected the transferability and usefulness of the model if unaccounted. Per the EIT, f*orest management* accounts for alterations to the overall natural fire regime, salvaging logging, and suppression logging. Historically, northern Rockies' forests were intensely managed resulting in forest structural (74) and fire regime changes (75) throughout. The ubiquitous affect across the landscape and lack of spatially explicit historical management information would have resulted in a relegation of the region to the *poor* indicator level for modeling purposes. This would have rendered the *forest management* indicator uninformative for model inclusion. Confounding this was the lack of spatially explicit harvest data to assess *timber harvest* thresholds. The solution was to use the LANDIS-II modeled stand ages at two threshold levels to inform the *timber harvest* and *stand age* (Table 2). This allowed for identification of older stands indicative of long fire return intervals and lack of harvest. As a result, the areas meeting these thresholds were assumed to be "unmanaged" providing a proxy for the f*orest management* important indicator. Though, we implemented solutions to improve transferability and applicability, model validation was still a concern.

Model Validation

The LANDIS-II informed habitat suitability map of the Flammulated Owl model was validated against the same niche model informed with an independent dataset (Figure 2.2-F). However, both habitat suitability maps were not completely verified with independent observation data (Figure 2.2-G), since the available observation data was affected by sampling bias. In contrast to the Flammulated Owl model, there was no procedure to quantitatively validate the American Three-toed Woodpecker model with an alternatively informed model (Figure 2.2-F). The validity of the model depended on the success of the initialized landscape to accurately reflect contemporary forest composition and structure. The landscape initialization process (76) was informed by FIA data and produced a forest composition and structure that agreed with FIA data (Table 3.5 and 3.6). Further, the validation of the Flammulated Owl model (Figure 2.2-F) supports the validity of the initial LANDIS-II modeled landscape. The LANDFIRE and LANDIS-II informed models agreed (Figs 4 and 5), therefore the LANDIS-II model spin-up used to inform the American Three-toed Woodpecker model is reflective of the contemporary landscape. In addition, the FIA plots meeting the suitability criteria were generally associated with the areas identified by the model (Figure B.2.4). In this case, the validity of the suitability predictions would be a function of the model capturing the habitat use dynamics of the American Three-toed Woodpecker in the Northern Rockies Ecoregion and not the data used to inform it. The caveat to this assumption: the *snag density* predictions were not verifiable or comparable to the Flammulated Owl model, and they represent input data that is uncertain. We are not concerned as these data are temporally dynamic and do not represent more long-term core habitat features further discussed.

Both models required variables to be derived from LANDIS-II outputs because of a lack of direct informative data. Canopy cover (Flammulated Owl), forest type (Flammulated Owl), and snag density (American Three-toed Woodpecker) all required secondary modeling. We implemented a RF model for each variable, because 1) we assumed complex and strong interactions among the predictor variables, which are notably handled by RF (77); 2) prediction and not inference was our objective, making a machine learning process more advantageous (69). The canopy cover model was the least robust, though this did not affect the Flammulated Owl habitat suitability map predictions (Appendix B.1.1). RF has been used with success to predict canopy cover, but the predictor variables were more informative and based on data not derivable from LANDIS-II (78). The secondary modeling introduces additional variability into the final potential and realized niche predictions, however models not informed by the RF data (Flammulated Owl) indicated the moderate error within the RF model (canopy cover) had minimal effect on predictions (Appendix B.1.1). Only the snag RF model could not be independently assessed, which is likely to have little effect on the information derived from the American Three-toed Woodpecker potential niche model because of the nature of the snag variable.

LANDIS-II

The process of using LANDIS-II to produce spatially explicit data for use in other models has been done before (79), provides a means to simulate landscape level data that is otherwise unavailable, and has its limitations. LANDIS-II estimates spatially explicit data that were unavailable over large spatial extents from alternative datasets. Integrating LANDIS-II allowed for the application of the American Three-toed Woodpecker model to the Northern Rockies Ecoregion. Data to inform the Woodpecker model was otherwise unavailable except for FIA plots, which would have limited the spatially explicit predictions possible via LANDIS-II. Using LANDIS-II in this integration provided opportunities, however it also presented limitations.

Restricted outputs from LANDIS-II presented a major limitation to implementation of the proposed framework. This limited the scope of species and model types (80–82) that were feasible, because predictor variables (e.g., normalized burn ratio NBR) had no analog with or could not be derived from LANDIS-II. Management of species of conservation concern like the Lewis’s Woodpecker (*Melanerpes lewis*) (83) would benefit from model integration. However, the available models (82,84) were not easily transferable because of geographic and variable differences, specifically measures of landscape level fire effects (e.g., NBR) more complex than burned area have no definitive analog in LANDIS-II fire processes. The data mismatches between avifauna-forest models and LANDIS-II limited the integration potential of ACN niche models.

A lack of suitable ACN niche models for integration can be addressed though development of *in situ* niche models based on habitat predictor variables easily sourced from forest landscape models (36,79,85). Better integration through ACN predictor variable fit (Figure 2.2-B) is possible through the use of alternative forest landscape models like LANDIS-PRO (86), which can simulate density and basal area providing a better mechanism to estimate predictor variables like canopy cover (36). Integrating LANDIS-II or other forest landscape models in the initial research development stages will likely minimize the constraints associated with data mismatches and transferability.

Habitat Suitability Maps

In Idaho, the Flammulated Owl is widely distributed in montane habitats but locally abundant with clustered spatial distribution of breeding sites (87). This general pattern was exhibited in the predicted realized niche and the IDFG observation points (Figure 2.3). The increased probability of occupancy was generally not associated with observed locations and associated habitat use buffers (Table B.2.2). The lower occupancy probabilities associated with the observed locations could result from uneven temporal recording intensity, uneven spatial coverage, uneven sampling effort, and uneven temporal and spatial detectability, i.e., biased data (88). It is likely these data are a function of these biases. Most of the data were incidental/opportunistic sightings spanning a 32-year period. Probability of detection is high for the Flammulated Owl among trained observers, though it is influenced by noise (49) and can decline significantly outside of the pair-bonding and incubation period (89). The realized niche predictions may represent contemporary habitat suitability and the observation data may not represent contemporary habitat use because of less than perfect detectability and a likely shift in temporal habitat suitability over the 32-year period.

Alternatively, the niche suitability model may poorly approximate the realized niche in the novel study region because of resource use variations. Resource selection can vary between locations based on availability differences resulting in poor predictability of habitat use (90). This can cause poor transferability of habitat suitability models (80). The transferability assessment showed little difference between the model's training region and the study area (Figure B.2.1 and B.2.2) except in the covariance structure between ponderosa pine cover and two other variables (non-forest cover and canopy cover) (Figure B.2.2). However, prey availability, snag density, and stand density, which are associated with Flammulated Owl habitat, may influence resource selection, and are related to stand age and disturbance regime (91), which were not directly modeled. The age and forest structure underling the density of ponderosa pine and Douglas fir forest cover (included variables) is likely affecting habitat use due to resource availability differences between the model development and our study region. This is observed in the data since older stands were associated with the habitat use buffers. We did not assess if this represents a habitat use difference compared with the entire landscape, as this was beyond the scope of this research. The habitat suitability map is still useful in the management and protection of suitable habitat by focusing on those areas that are most suitable (49), or by focusing population trend and habitat suitability research needs (92) on areas of increased occupancy.

Assessing population abundance and trends for the American Three-toed Woodpecker is difficult; they are a highly irruptive species because of an association with newly (< 5 years old) burned forest patches (59). Often associated with shifting food resources (93), irruptive species have irregular movement patterns making predictions of spatial habitat use patterns also difficult (94). We found little value in comparing the known locations to the habitat suitability map, because of the irruptive characteristics and resulting sampling biases (88). Any habitat suitability map will be highly temporally constrained and likely biased if disturbance characteristics resulting in shifting prey availability are not accurately modeled. However, land management and conservation activities will benefit from the spatial identification of habitats with key non-temporally sensitive niche characteristics (e.g., mature spruce forest). These landscape areas have the potential to confer suitable habitat after interacting with natural and anthropogenic disturbances. Focusing contemporary management and conservation activities on these core habitat areas is an investment in future suitable habitat.

The niche attributes within the American Three-toe Woodpecker model that are temporally constrained but confer habitat suitability are snag density and time since last burn. The less temporally dynamic niche attributes are the mature/old growth forest, spruce forest cover, elevation, and areas devoid of harvest. The intersection of these niche attributes represents the core habitat areas to focus contemporary management activities. We found that these areas were aggregations of spatially fragmented forested blocks (Fig 7), which fragmentation and habitat loss are the main concerns for this species in Idaho (95). Land management activities such as snag retention, fire management, and minimized timber harvest especially of mature/old growth forest would be best focused on these areas. In addition, future scenario modeling could evaluate the degree of impact of climate change and disturbance event interactions on the core habitat.

Conclusion

The presented framework for the integration of ACN and forest landscape models based on the transfer of existing niche models is viable. Transferability was hindered by limitations such as model training and application landscape similarities and forest landscape model output variables. We addressed these limitations through the criteria of selecting appropriate niche models, evaluating training and application landscape similarities, and secondary modeling of niche model inputs from the forest landscape model outputs. The framework proved useful when niche models are not easily transferable to a landscape due to data constraints. LANDIS-II estimated spatially explicit landscape information (e.g., stand age distributions) that were unavailable from other datasets, and the framework included the process of validating habitat suitability maps and underlying data. This increased the application of avian niche models across a broad landscape improving habitat conservation information for land managers. Finally, this framework provides a process to ascertain species responses to climate change and management scenarios while providing forest ecosystem modelers with a means to account for wildlife habitat suitability.

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Table 2.1. The variables used to inform the Flammulated Owl realized niche model reported by Scholer et al. (2014).

Parameter	**Original Model Data Source**	**LANDIS-II Model Data Source**	**Original Model Coefficient (logistic)**
Aspect (cosine)	Digital elevation model derivative	Digital elevation model derivative	-2.544
Canopy	U.S. Forest Service LANDFIRE Forest Canopy Cover (54)	A Random Forest model of canopy cover based on LANDIS spin-up biomass estimates.	0.064
Diversity*	Shannon Diversity Index of the LANDFIRE Existing Vegetation Type classes of the study area	Shannon Diversity Index of the Random Forest modeled cover types.	-1.209
Douglas -Fir*	U.S. Forest Service LANDFIRE Existing Vegetation Type (54)	Proportion of Douglas-fir from the Random Forest modeled cover types.	0.994
Non-forest*	U.S. Forest Service LANDFIRE Existing Vegetation Type (54)	Proportion of non-forest from the Random Forest modeled cover types.	-0.021
Ponderosa Pine*	U.S. Forest Service LANDFIRE Existing Vegetation Type (54)	Proportion of ponderosa pine from the Random Forest modeled cover types.	0.013

*A Random Forest model was used to assign the land cover types of each grid cell to be similar to the original model's LANDIFRE Existing Vegetation Type categories. The model was informed using the species composition and live biomass of each grid cell at spin-up.

Table 2.2. The variables used to inform the American Three-toed Woodpecker potential niche model reported by Oliver and Tuhy (2010). The provided parameter values are those associated with the category "very good habitat".

Parameter (Indicator)	**Value**	**LANDIS-II Model Data Source**
Tracts of old-growth forest	Continuous tracts of land with a cumulative area > 1,000 km^2 (*very good)*; area 600 – 1000 km^2 (*good*)	First simulated time step: all continuous grid cells with an average forest age >=125
Plant associations*	Spruce (*Picea* spp.) forest (*very good*); Spruce and Mixed-conifer/Douglas-fir (*good*)	The area of forest cover resulting from the first simulated time step. The forest type dataset was the same as the Flammulated Owl model.
Stand age*$^+$	>=125 yrs (*very good*) >= 90 yrs (*good*)	First simulated time step: all grid cells with an average forest age meeting the criteria
Snags and decadent trees, especially those with heartrot*$^{++}$	>1.2 snags/ha (this fulfills *very good* and *good* levels)	First simulated time step: a binary variable predicted using a Random Forest model with live above ground

		biomass, average forest age, elevation, slope, and aspect as predictor variables.
Natural forest disturbance*	Disturbed <=5 years (this fulfills *very good* and *good* levels)	First simulated time step: burned grid cells
Elevation*+++	4300-9000 ft	DEM
Timber Harvest*	Rotations > 100 yrs. (this fulfills *very good* and *good* levels)	First simulated time step: all grid cells with an average forest age meeting the criterion

+ The stand age was parameterized as a categorical value (old-growth and mature) in Oliver and Tuhy (2010). We associated a value of 125 years from a reference in Tremblay et al. (2018b).

++ The snag density was parameterized as a categorical value (abundant) in Oliver and Tuhy (2010). We associated a value of 1.2 snags/ha based on Zapisocki et al. (2000) American Three-toed Woodpecker habitat suitability model.

+++ The elevation proposed by Oliver and Tuhy (2010) was specific to Utah. The best information on elevation gradients in Idaho indicate mid-elevation habitat use and across the American Three-toed Woodpecker western distribution an elevation range of 4300' – 9000' (59).

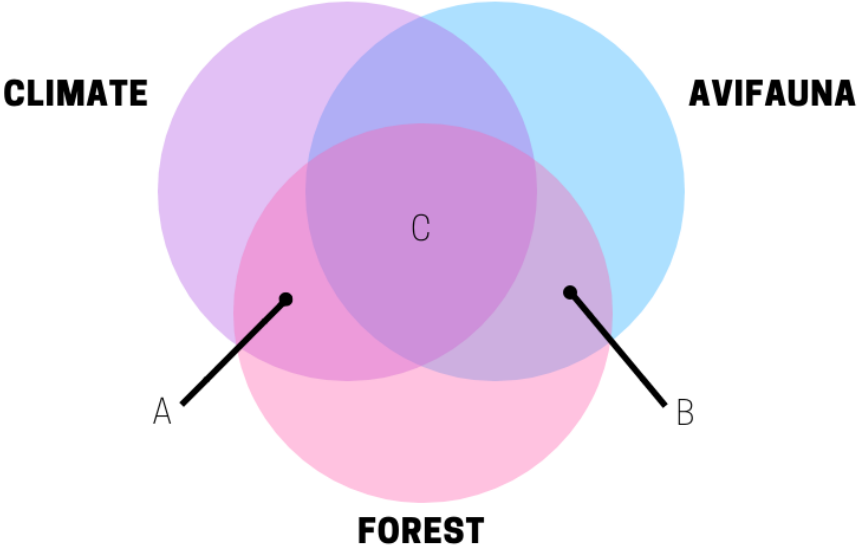

Figure 2.1. The conceptual diagram of climate-avifauna-forest model integration. A) Spatially explicit forest landscape models with dynamic ecosystem processes that modulate processes via dynamic climate integration like LANDIS-II; B) Avifauna-Forest models that integrate with Climate-Forest models and are not constrained by transferability to novel regions; C) the integration of two different model types to produce emergent results that accounts for climate, vegetation, and biodiversity.

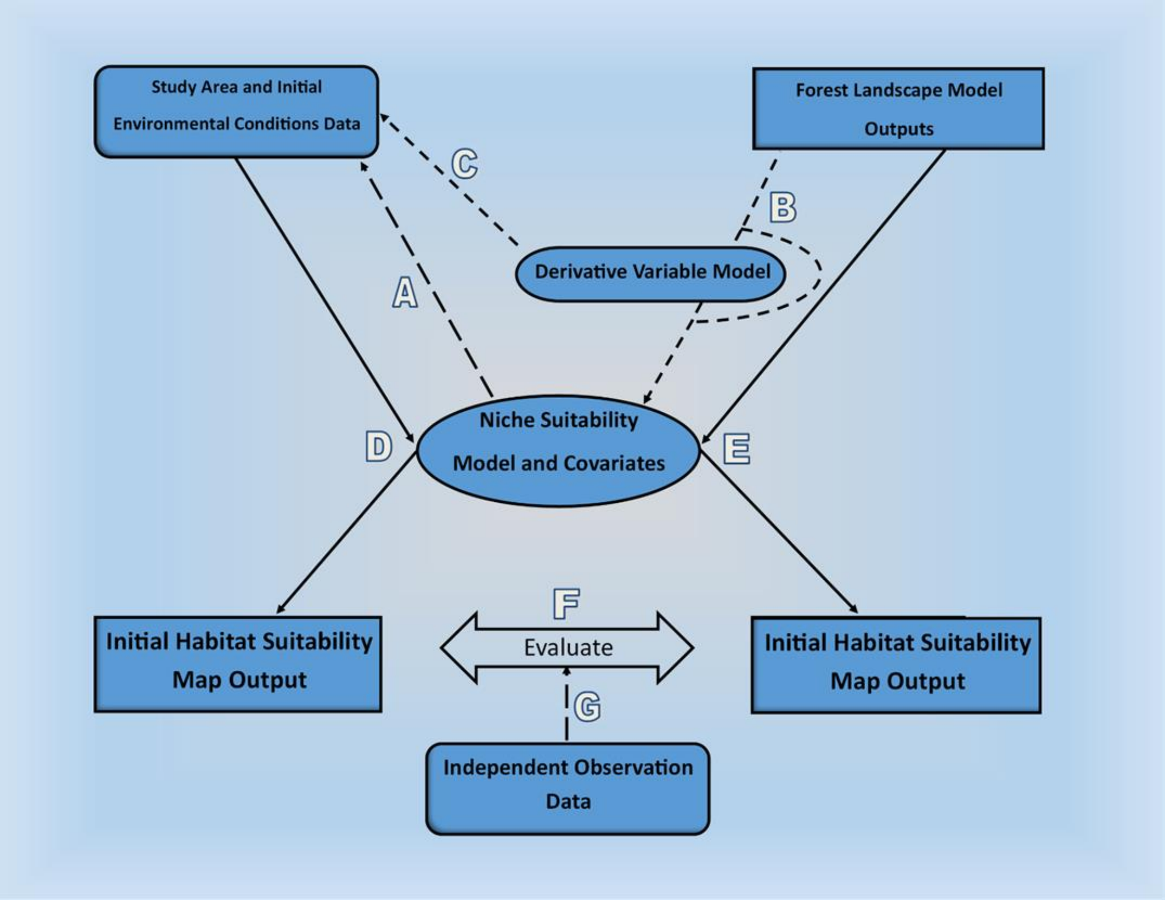

Figure 2.2. The framework for linking existing niche suitability models with forest landscape models to achieve integration (Figure 2.1). Evaluate the transferability of the niche suitability model to the new study area (A) and the ability to inform the model with outputs of the forest landscape model (B). Niche suitability variables that are not direct outputs of the forest landscape model may be derived through additional modeling, and then verified against corresponding study area conditions (C). The niche suitability model is informed using datasets of initial environmental conditions as prescribed in the original model (D) and using initial conditions simulated by the forest landscape model (E). The forest landscape model habitat suitability map (E) is verified against the original model habitat suitability map (D). When available observation data can be used to evaluate the habitat suitability maps (G).

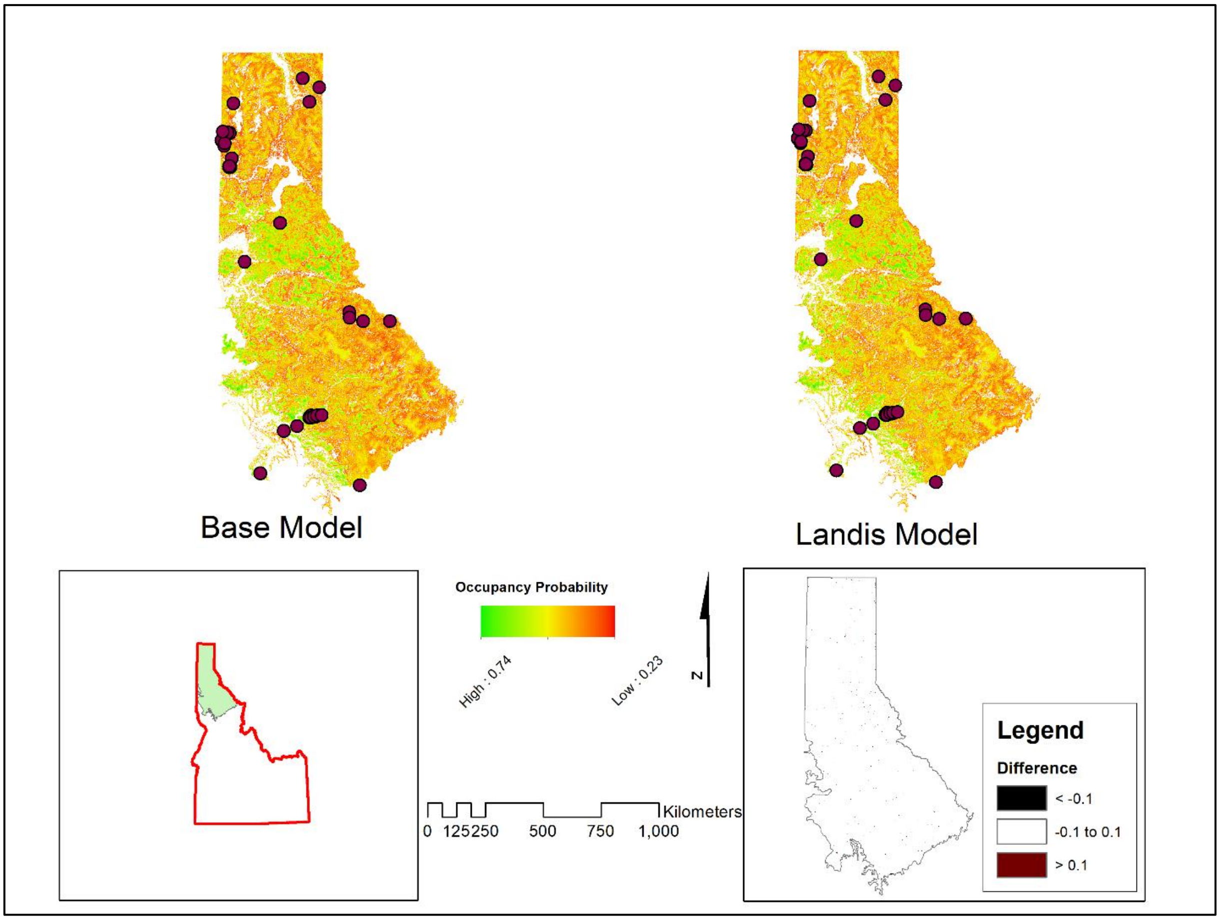

Figure 2.3. The contemporary habitat suitability map (HSM) of the Flammulated Owl across the Northern Rockies Ecoregion of Idaho with observed locations. The HSMs were based on the occupancy probability using the realized niche suitability model described in Scholer et al. (2014). Two data sources were used to inform the niche model: original sources as described by Scholer et al. (2014) and data sourced from the LANDIS-II forest landscape model. Differences greater than +/- 10% between models informed with the differing data sources are identified (inset map).

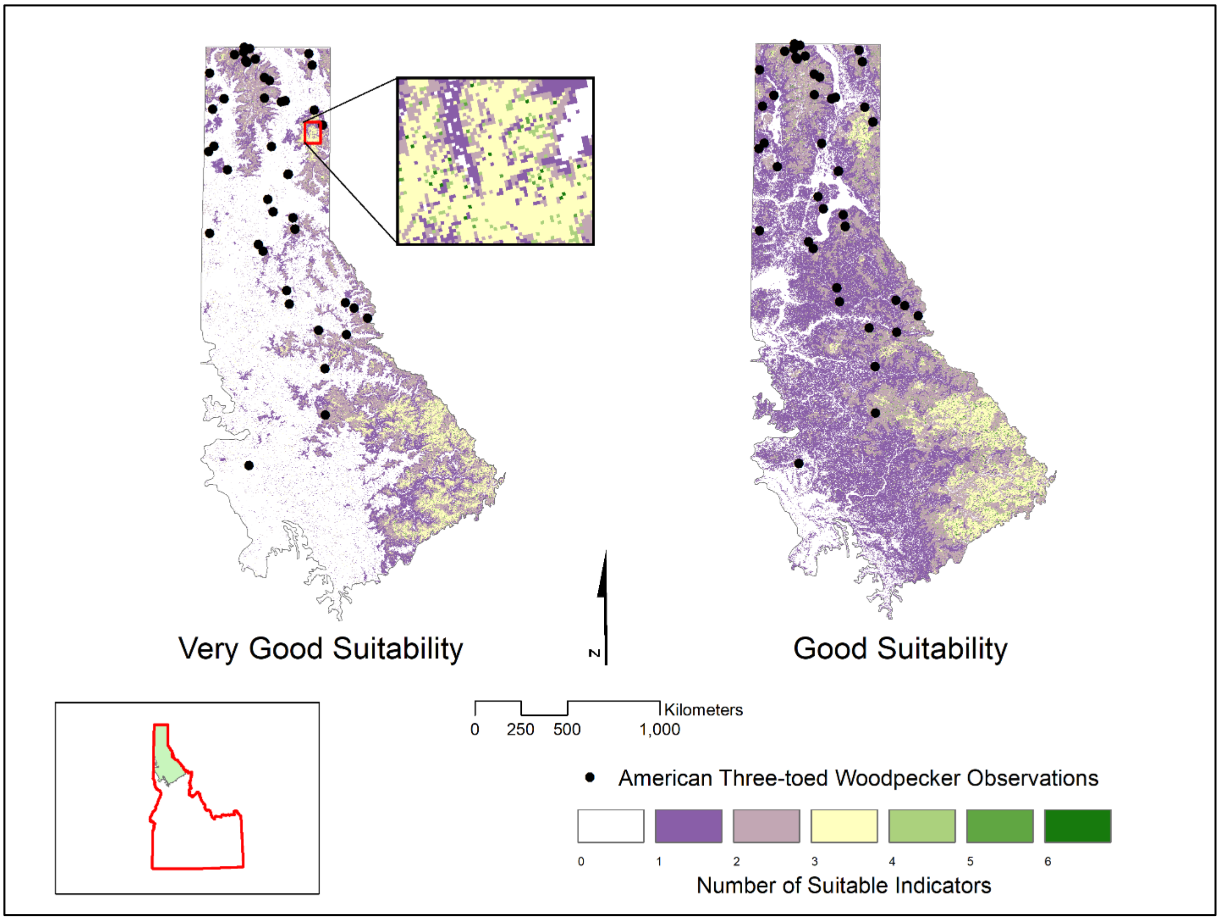

Figure 2.4. The number of American Three-toed Woodpecker potential niche ecological indicators intersecting across the Northern Rockies Ecoregion for two suitability levels. Expanded inset map depicts the disjunct areas of increased suitability.

Chapter 3: Future climate change and the Northern Rockies Ecoregion: Carbon and avian cavity nester responses

Abstract

Forest ecosystem services (e.g., carbon and nutrient cycling, biodiversity, and wood products) will be strained by climate change and maintaining these services, increasing resiliency, and conserving wildlife habitat will depend on climate change adaptive forest management strategies. Modeling frameworks that couple biodiversity and forest productivity responses will be critical for evaluation of management strategies. We present an integrated framework of forest landscape and niche suitability modeling tested in the Northern Rockies Ecoregion of Idaho (NRE). We report on the interactive effects of climate change, fire, and harvest management on carbon cycling and the distribution of suitable habitat of two avian cavity nesters (Flammulated Owl (*Psiloscops flammeolus*) and American Three-toed Woodpecker (*Picoides dorsalis*). The NRE was projected to maintain a sink potential to the end of the century with fire and harvest disturbances interacting; it was enhanced by harvest and only weakened under a warming climate when simulation of harvest was halted. The aboveground biomass of the NRE increased the most under the highest emissions scenario (RCP 8.5) with a projected 1/3 increase in biomass at the end of the century. Climate warming interacting with harvest resulted in an increase in *Pinus ponderosa, Pinus monticola, Larix occidentalis,* and a decline in *Pseudotsuga menziesii* biomass with the latter increasing with harvest halted. This shift in composition increased the realized niche area of the Flammulated Owl and potential niche of the American Three-toed Woodpecker. These species were projected to have more suitable niche habitat at the end of the century, highlighting the potential for the NRE to be viable wildlife habitat in a warming climate. This research highlights the importance of further development and integration of forest and species niche models to aid in balancing multi-objective forest management to produce adaptive environments in a changing climate.

Introduction

More than half of the North American forests will experience future climates that differ from historical growing conditions (Charney et al. 2016). This will result in structure and composition shifts due to climate-induced changes in precipitation, temperature (Lenihan et al. 2008), fire (Abatzoglou and Williams 2016), and biological disturbances (Weed et al. 2013). These climate and habitat changes will likely have biodiversity implications (Jetz et al. 2007, Langdon and Lawler 2015), since forest composition and structure are integral to biodiversity (McElhinny et al. 2005). Maintaining ecosystem services, resiliency, and biodiversity will depend on climate change adaptive forest management strategies (i.e., an iterative decision-making process that is evidence based either experimentally or via adaptive management (Holmes et al. 2014)).

Forest management can improve ecosystem services through increasing sequestration of atmospheric CO_2 (Murray et al. 2005, Mckinley et al. 2011, Law et al. 2018), increasing suitable wildlife habitat (McComb 2015), reducing wildfire hazard (Charnley et al. 2017), and managing hydrologic dynamics (del Campo et al. 2014). Climate adaptive management practices aimed at increasing carbon sequestration through protection of large tracts of land could enhance ecosystem biodiversity (Strassburg et al. 2010, Thomas et al. 2013) resulting in a positive relationship between ecosystem carbon levels and species diversity (Wright 1983). However, climate change adaptation focused only at increasing forest production (a strategy for increasing carbon uptake) via maximizing growth and minimizing disturbances is not necessarily conducive for biodiversity conservation (Siikamäki and Newbold 2012, Lawler et al. 2014, Felton et al. 2016). Such single-objective management strategies without explicit wildlife diversity consideration could simultaneously decrease biodiversity (Onaindia et al. 2013). Multi-objective climate adaptation strategies developed and evaluated in a forest ecosystem modeling framework provide a solution.

A forest ecosystem modeling framework that couples biodiversity and forest productivity responses is critical for climate adaptation management (Strassburg et al. 2010, Siikamäki and Newbold 2012, Onaindia et al. 2013). Integrating biodiversity and habitat change into climate and carbon cycle models requires information about the potential response (e.g., geographic range distributions, occupancy, etc.) of wildlife to climate change and forest ecosystem shifts. These coupled vegetation-wildlife models have improved forecast species distribution models (Veloz et al. 2013), informed forest management scenarios (Di Febbraro et al. 2015), and evaluated climate change-management scenario interactions (LeBrun et al. 2017, Tremblay et al. 2018). Biodiversity and forest resiliency in a forecast framework can be evaluated specifically using the distribution or population responses of avifauna cavity nesting species (e.g., owls, woodpeckers). Woodpeckers and top vertebrate predators are functional indicators of ecosystem biodiversity and resiliency (Sergio et al. 2006, Drever et al. 2008).

LANDIS-II (hereafter, LANDIS) is a process-based spatially explicit forest landscape model, which provides the foundation to model forest ecosystem processes and integrate avifauna species distribution models at multiple points (Figure 2.2). It is a flexible model that can simulate a variety of ecosystem processes at multiple scales and over large spatial and temporal extents. It can provide detailed habitat responses (Shifley et al. 2008) and has been used in conjunction with population (Scheller et al. 2011b) and habitat suitability models (Shang et al. 2012), specifically avifauna (Martin et al. 2014, Di Febbraro et al. 2015, LeBrun et al. 2017, Tremblay et al. 2018). Importantly, it provides information at the spatial grain of management implementation for decision support tools (Larson et al. 2004, Scheller et al. 2011b).

In this study, our objectives were to 1) model the interactive effects of climate change, fire, and timber harvest on the forest carbon cycle, composition, and structure of the Northern Rockies Ecoregion of Idaho, USA; 2) model the niche distribution change of two avifauna cavity nester species, the Flammulated Owl (*Psiloscops flammeolus*) and American Three-toed Woodpecker (*Picoides dorsalis*). We hypothesize that: 1) increased warming interacting with disturbance events will alter the carbon cycle by decreasing carbon storage potential of the Northern Rockies Ecoregion; 2) forest carbon decreases will be partially offset by increased productivity of undisturbed forests; 3) niche suitability will have a positive association with increases in fire frequency (Hutto and Patterson 2016) and U.S. Forest Service land.

Materials and Methods

Study Area

The study area was the Environmental Protection Agency Level III Northern Rockies Ecoregion (Omernik and Griffith 2014) (Figure 3.1). This area covers 3.1 million hectares and is 88% forest land cover. The region is 61% publicly held with 76% of the public land managed by the U.S. Forest Service. It has distinct climatic and vegetation conditions due to the marine-influence of the Pacific with a mean annual precipitation of 214 cm and a mean annual temperature of 5.1° C (Figure 3.2) (Maurer et al. 2002). The climate varies across topographic gradients from cooler-wet (mean elevation: 1406 m) to warmer-dry (mean elevation: 925 m) (Figure 3.3 and 3.4). Historically, the driest and warmest months are July, August and September (Figure 3.5). This climate results in forests comprised of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), western white pine (*P. monticola*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophylla*) with differing biomass distributions across the region (Table 3.1).

The region historically had a mixed-severity fire regime with low/moderate severity fire rotations of < 20 years in the low to mid-elevation forests (Fryer 2016) to high severity fires occurring every 150-500 years across elevation gradients (Smith and Fischer 1997, Odion et al. 2014). Most of the 20th century area burned was substantially smaller compared to the late 19th and early 20th century (Figure 3.6 and Table 3.3) (Gibson 2005). Several years since 1960 have been marked by increased burned area (Figure 3.7), however these are substantially smaller than the turn of the 19th century fire extents. Finally, this region accounts for approximately 85% of all timber harvested in Idaho with private industrial and non-industrial accounting for 65.8% of the total annual harvest (2015 data; total timber harvested is adjusted for the Northern Rockies Ecoregion; private harvest was not adjusted) (Simmons and Morgan 2017). This results in a forest dominated by age groups 45-50 (Figure 3.8).

Climate

We simulated a historic climate (1980-2010) (Abatzoglou 2013) as a baseline for comparison and two radiative forcing scenarios: representative concentration pathways (RCP) 4.5 and 8.5. For historic climate simulations, the LANDIS Climate Library assigned a randomly selected year (aggregated monthly climate data) to each timestep of the simulation without regard for chronological order. For future climate scenarios, we implemented monthly climate date from the Canadian Earth Systems Model version 2 (CanESM2) and the NCAR Community Atmosphere Model (CAM5) in chronological order.

These general circulation models were selected because they capture the climate variability of the northwest region of the United States (Rupp et al. 2013). For the study area, the CanESM2 projects an increase in mean annual temperature of 3.7° C (RCP 4.5) to 6.2° C (RCP 8.5) (2070-2100) above historic temperatures (1980-2010), while the CAM5 projects an increase of 3.5° C (RCP 4.5) to 5.6° C (RCP 8.5) for the same periods. The growing period is projected to increase on average from 36 – 50 days depending on RCP scenario 4.5 and 8.5, respectively. The annual change in precipitation for this region is less pronounced, however, during the growing season (June-September) there is a decrease in precipitation with a corresponding increase in temperature (Rupp et al. 2017), increasing the stress from drought and fire conditions. All climate data were processed for the study area using the USGS Data Portal (Blodgett, David L. et al. 2011).

Model Description

We simulated forest succession and carbon dynamics using the LANDIS-II (v.6.2.1) forest landscape model (Scheller et al. 2007). A library of extensions facilitates the simulation of multiscale ecosystem processes with spatial interactions and dynamic communities at scales of 10^4-10^7 ha. These multiscale processes and dynamics are simulated at variable timesteps within an interacting gridded landscape with each cell representing aggregates of species-age cohorts and respective biomass. The ecosystem processes of establishment, growth, and senescence are a function of species life-history characteristics (Table C.1.1), disturbance processes, site conditions, and competition for resources.

Ecosystem processes were simulated at a grain resolution of 200 m (4 ha) with each gridded cell being assigned to an ecoregion that represents similar climate and soil conditions. The delineated ecoregions were based on an ArcGIS Cluster Analysis (Scott and Janikas 2010) of historic (1979-2014) total precipitation and minimum and maximum temperature during the growing season (May-September) (Abatzoglou 2013), elevation, and SSURGO soil water availability (Soil Survey Staff 2015). Two ecoregions were identified that roughly corresponded to elevation-climate gradients, which could be characterized as cool-wet (CW) and warm-dry (WD) (Figure 3.1). Only grid cells coded as forest landcover (LANDFIRE 2014) were active for simulations.

Twelve tree species were modeled (Table 3.1), based on a threshold biomass of >1% of the landscape total as calculated from Forest Inventory and Analysis (FIA) (U.S. Department of Agriculture 2015). We initialized the species-age cohort landscape using FIA data and Landscape Builder (Dijak 2013), which is a program that develops a spatially representative landscape from FIA data. Landscape Builder assigns species to each grid cell as a function of FIA geographic unit, landform, forest type, and size class. Each species is then assigned an age using a tree record DBH in a regression equation. The regression equation for each tree species was estimated in R (Team R Core 2018) using the FIA tree record DBH and age data. This process does not assign biomass totals to each grid cell, which is completed during the LANDIS-II spin-up process. Thus, biomass totals post spin-up are then evaluated against FIA estimates, which are independent of the initialization process.

Extensions

Succession

The Net Ecosystem Carbon Nitrogen extension (NECN) v.4.2.4 (formally the Century Succession extension) (Scheller et al. 2011a) was implemented in five year time steps to model forest carbon pools (above and below-ground) and fluxes (net ecosystem exchange (NEE), net primary production (NPP), and respiration (HR); see Table 3.2 for description of ecosystem carbon dynamics nomenclature. NECN is based in part on the globally utilized CENTURY soil model (Parton 1996) and simulates the establishment, growth, and mortality of species, accumulation and decomposition of wood and litter, soil carbon pools, and water availability (Scheller et al. 2011a, 2012).

The NECN extension is parameterized at three ecosystem scales (tree species (Table C.1.2), tree functional groups (Table C.1.3), and landscape ecoregions (Tables C.1.4, C.1.5, C.1.6)) based on published values (Thompson et al. 1999, Hessl et al. 2004, Scheller et al. 2011b, Loudermilk et al. 2013, West 2014, Creutzburg et al. 2015, Soil Survey Staff 2015) and expert opinion. Species were aggregated into functional groups based on the Atlas of Relations Between Climatic Parameters and Distributions of Important Trees and Shrubs in North America (Thompson et al. 2015) and the Northern Rockies forest community summaries (Arno 1979). The simulated ecosystem processes are modulated by a dynamic climate library, which allows for explicit climate change modeling over an entire simulation. Landscape soil metrics are necessary to initialize the model during spin-up (the process of estimating spatially explicit soil and biomass values based on the initial species-age cohorts). These initial soil inputs were from soil studies of the study region (Harvey et al. 1987, Page-Dumroese and Jurgensen 2006) with the subsequent soil organic matter pools (SOM) (slow, passive, and fast) (Table C1.4) calculated from the CENTURY manual algorithms (Metherell et al. 1993).

The NECN model initial conditions were calibrated by comparing the spin-up and initial output to literature values and expert opinion using the historic climate (1950-2010) (Maurer et al. 2002) simulations. The following model outputs were used in the calibration process: nitrogen deposition (Zhang et al. 2012), denitrification rate, tree functional group biomass curves, woody mortality rates (Harvey et al. 1987, Keane 2008), litter fall rates (Keane 2008), nitrogen content of dead wood (Page-Dumroese and Jurgensen 2006), initial landscape AGB totals (Jenkins et al. 2003, U.S. Department of Agriculture 2015), initial soil organic carbon totals, and initial soil inorganic nitrogen (Harvey et al. 1987, Page-Dumroese and Jurgensen 2006). NPP and NEE were not explicitly calibrated, because the study region is void of direct ecosystem flux measurements.

The succession model was validated by comparing initial spin-up above ground biomass under historic climate simulations to FIA estimates (U.S. Department of Agriculture 2015) and the National Biomass and Carbon Dataset (Kellndorfer et al. 2013). Though FIA species composition data were used to initialize the landscape, FIA biomass was not used in landscape initialization. We evaluated the historic climate scenarios without disturbance to ensure that the forests biomass would increase through time as would be expected. In addition, the initial simulated NEE was compared to the best regional landscape estimate available (Xiao et al. 2011). There is no independent more robust dataset that reports NEE in Idaho (e.g., eddy-covariance tower data). All extension parameterizations were considered validated when key metrics were within 25% of observed values.

Fire

Fire disturbance events were simulated using the Dynamic Fire and Fuels System (DFFS) to favor a mixed-severity fire regime. The DFFS extension is based on the Canadian Wildland Fire Information System and modulates fire events based on fuel types, fire-weather, ignition probability, and topography (Sturtevant et al. 2009). Fuel types are assigned to each grid cell using species composition and biomass, fire-weather is a derivative of climate data, and ignition probability is a function of historic data.

DFFS allows for temporally dynamic fire-weather and active fire regions. The landscape was divided into two fire regions and constrained the model for all simulations. The active fire region encompassed the known historic fire extents between 1889 and 2013, which 79% of this area had burned by 1920 (Table 3.4). Thus, in the study area, there has not been a consistent nor abrupt increase in the areas subject to fire events within the previous 94 years. Fire regime characteristics have changed since the early part of the 20th century; fire ignitions, individual fire size, and annual median area burned have declined (Table 3.3). To account for these shifts, we calibrated the model to the 1960 and 2010 fire regime conditions of the Northern Rockies Ecoregion (Table 3.3) (fire occurrence, fire extents (mean annual area burned), fire rotation period) using the method described in Sturtevant et al. (2009). This period was selected because it balanced the rare large and predominate small fire years with the fine-scale weather data necessary to inform the model. The spatially explicit burned areas as reported by Gibson (2005) (1889-1984) and Forest Service Region 1 (2015) (1985-2010) were used to inform all fire modeling.

DFFS can constrain each fire event based on duration or size. Duration is more conducive for climate change modeling, however the historic fire data lacked duration information. To parameterize the fire model to be based on historic durations, an initial DFFS model was calibrated to the historic fire extents, and the simulated duration data were used to calculate the initial statistical parameters for duration-based model calibration. Fuel-types characterized in the Canadian Wildland Fire Information System were adapted to the vegetation types of the landscape and fire-weather was calculated from climate datasets corresponding to the scenario. For the historic climate (1980-2010) simulations, the fire-weather data was based on the historic climate data (1980-2010) (Abatzoglou 2013) and applied across the entire simulation. For the climate change scenarios, a new fire-weather dataset was activated at each DFFS time step, which was temporally consistent with the climate data, i.e., DFFS time step 1 (2010-2015) fire-weather corresponded to climate data from 2010-2015, etc. The model calculates a fire severity metric ranging 1-5 based on the fraction of the crown burned, where 1 and 2 are surface fires and 5 represents >= 90% crown fraction burned. We report the mean annual burned area, the percent of area burned (the mean annual area burned/the entire study area), and the mean annual emissions for the replicates of each scenario.

Harvest

Harvest disturbance was simulated with the Biomass Harvest extensions. The extension simulates multiple prescriptions across differing management units and sub-units (stands). The landscape was divided into management units corresponding to the major ownership entities (U.S. Forest Service, state of Idaho, U.S. Bureau of Land Management, and private; there were no available spatial data to subdivide private into industrial and non-industrial forests). Stands were identified using the U.S. Forest Service Vegetation Mapping Program VMap Database (U.S. Forest Serice 2017). Prescriptions (Table C.1.7) were based on management plans (Krueger et al. 2015), forest service personnel and other expert opinions. Harvest was implemented in five-year time steps across all management areas in qualifying stands. The first two harvest time steps (i.e., 10 years of harvest) were calibrated to be within 10% of the average harvested biomass for each ownership group from 2001 to 2015 (Simmons and Morgan 2017). The average biomass estimates of historic harvest were calculated from the reported high and low board foot estimates (Simmons and Morgan 2017). The calculation of biomass was the following:

$$\text{Equation 1: } HB = BF \times pctH \times Scf \times WTV \times DBc \times conv$$

where *HB* is harvested biomass, *BF* is the reported board feet harvested (MBF Scribner), *pctH* (85%) is the percent of the board feet harvested in the Northern Rockies Ecoregion, *Scf* (226.7) (Spelter 2002)is the conversion factor for MBF Scribner to cubic feet, *WTV* (1.898) (Birdsey 1992) is the ratio of total tree volume to merchantable volume, *DBc* (26.1) (Janowiak 2008) is the conversion to above ground dry biomass, and *conv* is the conversion factor for lbs to Mg of biomass.

An alternative biomass estimate was provided by research conducted in our lab and compared to the estimate from Equation 1. The final biomass harvest total used for calibration was the average of the two estimates.

Scenarios

We conducted a nested study to compare the changes in landscape carbon dynamics and forest composition among climate and disturbance scenarios. We isolated the effects of disturbance and climate by comparing future climate to the historic climate scenario with the disturbance events turned on and off. This resulted in historic climate, two GCMS, two RCP trajectories, and four scenarios (no disturbance, harvest only, fire only, fire and harvest) for a total of 20 scenarios. The scenarios were simulated to the year 2100 and replicated five times to account for model stochasticity; the reported data are an average of the replications. The disturbance scenarios were not varied to assess alternative management prescriptions.

Biodiversity Measure

We implemented the ecological niche models from chapter two to assess the effects of climate change on the Flammulated Owl and American Three-toed Woodpecker and provide a measure of biodiversity within the forest landscape modeling framework. The avian models were applied to the fire only and fire-harvest interaction scenarios under historic, RCP 4.5 (mean), and RCP 8.5 (mean) climates at the mid (2050) and end (2100) of the century. These were selected to evaluate the effect of no harvest on avifauna habitat response against full disturbance interactions. To determine the change in realized niche suitability among the scenarios, we report the percent of area that was associated with a change in occupancy probability of +/- 10%.

For the American Three-toed Woodpecker, we modeled the ecological indictors that are less temporally dynamic (plant associations, stand age, elevation, timber harvest (modeled as stands > 100 years old were considered void of harvest) (Table 2.2). We focused on the intersection of these ecological indicators because they represent the core habitat associations that have the potential to confer suitability after appropriate disturbance events, e.g., fire. The core habitat refers to areas with all four ecological indicators and are presented as the attributes that confer the suitability level *very good*. The suitability level *good* was modeled with the results not being presented, because these areas were more generalized and were less informative of niche shifts. To determine the change in potential niche suitability between scenarios, the percent area change of the intersection of all four ecological indicators (core habitat) between each scenario and initial landscape conditions was reported.

Results

Validation

The average AGB at spin-up was within 9% of the reported biomass of the region (Table 3.5). The distribution of biomass among the NECN ecoregions was slightly different with less correspondence between the modeled and reported CW ecoregion (22% difference (Table 3.5). The distribution of biomass of each modeled species among the ecoregions were mostly consistent, however more *T. plicata* biomass was initialized within the CW region compared to the WD region than reported in the FIA data (Table 3.6).

The DFFS model under historic climate with fire and harvest disturbances turned on performed slightly below historic conditions (Table 3.7). All values were within the acceptable range (i.e., 25%), and the highly stochastic fire model exhibited moderate variation among replications. Because we lacked an independent dataset to evaluate the calibrated model against, we could only compare emission results to published values. The mean yearly amount harvested in the first two simulated time steps corresponded well for the private and public other (State of Idaho and Bureau of Land Management) ownership groups, however the National Forest prescriptions resulted in an above normal historic average (Table 3.8). This was necessary to achieve the benchmarks in the Idaho Panhandle Forest Plan.

Carbon Dynamics

Total AGB under baseline historic climate conditions with fire and harvest interacting was projected to increase 15.0% (Figure 3.9 and 3.10) by the end of the century. No-disturbance, harvest, and fire disturbances individually accounted for an increase in AGB of 8.1%, 17.3% and 10.6%, respectively. Under climate forcing, AGB increased above historic climate with all RCP 4.5. and 8.5 models predicting a mean increase of 25.8% and 32.6%, respectively. The increase among the climate forcing scenarios generally diverge from historic simulations (fire-harvest interacting) (Figure 3.10) and were greatest among simulations that excluded harvest. The simulated ecoregions exhibited slightly different responses. There was a decrease in biomass at midcentury in the warm-dry region across all climate scenarios. The projected decline was slightly weakened under climate forcing and was offset at the landscape level by the cool-wet ecoregion (Figure 3.9). The projected change in warm-dry biomass appears to be mostly driven by harvest; the signal was not present under fire only disturbances (Figure 3.11) and was present under harvest only (Figure 3.12)

Under historic climate conditions with fire and harvest interacting, the proportion of *L. occidentalis, A. grandis,* and *P. menziesii* changed by 25.7%, -14.4%, and -13.8%, respectively compared to the entire initial landscape composition (Figure 3.13). These responses occurred across all fire-harvest interacting scenarios. The projected changes in composition under historic climate conditions occurred under increased warming, though the increase of *L. occidentalis* was tempered and *Ps. menziesii* increased in the cool-wet ecoregion (Figure 3.9). Changes in proportion of species biomass were predominantly associated with the warm-dry ecoregion (Figure 3.13) and followed the same pattern seen in total biomass shifts; harvest was the predominate driver (Figure 3.13).

The median stand age in the Forest Service management areas was 73, 77, and 81 by the end of the century under fire and harvest interactions for historic, RCP 4.5, and RCP 8.5, respectively. All are significant deviations from initial conditions, which was 49. Overall the median stand age across the study region was 33, 23, and 23 among historic, RCP 4.5, and

RCP 8.5 climate scenarios, respectively. Overall, this was a departure from the initial landscape median stand age of 46. This is driven in part by the median age of private forest, which averaged 10 among all harvest scenarios and 69 without harvest; a departure from the initialized landscape median age of 39.

The ecosystem carbon balance of the Northern Rockies Ecoregion generally trended towards a strengthening or stabilizing carbon sink potential (Figure 3.14) with fire and harvest interacting. Harvest interactions in a warming climate caused the sink potential to converge with historic climate projections. Scenarios without harvest interactions weakened the carbon sink potential. Aboveground NPP (ANPP) increased through the century among all simulations (Figures 3.15 and C1); though all warming scenarios were greater than historic climate, most were within the variation of historic simulations (fire-harvest interacting) (Figure 3.15). In addition, overall total NPP increased (Figure 3.16) among all scenarios through the century and NEP had a mixed response; more scenarios projected lower NEP rates at the end of the century compared to the begiing as respiration increased (Figure 3.17 and 3.18) (Table 3.10). The greatest increase (last third of the simulation compared to the first) of NEP (49.4%) was associated with historic climate with fire and harvest interacting; RCP 4.5 and 8.5 tempered this response to 4.1% and 16.4% for multi GCM mean, respectively (Table 3.10). Climate warming had a significant effect on total ecosystem respiration increasing at the end of the century among all scenarios by 40.9% - 46.0% (RCP 4.5 and 8.5, respectively). In contrast, historic climate scenario ecosystem respiration rates increased a mean 21.6%. At the end of the century there was a projected decline in ANPP and ecosystem productivity did not differ from the variance of historic conditions with fire and harvest interacting (Figure 3.16 and 3.17). The replication variance was greatest for historic climate runs (Figure C1) as would be expected, since the LANDIS-II Climate Library randomly selects historic climate data throughout the baseline historic scenario.

Disturbance

Warming climate scenarios predicted a slight increase in the mean annual burned area (ha) (Figure 3.19); there was no temporal trend in burned area (Figure 3.20). Overall, the mean annual burned area did not differ among warming scenarios or from historic climate because of the variation within each scenario (Figure 3.19). The variance was greatest in the first third of the century in the historic climate fire-harvest interactions (Figure 3.20) and this relationship was consistent among all other fire scenarios. This increased fire incidence at the early part of the century producing higher emissions (Figure 3.21) with an overall mean fire severity of two on a scale of 1-5 for all scenarios.

Harvest dynamics differed among scenarios and land ownership groups. Under historic climate projections, harvest totals on private lands declined by 55.6% at midcentury and then increased towards the end of the century to 69.6% above initial harvest totals (Figure 3.22). This general pattern occurred among all climate scenarios. Harvest levels remained consistent on Forest Service lands until mid-century among harvest only models and the end of the century for fire-harvest scenarios.

Avifauna Distributions

There was an increase in area of the Flammulated Owl realized niche by the end of the century under all climate scenarios with fire and harvest interacting (Figure 3.23). Historic climate, RCP 4.5, and 8.5 projected an occupancy increase (>10% change in occupancy probability) across 25.5%, 19.0%, 18.7% of the study area, respectively. Likewise, there was a projected decrease (>10% change in occupancy probability) across 9.3%, 14.4%, and 13.7% of the study area respective of the climate scenario (historic, RCP 4.5, and 8.5) (Figure 3.24). Among all climate scenarios, almost a third (22.2% - 29.5%) of the increased areas of suitability were associated with Forest Service management areas. In the absence of harvest, fire only models exhibited mixed results. Historic climate simulations projected 1.6% of the study area had a >10% increase in occupancy, however 11.3% of the study region had an occupancy probability decline. Climate change offset these loses, increased warming caused an occupancy probability increase across 10.2% and 7.4% of study area with declines in occupancy across 0.6% and 0.9% of the study area for RCP 4.5 and 8.5, respectively. Under climate warming (RCP 4.5 to 8.5, respectively), 75.0% to 70.3% of all areas with increased occupancy were relegated to Forest Service management areas.

The potential niche core habitat (four ecological indicators) of the American Three-toed Woodpecker was projected to increase by 262% and areas with three indicators increased by 241% under historic climate conditions (Figure 3.25). Moderate climate warming (RCP 4.5) had little effect compared to the historic climate scenario on areas with four indicators (264% increase), however under RCP 8.5, the area of core habitat increased by 324%. Approximately 96% of the region with four ecological indicators was associated with Forest Service management areas under all climate scenarios. Lack of harvest increased the core habitat area by the end of the century to 3050%, 295%, and 513% among the historic, RCP 4.5, and 8.5 scenarios, respectively. The suspension of harvest also increased the core habitat among other land management entities; the Forest Service lands were associated with 82.3% of the core habitat increased area.

Discussion

The Northern Rockies Ecoregion is a substantial forested landscape, is comparable to the Pacific Northwest Cascade Ecoregion (~29k km^2) but has been the focus of few forest biogeochemical studies, especially those with dynamic fire-vegetation-climate change interactions (Rocca et al. 2014). This research highlights the cumulative impacts of climate change, harvest, and fire on a significant forested region of the Pacific Northwest. The future forest growth dynamics of this region are likely a function of the historic anthropogenic activities like logging and fire exclusion, which has been the mechanism affecting carbon dynamics globally (Houghton 2003). Forests in other regions of the United States have the potential to continue to sequester carbon (Rhemtulla et al. 2009) due to logging and agriculture land conversion, which is similar to the finding of this research. The forest ecosystem of the Northern Rockies of Idaho was projected to increase in biomass even under historic climate conditions. The forest growth projected in this study appears to offset the effects of climate change by maintaining a carbon sink despite increases in heterotrophic respiration. In addition, the continual growth, aging of public forests, and shifting of species composition increased avifauna niche distributions and the habitat suitability of the Northern Rockies Ecoregion of Idaho.

Forest Dynamics

Harvest was an important driver of forest carbon dynamics in the study area. It increased the sink potential, increased ANPP and NPP, offset the effects of a warming climate, and shifted species composition. LANDIS-II models tree growth as a function of age, such that older trees are less productive. Harvest and climate warming shifted the NPP and ANPP responses upward, however this did not result in a synergistic interaction. Climate warming increased ecosystem respiration, and this offset the ecosystem productivity gains due to harvest (Table 3.9). The total interaction of climate warming, harvest, and fire produced a trajectory that maintained the sink potential of the study area consistent with a theoretical continuation of historic climate (Figure 3.14).

Climate warming caused a shift in percent composition of species (function of the total biomass) at the end of the century that were offset by harvest (Figure 3.13); *P. menziesii* was projected to increase and harvest caused a decline; *L. occidentalis* was projected to increase and harvest magnified the response; and similarly, *A. grandis* was projected to decline and harvest magnified the decrease. *P. menziesii* is the only species that increased if not for historic climate conditions or harvest. *P. menziesii* is unique among the species modeled because of this response. *P. menziesii* is limited by growing season dryness (low precipitation and high temperatures) (Gower et al. 1992, Littell et al. 2008) and benefits from increased November temperatures and soil wetting because of winter photosynthesis potential (Chen et al. 2010). Climate change is overall likely to not impact this species in the study region (Chen et al. 2010), which is in agreement with the this study. The climate only simulations resulted in the smallest change in percent composition (Figure 3.13). However, the growing season is predicted to increase among the climate warming scenarios, increasing the likelihood of warmer Novembers at the end of the century, which is evident by the increase of *P. menziesii* at the end of the century among models lacking harvest disturbance.

The response of *L. occidentalis* to harvest and fire are consistent with the species being an early seral species that is shade intolerant (Milner 1992) and fire tolerant. The response of *L. occidentalis* to climate warming has been mixed among modeling studies as range contractions have been projected but upward slope migration is expected (Keane et al. 2018). The projected increase among the climate warming models presented here may be related to growing season increase; *L. occidentalis* seedling and sapling survival is related to warmer autumns with low probability of cold snaps (Rehfeldt 1995). The slight decline in percent composition *A. grandis* occurs after a mid-century increase, which modeling studies project both major declines and possible increases because of increases in productivity from warming (Keane et al. 2018). *Tsuga heterophylla* is projected to decline significantly in percent composition, especially with fire interaction (Figure 3.13). This is consistent with some projections, because the species seed establishment is sensitive to warming and area burned can reduce distribution (Keane et al. 2018).

The USFS Idaho Panhandle National Forest Plan 2015 (Krueger et al. 2015) provides vegetation goals to increase resistance and resiliency of the forests to natural and man-made disturbances. Several management objectives within those vegetation goals were implemented in this study. These included an increase in dominance of *P. monticola*, *P. ponderosa*, *L. occidentalis, P. albicaulis* (FW-DC-VEG-01) and *P. Ponderosa* (FW-OBJ-VEG-01**)** with a substantial amount of old growth stands (FW-DC-VEG-03**)**; decrease of *A. grand, T. heterophylla, Thuja plicata, P. menziesii, P. contorta,* and *A. lasiocarpa*; more of the forest is dominated by stands occurring in the seedling/sapling size class and large size classes while less of the forest is dominated by stands that occur in the small and medium size classes (FW-DC-VEG-02). *P. monticola*, *P. ponderosa*, *L. occidentalis*, *P. Ponderosa* all increased as prescribed; *P. albicaulis* did increase in the cool-wet ecoregion, though the initial biomass was extremely low resulting in a negligible increase. The increase of these species was not as pronounced without harvest management (Figure 3.9). The only species prescribed to decline but was simulated to increase was *P. contorta,* though the increase was associated with a warming climate, harvest reduced the increase (Figure 3.13). As implemented, the median forest age also increased across Forest Service lands and assuming age is a proxy for size class, then more of the forest was in the larger size class.

Climate change interacting with fire had subtle effects on forest carbon dynamics. Mean annual area burned among low and high emission scenarios with harvest interactions increased by 13% and 29%, respectively. This was a deviation from the 48% predicted for the region using an explicit fire model with vegetation functional types and moderate climate warming (Riley and Loehman 2016). Other fire projections include a doubling of area burned in the Northern Rockies under a 1° C mean annual temperature increase (National Research Council 2011) and an increased percent area burned of 0.62 – 0.67 over the greater region that encompasses the Northern Rockies Ecoregion (Sheehan et al. 2015). The discrepancies between this study and others are likely due to the different model approaches especially with regards to vegetation feedbacks. Vegetation modeled as functional types do not capture the specific dynamics between climate change and forest types that dictate specific fuel types (Rocca et al. 2014). In addition, the areas modeled included the entire Northern Rockies Ecoregion, however I focused on only the areas that have burned since 1889. Such a narrow spatial focus, can minimize the likelihood of future fires, reoccurring fires, or severity increases, if post-fire fuel loads and conditions do not develop (Parks et al. 2016). The fire simulations produced initial carbon emission of 17.5 g C/m^2 which is similar to the estimated carbon emissions from 2001 – 2008 (18.6 g C/m^2) (Wiedinmyer and Hurteau 2010). The projected emission declines (Figure 3.21) was a function of the decline in fire severity, since burned area was not projected to decline through the century. The subtle increase in area burned reduced ANPP and NPP in comparison to similar climate scenarios with no disturbance or harvest interactions (Table 3.9). Fire decreased NEP particularly at the end of the century, this is related to the increase in area burned around 2075 (Figure 3.17 and 3.20).

Biodiversity Responses

The results indicate that harvest interacting with climate change will play an important role in habitat suitability of the avifauna species reviewed. The Flammulated Owl niche projections showed increases in suitable area under a warming climate and harvest is projected to interact synergistically with warming to further increase niche suitability. This occurred because *P. ponderosa* and *P. menziesii*, key species of the owl's niche suitability model were projected to increase under a warming climate (Figure 3.13). This increase is consistent with other projections of these species for the region (Coops et al. 2005, Coops and Waring 2011, Keane et al. 2018). Harvest, synergistically increased the *P. ponderosa* response, however even with the composition decline of *P. menziesii* caused by harvest, niche suitability increased with the addition of harvest (Figure 3.23). This is likely, because *P. menziesii* increased in the cool-wet ecoregions even with the decline in the warm-dry, and *P. ponderosa* was associated with the state and private land management units, which accounted for 70% of the total area that increased in suitability under fire and harvest interaction simulations. Thus, management of private and state lands will be important for Flammulated Owl niche persistence.

The Flammulated Owl is a cavity nester and requires nesting sites (e.g., snags) in mature forests with large diameter trees (31 cm) (Groves et al. 1997). The niche model applied did not account for such habitat features either directly or indirectly, e.g., stand age, time since disturbance. However, this research indicates that harvest prescriptions prescribed per the Idaho Panhandle Forest Plan will result in a median forest age consistent with mature forests. However, these areas are not in complete overlap with the stands most associated with the owl's realized niche habitat, as state and private lands are projected to have a median age consistent with early seral stages. There is little evidence on the vulnerability of this species to climate warming except that a loss of larger diameter trees would increase the stress on nest establishment and reproductive success (Mckelvey and Buotte 2018). Future modeling focused on incorporating an age or tree size component may better refine the results presented here.

The American Three-toed Woodpecker potential niche projections were also strongly associated with harvest. Simulations with suspended harvest projected an increase in potential niche, because more cohorts matured. The maturing affected the responses of the stand age and timber harvest ecological indicators. Plant associations, specifically the spruce-fir land cover was not substantially different between historic climate and RCP 8.5 end of century projections with fire and harvest interacting. In contrast, spruce-fir land cover was greater among the fire only models and greatest for the historic climate scenario. The decreased harvest intensity and prescribed harvest plan to increase stand age of the Forest Service management areas increased the suitability of these regions. Harvest management relegated almost all suitable lands to the Forest Service management areas, because harvest on private lands produced young forest. RCP 8.5 climate warming devoid of harvest increased area suitability above historic climate projections. *Picea engelmannii* and *A. lasiocarpa* decreased in percent composition of the landscape under high emissions with harvest and fire interacting and remained stable with no harvest (Figure 3.13). Interestingly, the spruce-fir land cover type (predicted from Random Forest) increased, which appears counter to these results. The intersection between the LANDIS-II biomass maps of each species and the reclassification of the LANDFIRE Existing Vegetation Types classes to the landcover types used in the Flammulated Owl model is a possible cause of the error. However, the spruce-fir cover class was predicted by the Random Forest model with a low error rate (Table B.1.2.4), therefore there was good agreement between the LANDIS-II biomass maps converging and the original LANDFIRE data cover classes. It is possible that species other than *Picea engelmannii* and *A. lasiocarpa* were important in the Random Forest model to predict the cover class spruce-fir. This reflects the nature of the LANDFIRE data, which broadly classifies forest types across a heterogenous landscape of stands. This highlights the need for the Random Forest model to predict the landcover types for the avifauna models, because the direct reclassification of the LANDIS-II species-biomass maps was at a scale too fine to inform the Flammulated Owl niche model. The identified core habitat should then be interpreted as the broad scale areas that potentially confer niche suitability without focusing on specific stands as being important.

The American Three-toed Woodpecker is projected to lose substantial climatically suitable range by the end of the century (Langham et al. 2015). Though the models presented project niche suitability in the Northern Rockies of Idaho to increase under climate warming; the areas identified with these models do not represent habitat that confer all necessary niche resources. This species is a disturbance specialist and have irruptive population dynamics in response to fire events. Managing for these core areas would increase the adaption potential in the future by managing the habitat for future fire events. Burn severity, tree size, and beetle occurrence determine habitat use and managing for mixed-severity regimes is important (Kotliar et al. 2008). Biological disturbance modelling is available in LANDIS-II and could provide further niche information when included. However, the models presented did not address changes in burn severity or the heterogeneous nature of fire across the landscape. Burn severity is not a consistent measurement especially between modeling and observation-based studies. For example, observation studies use the normalized burn ratio to measure severity (Kotliar et al. 2008, Latif et al. 2016), which is based on reflectance and has no analog with LANDIS-II fire metrics. Informative fire modeling to further assess the potential niche would need to address the severity of projected fires, the spatial heterogeneity of those projections, and the relationship between modeled and observed fire severity. Though climatically suitable range may contract, there is evidence that attributes of the potential niche will persist to the end of this century and managing for them is important.

The projections of these cavity nesters with regards to harvest, fire, and climate change interacting are region specific, since assessment of a different boreal woodpecker species found differing responses (Tremblay et al. 2018). However, the northern Idaho has the potential to provide habitat to other co-occurring species as the climate warms, because wildlife species that are projected to loose suitable habitat due to climate change and forest disturbance interactions (Drever et al. 2008, Tremblay et al. 2018) have geographic ranges that intersect with the Norther Rockies Ecoregion of Idaho. In the context of the projected loss of boreal avifauna biodiversity (Mahon et al. 2014), a focus on wildlife habitat management of the Northern Rockies is important, particularly for species with ranges that intersect boreal and Northern Rockies forest ecosystems. The probability of the study region conferring future wildlife habitat for species impacted by climate change is predicated on the implementation of the Idaho Panhandle Forest Plan, which produced many of the key habitat characteristics through implementation of harvest prescriptions recommended. The management scope of the plan and the effectiveness of past plans and actions to create, restore, and maintain critical habitat is beyond the scope of this research. However, any research including modeling that can improve conservation planning and cumulative effects analysis are foundational for adaptive management (Schultz 2010).

Simulation Limitations

This research provided insight into the interacting effects of climate change, fire, and harvest on forest ecosystems and avifauna niche responses. These simulations are representative of complex processes and interactions that occur at multiple scales and thus there are caveats to the results. The stochasticity of the ecosystem processes and climate was captured through multiple runs of two GCMS to account for this variability. The uncertainty of the climate was considered through the implementation of two GCMs that model the region well but provide a range of temperature and precipitation projections. The dynamics of climate were integrated through a downscaled model of the GCMs, but at a resolution coarser than the ecological processes applied through LANDIS-II, i.e., the climate condition of any randomly selected simulated 4 ha grid cell likely matched its neighbors. Additionally, the 4-ha resolution likely reflects the upper limit of the forest processes modeled in LANDIS-II, e.g., seed dispersal, fire spread, to be ecologically interpretable.

The implementation of fire is an area of uncertainty and was a stochastic ecosystem process. Fire modeling depended on the historic fire regime to bound future fires to a specific statistical distribution. I based the fire statistics on the latter half of the 20th century, which did not represent the fully dynamic fire regime of the Northern Rockies Ecoregion of Idaho. The late 1800's and early 20th century was marked by large fires including the 1910 Fire, an extreme and unparalleled fire event (Arno 1976). Other studies of the Northern Rockies have considered the entire available fire regime when calculating statistical distributions (Sheehan et al. 2015, Riley and Loehman 2016). Inclusion of the major fire events of the early part of the 20th century would have increased the subsequent modeled fire extents, and the altered the effects of fire on ecosystem processes. The probability of such events occurring in the future is debatable and an area of research need. Thus, it is probable the fire regime implemented is conservative and future research can evaluate the effects of altering the fire regime with respect to the historical record.

The research did not include the dynamics of drought stress, biological disturbance, drought induced mortality, or CO_2 seeding, which will impact ecosystem dynamics (Ciais et al. 2005, Harvey et al. 2014, Reyer et al. 2017), tree species (Adams et al. 2009, Silva et al. 2010, Keane et al. 2018), and cascading effects on avifauna (Sekercioglu et al. 2012, Jenouvrier 2013, Bennett et al. 2014). The results likely represent an overestimation of productivity without the effects of such disturbance events, since drought can affect productivity and forest composition (Ciais et al. 2005, Zhao and Running 2010, Anderegg et al. 2013, Gustafson and Sturtevant 2013). These dynamics may affect the carbon balance (Noormets et al. 2008) altering source-sink dynamics because of legacy effects on productivity post drought (Anderegg et al. 2015) rending the ecosystem carbon neutral or source earlier in the 21st century.

The avifauna models integrated a niche suitability response with the biogeochemical responses of the forest ecosystems. The niche models, either potential or realized assessed suitability based on habitat or distribution potential, respectively (Sillero 2011) assuming that the observed contemporary relationships with environmental covariates persist (niche conservatism). These models have uncertainties associated with them, such as transferability and parsimony as discussed in Chapter Two. However, the models applied in this study only account for a narrow range of ecological characteristics that define the fundamental niche of the species and assume the niche space is stable (Wiens et al. 2009). Avifauna exhibit local adaptation and plasticity to changing conditions (Martin 2015); a potential violation of niche space stability. In addition, these models did not address vital rates, density dependent factors, migration, and predator-prey dynamics that augment fitness and habitat suitability.

Climate change interacting with forestry and land use practices impacts avifauna population dynamics with emergent and complex results (Selwood et al. 2015, Layton-Matthews et al. 2018). Suitability based on vegetation and landscape characteristics may purport future habitat, however induced changes (directly climate related or otherwise) to prey resources (Schiegg et al. 2002, Wiebe and Gerstmar 2010), breeding (Halupka et al. 2008), diseases (Liao et al. 2017), and community predator dynamics (Rees et al. 2018) will affect fitness and population viability. The models presented provide insight into managing the landscape and not the species populations.

Conclusion

This research analyzed multiple forest ecosystem processes and climate change in the Northern Rockies Ecoregion of Idaho and subsequent habitat responses of two avifauna cavity nesters. The integration of a forest landscape and avifauna niche models is emerging (Martin et al. 2014, LeBrun et al. 2017, Tremblay et al. 2018) and is providing a process to evaluate biogeochemical and biodiversity responses to climate-vegetation-disturbance interactions. Our results suggest the study area will maintain a carbon sink potential through to the end of the century, that harvest was an important factor affecting carbon dynamics and habitat suitability, and burned area will increase slightly under a warming climate. Harvest was the most important disturbance interaction, especially on Forest Service lands, because it resulted in an increase in mature forests and tree species of management focus. These changes resulted in habitat that was conducive for two cavity nesting species, which represent the potential for biodiversity persistence in the future. This research supports the proposition that the Northern Rockies Ecoregion of Idaho is a potential habitat refugia for avifauna and other forest dwelling species as the climate warms. The further development and integration of forest and species niche models will aid in balancing multi-objective forest management to produce adaptive environments in a changing climate.

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Table 3.1. The tree species modeled with the FIA species code and FIA percent of total biomass associated with the cool-wet (CW) and warm-dry (WD) simulated ecoregions.

FIA spcd	**Latin Name**	**Common Name**	**CW**	**WD**
17	*Abies grandis*	Grand Fir	17.5%	30.1%
19	*Abies lasiocarpa*	Subalpine Fir	9.6%	0.2%
73	*Larix occidentalis*	Larch	6.5%	9.0%
93	*Picea engelmannii*	Engleman Spruce	8.4%	0.6%
101	*Pinus albicaulis*	Whitebark Pine	<0.1%	<0.1%
108	*Pinus contorta*	Lodgepole pine	11.6%	3.9%
119	*Pinus monticola*	Western White Pine	1.5%	2.9%
122	*Pinus ponderosa*	Ponderosa Pine	0.9%	4.8%
202	*Pseudotsuga menziesii*	Douglas Fir	18.2%	32.0%
242	*Thuja plicata*	Western Redcedar	7.7%	12.0%
263	*Tsuga heterophylla*	Western Hemlock	8.6%	4.5%
264	*Tsuga mertensiana*	Mountain Hemlock	9.3%	0.0%

Table 3.2. The carbon cycling terms as defined by Chapin et al. (2006). Under their definition fire emissions are accounted in the NECB, however LANDIS-II NECN model reports NEE, which accounts for carbon losses due to leaching and fire emissions. Thus, NEE reported here is synonymous with NECB.

Acronym		**Description**
GPP	Gross primary productivity	Gross carbon fixation by autotrophic carbon fixing tissues
AR	Autotrophic respiration	The respiration of autotrophic organisms
NPP	Net primary productivity	Equal to GPP-AR (biomass accumulation and tissue turnover above and below ground)
HR	Heterotrophic respiration	The respiration rate of heterotrophic organisms
ER	Ecosystem respiration	The respiration of plants, animals, and microbes
NEP	Net ecosystem productivity	A sum of the fluxes of GPP, AR, and HR
NEE		The net CO_2 ecosystem exchange with the atmosphere. It diverges from NEP when carbon enters or leaves the ecosystem through vertical atmospheric exchange. This is the opposite sign of NEP because it is defined as a flux relative to the

		atmosphere, i.e., negative values indicate an ecosystem carbon sink.
NECB	Net ecosystem carbon balance	A sum of -NEE and lateral exchange, e.g., carbon leaching through the aquatic phase, carbon volatilization.
AGB	Above ground biomass	The living biomass above ground, which includes stem, stumps, branches, bark, seeds, and foliage

Table 3.3. Fire statistics for the Northern Rockies Ecoregion summarized from Gibson (2005) and Forest Service Region 1 (2015).

	1889-2013	**1889-1930**	**1931-1971**	**1972-2013**	**1960-2010**
Occurrence (mean)	16	30	7	6	6
Individual fire size (mean)	856	1033	576	456	485
Mean annual area burned	19081	39814	8947	1229	2683
Median annual area burned	1237	6588	306	419	417
Percent of area burned	1.8%	3.8%	0.9%	0.1%	0.3%

Table 3.4. The total unique fire extents burned each year from 1889 to 1919 with the percent of the total burned area extent being a function of the cumulative unique burned area per year.

Year	Total Unique Burn Area (ha)	Percent of total burned extents up to 2013
1889	83413	8.0%
1890	18135	9.7%
1894	24120	12.0%
1895	6250	12.6%
1898	16677	14.2%
1900	4334	14.6%
1902	352	14.6%
1903	369	14.7%
1904	2346	14.9%
1906	450	14.9%
1907	13	14.9%
1908	2610	15.2%
1909	4254	15.6%
1910	525021	65.6%
1911	342	65.7%
1912	74	65.7%
1913	202	65.7%
1914	9782	66.6%
1915	886	66.7%
1917	4917	67.2%
1918	4032	67.6%
1919	110220	78.1%
1920	9557	79.0%

Table 3.5. The biomass (g/m^2) at spin-up (Modeled) and observed (NACP Aboveground Biomass and Carbon Baseline) between the cool-wet (CW) and warm-dry (WD) NECN ecoregions.

	Modeled	**Observed**	**Difference**
CW	9537	12200	-21.8%
WD	12270	11700	4.9%
Landscape	10903	11950	-8.8%

Table 3.6. The ratio of biomass at spin-up (Modeled) and Forest Inventory Analysis (FIA) between the cool-wet (CW) and warm-dry (WD) NECN ecoregions. Values >1 indicate more biomass in the CW compared to WD. The ratios that differ between modeled and FIA are highlighted.

Ratio CW to WD	**Abies grandis**	**Abies lasiocarpa**	**Larix occidentalis**	**Picea engelmannii**	**Pinus albicaulis**	**Pinus contorta**	**Pinus monticola**	**Pinus ponderosa**	**Pseudotsuga menziesii**	**Thuja plicata**	**Tsuga heterophylla**	**Tsuga mertensiana**
Modeled	0.44	9.78	0.49	45.88	2.43	3.07	0.16	0.04	0.31	1.40	7.13	182.52
FIA	0.72	58.45	0.89	17.17	NA	3.66	0.00	0.23	0.70	0.79	2.34	502.94

Table 3.7. The modeled (fire and harvest disturbance turned on) fire statistics with standard deviation () compared to the observed.

	Modeled	**Observed 1980-2013**	**Difference**
Ignitions	14 (0.6)	15	-3.7%
Individual fire size (mean)	442 (180)	485	-8.8%
Total ha per year (mean)	6069 (2432)	7162	-15.3%
Fire rotation period (years)	172 (57)	151	14.4%

Table 3.8. The mean simulated harvest biomass (Mg) per year for the first ten simulated years compared to the mean harvested biomass reported.

Land Ownership Type	**Modeled**	**Reported**	**Difference**
Private	2328585	2768321	-16
National Forest	586625	346898	69
Public Other	913218	894138	2

Table 3.9. The ensemble mean percent change in ANPP, NPP, REP, and NEP in the final third of the century compared to the first third of the simulation.

	ANPP			NPP			Respiration			NEP		
	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5
No Disturbance	2.20%	14.43%	22.58%	1.69%	13.48%	19.70%	7.75%	42.07%	43.98%	-46.84%	-79.82%	-70.56%
Harvest	34.74%	34.78%	45.00%	33.79%	34.25%	42.06%	38.74%	46.58%	52.49%	10.02%	-10.38%	-1.92%
Fire	1.28%	5.15%	18.26%	1.81%	5.09%	15.68%	16.00%	18.23%	36.88%	-59.77%	-50.98%	-67.46%
Fire-Harvest	27.68%	34.77%	42.10%	27.85%	34.21%	38.90%	24.03%	42.03%	43.26%	49.43%	4.08%	16.43%

Table 3.10. The mean percent change in NEP in the final third of the century compared to the beginning third of the simulation.

	Current	**RCP 4.5**	**RCP 8.5**
No Disturbance	-46.84%	-79.82%	-70.56%
Harvest	10.02%	-10.38%	-1.92%
Fire	-59.77%	-50.98%	-67.46%
Fire-Harvest	49.43%	4.08%	16.43%

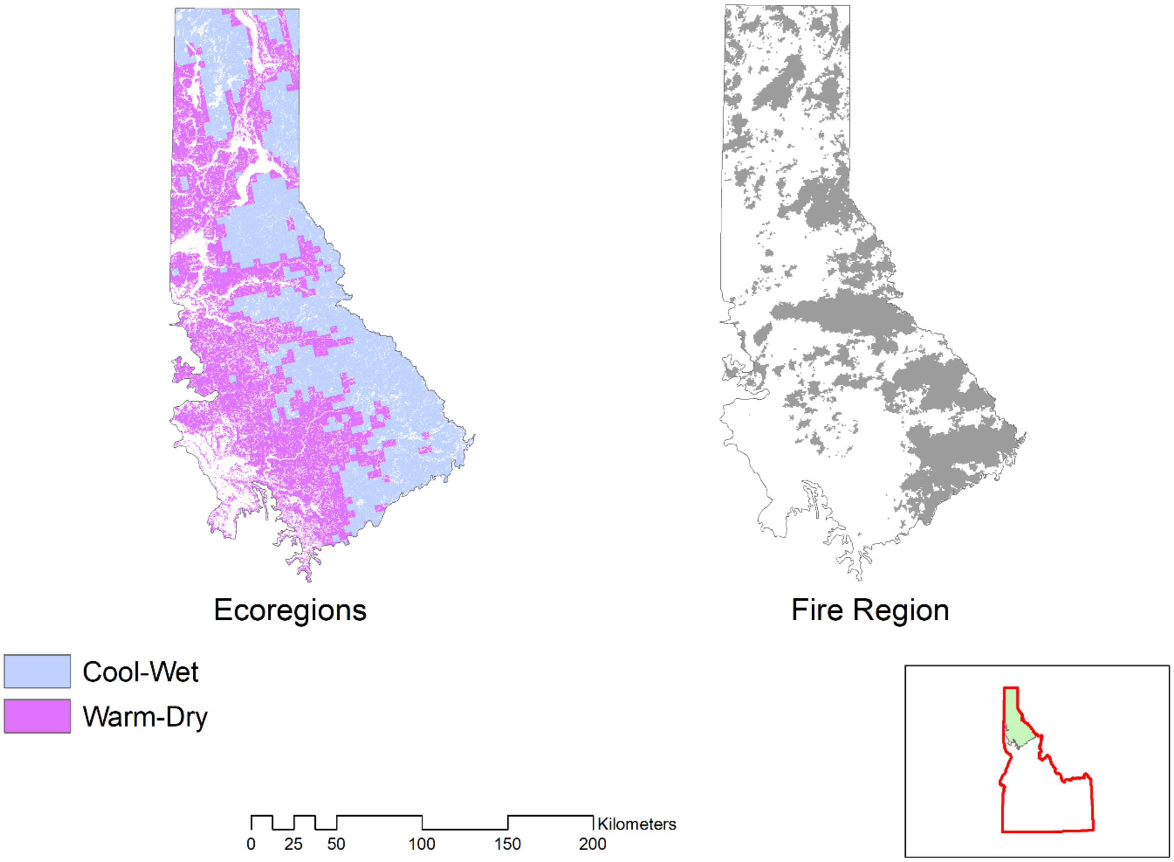


Figure 3.1. The study area (Northern Rockies Ecoregion of Idaho) with simulation ecoregions and modeled fire region.

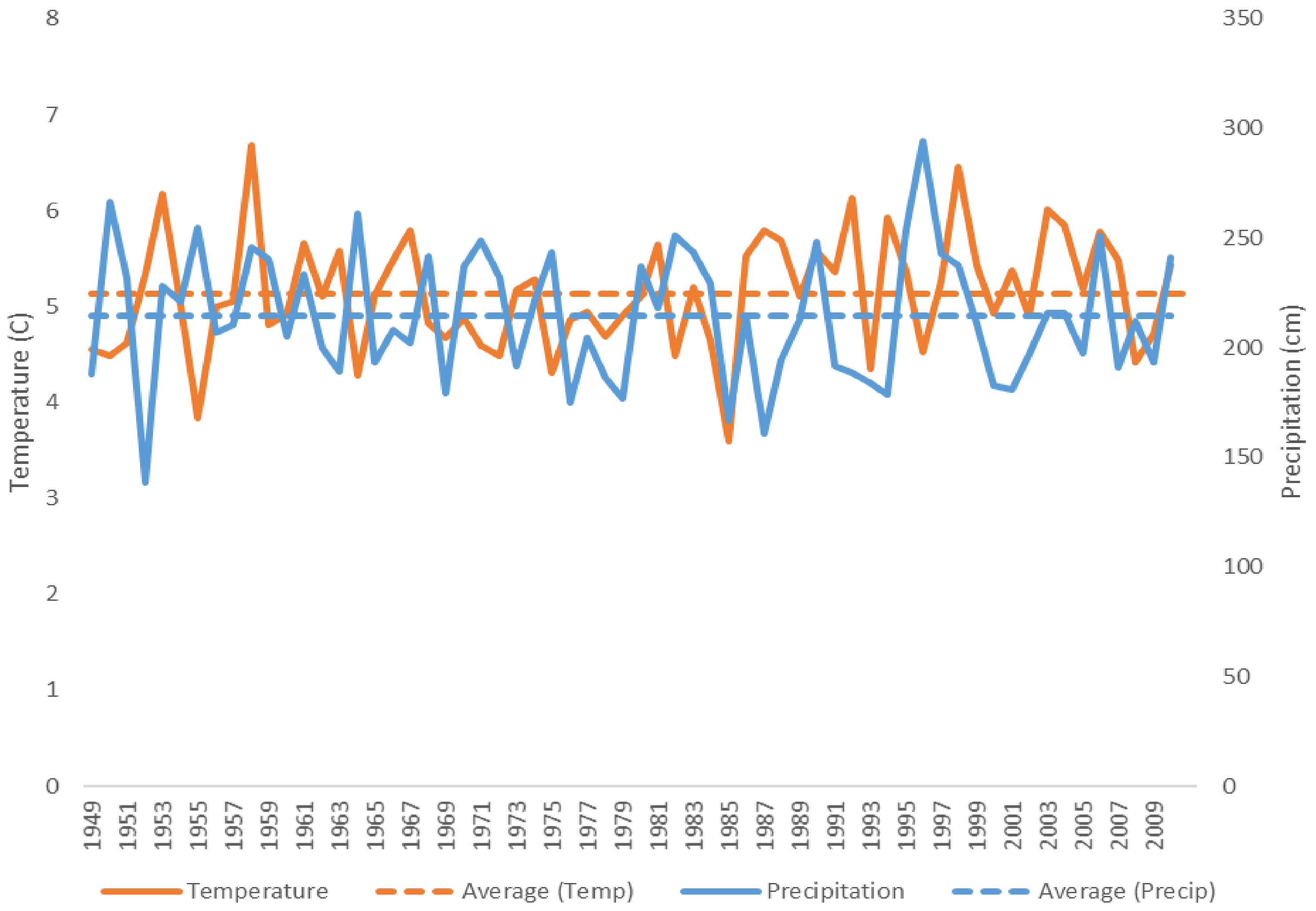


Figure 3.2. The total annual precipitation and mean annual temperature between 1949 and 2010 for the Northern Rockies Ecoregion of Idaho.

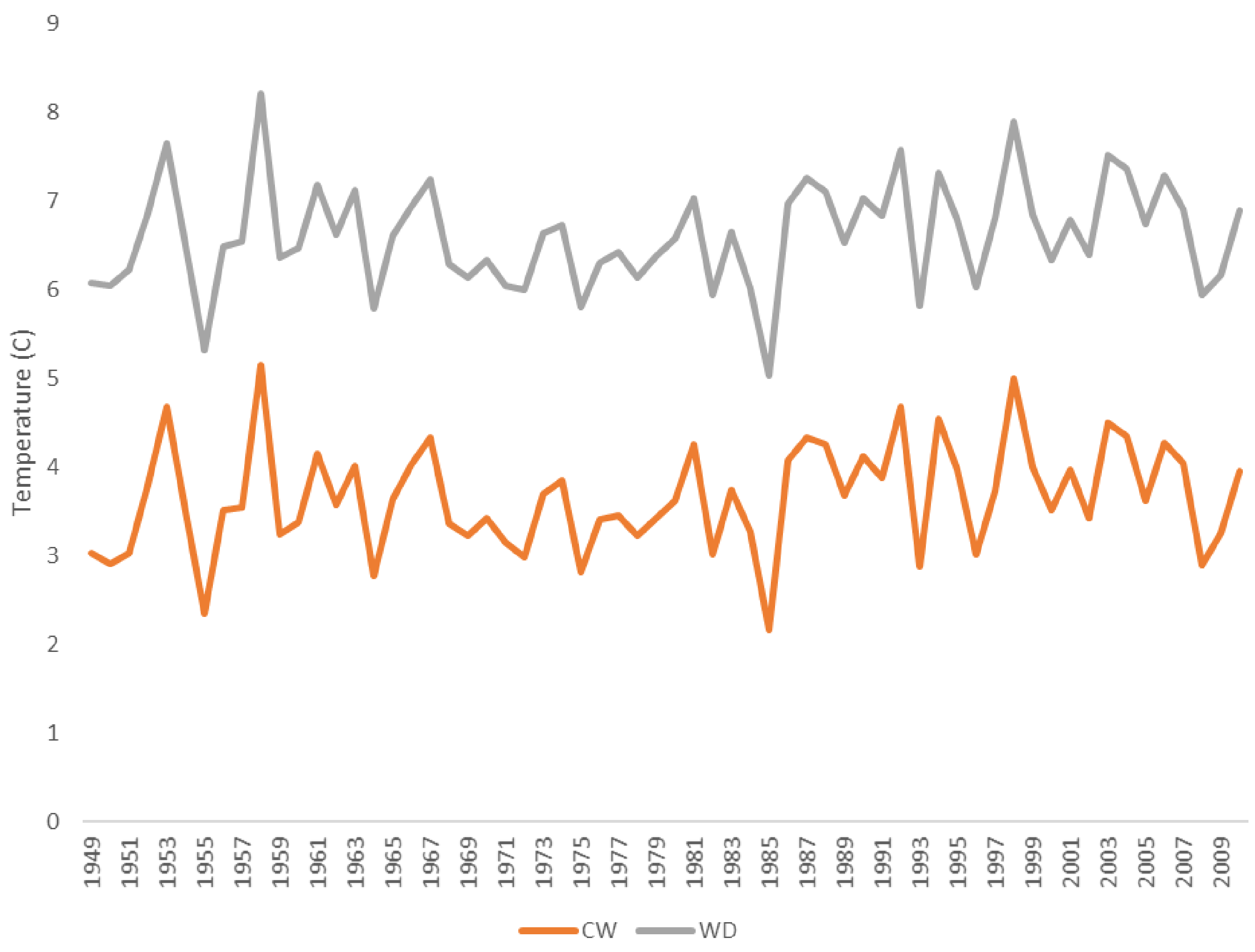


Figure 3.3. The annual mean temperature between 1949 and 2010 for the cool-wet (CW) and warm-dry (WD) simulation ecoregions.

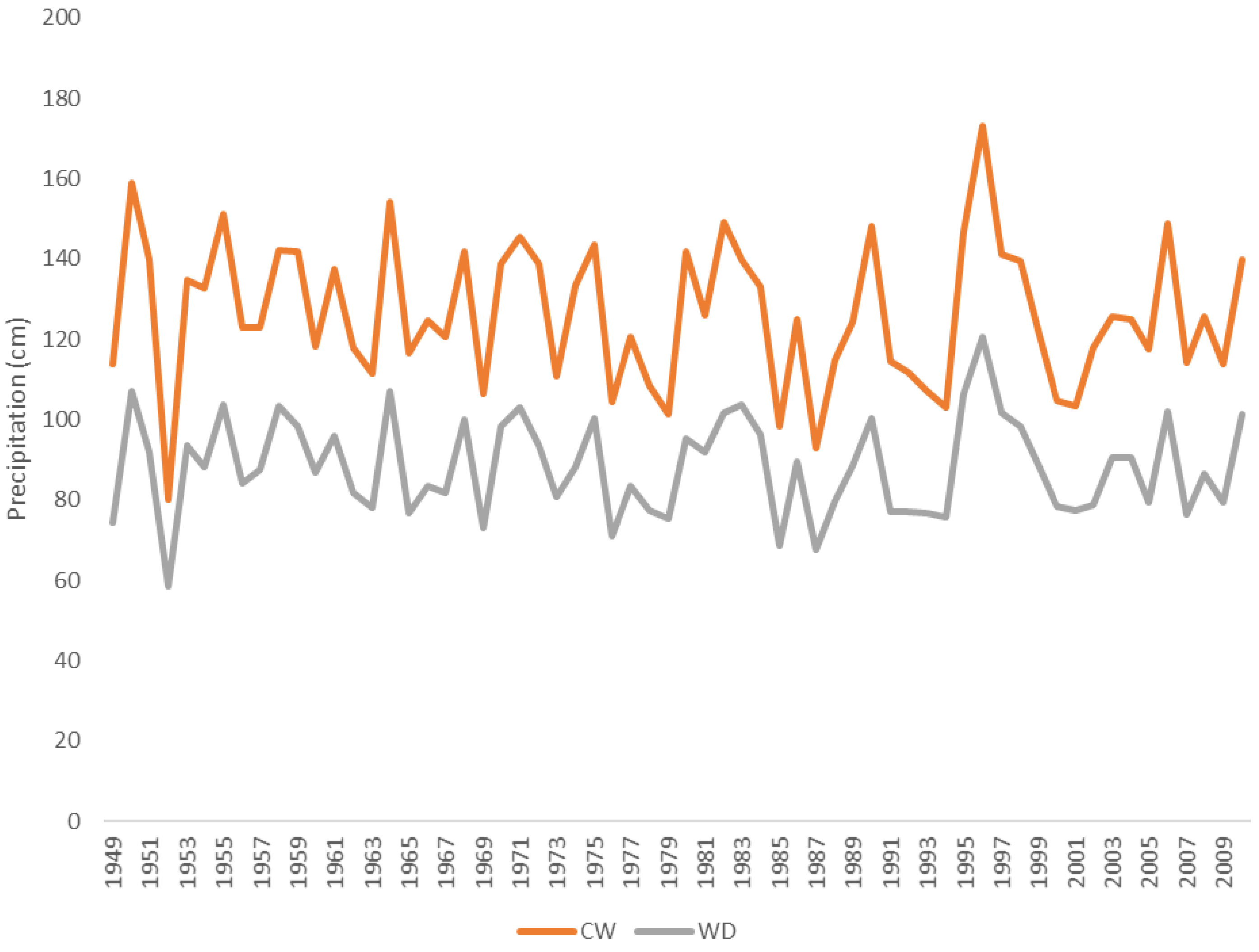


Figure 3.4. The total annual precipitation between 1949 and 2010 for the cool-wet (CW) and warm-dry (WD) simulation ecoregions.

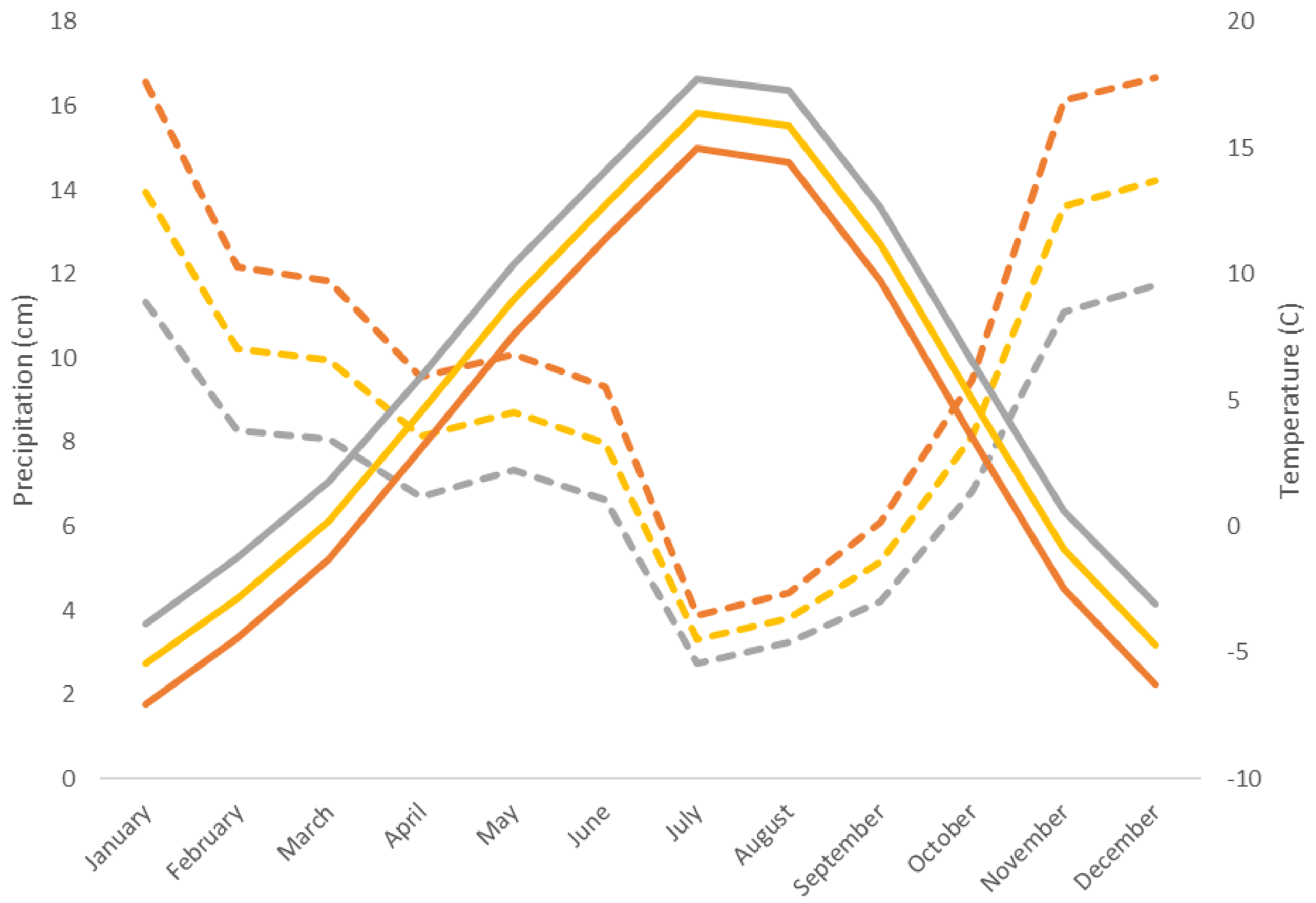


Figure 3.5. The average monthly precipitation (dashed lines) and temperature (solid lines) between 1949 and 2010 for the cool-wet (CW) and warm-dry (WD) simulation ecoregions.

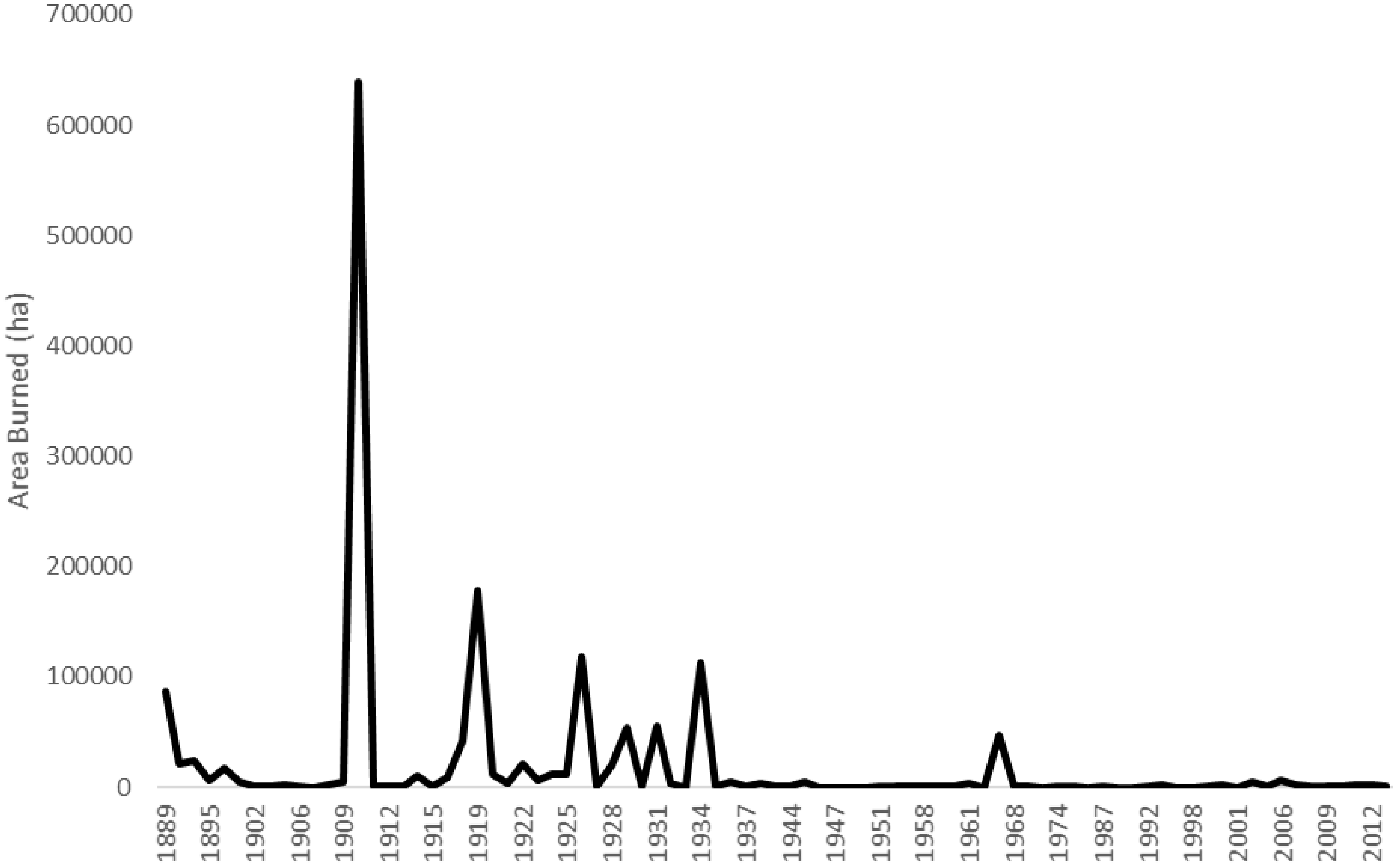


Figure 3.6. The yearly area burned from 1889 to 2013 of the Northern Rockies Ecoregion of Idaho summarized from Gibson (2005) and Forest Service Region 1 (2015).

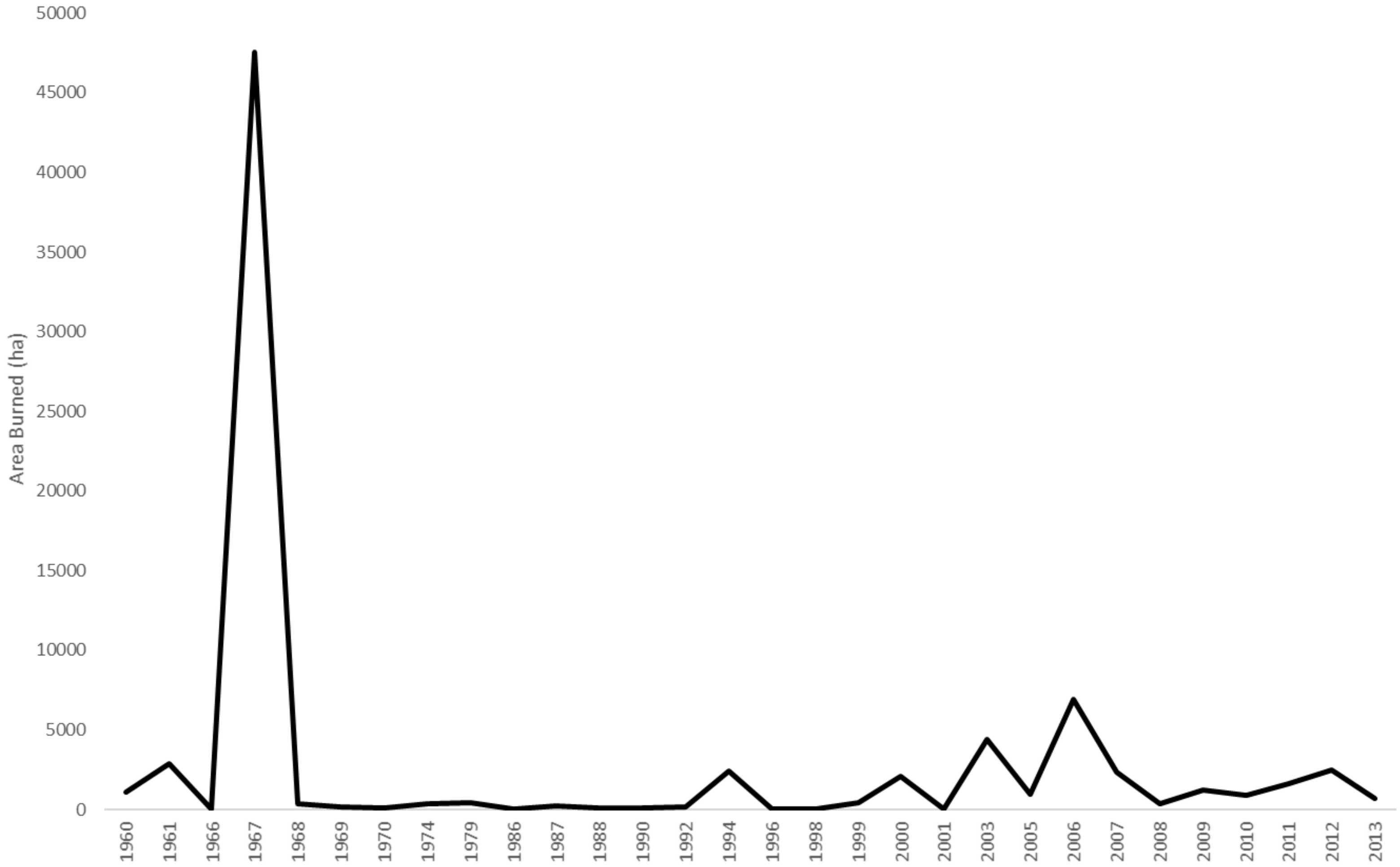


Figure 3.7. The yearly area burned from 1960 to 2013 of the Northern Rockies Ecoregion of Idaho summarized from Gibson (2005) and Forest Service Region 1 (2015).

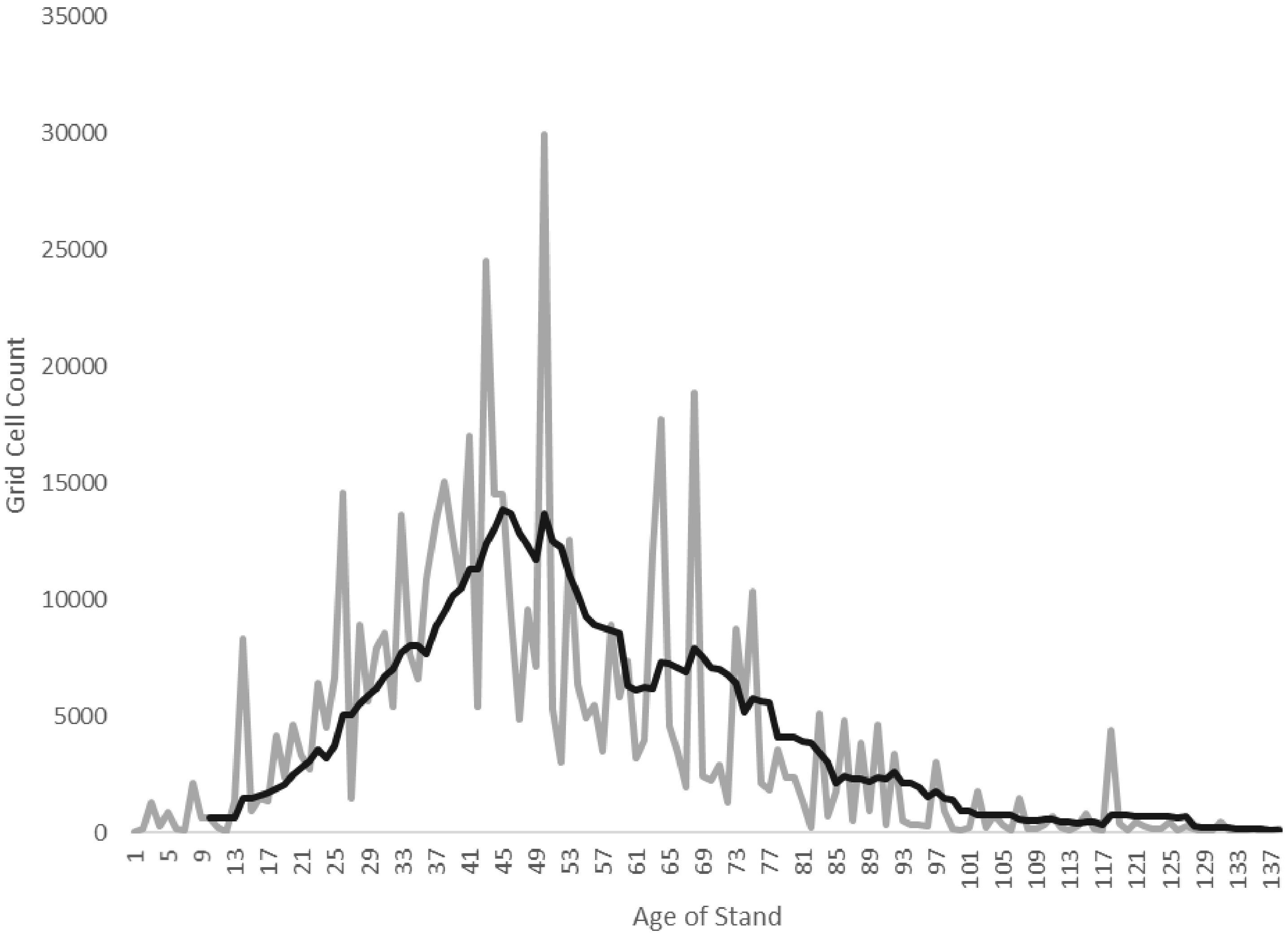


Figure 3.8. The distribution of grid cells among the average cohort age of each grid cell (gray line) with the smoothed average age (black line) calculated from the Landscape Builder assessment of the FIA data.

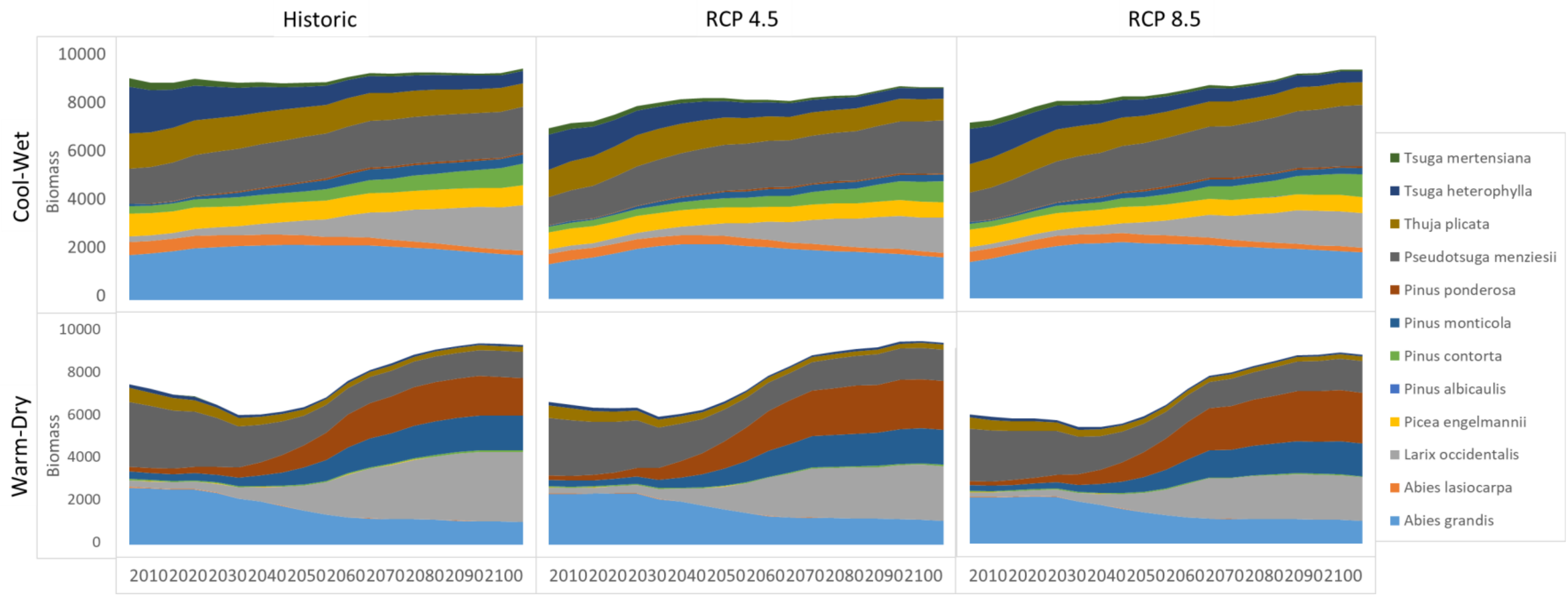


Figure 3.9. The modeled AGB (g/m^2) of each species under historic climate conditions and warming scenarios RCP 4.5 and 8.5 with harvest and fire interacting.

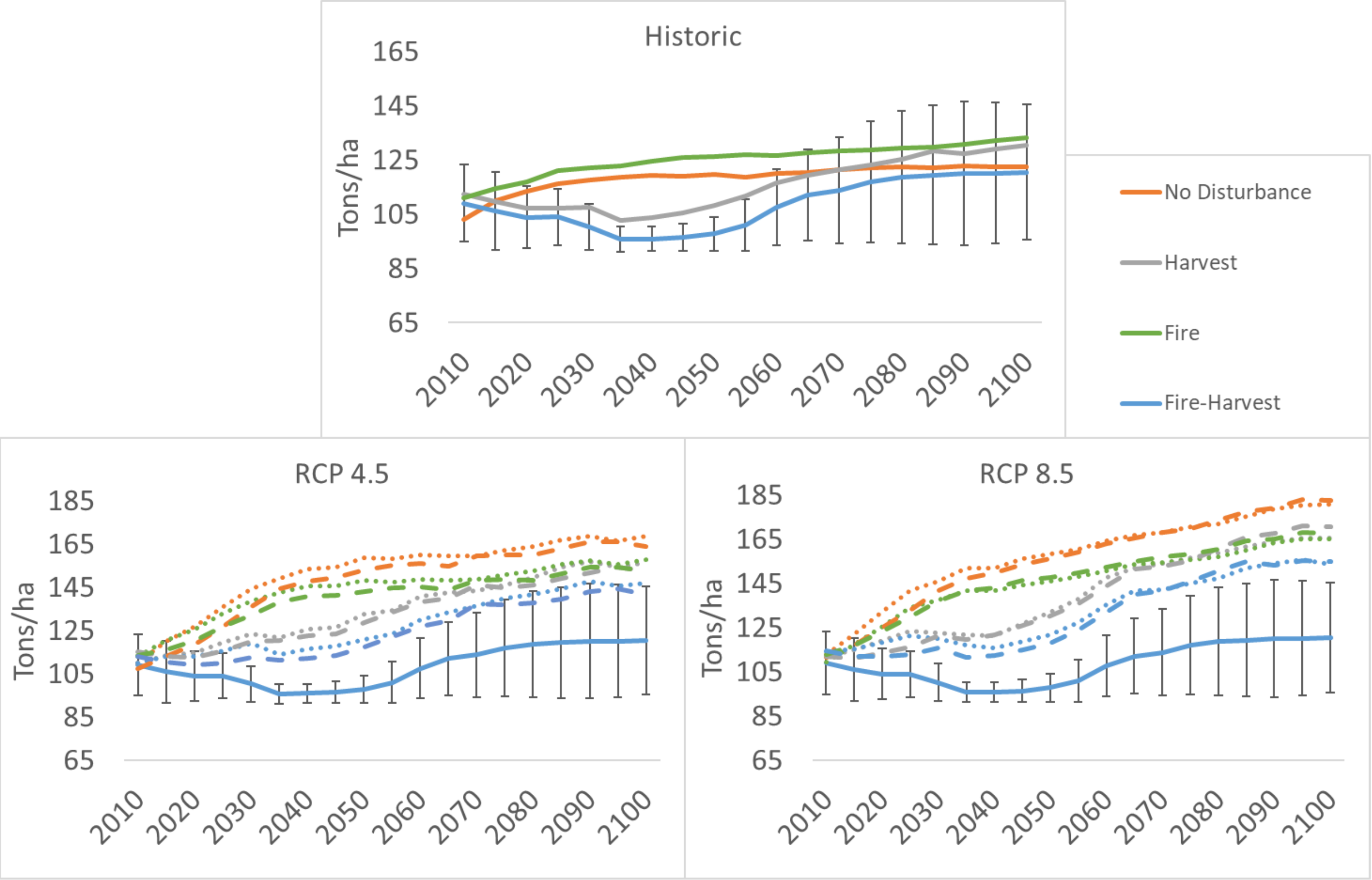


Figure 3.10. Projected AGB totals for all climate scenarios. Dotted lines are CanESM and dashed are CAM5 GCMs; error bars are the standard deviation of the replicated scenarios.

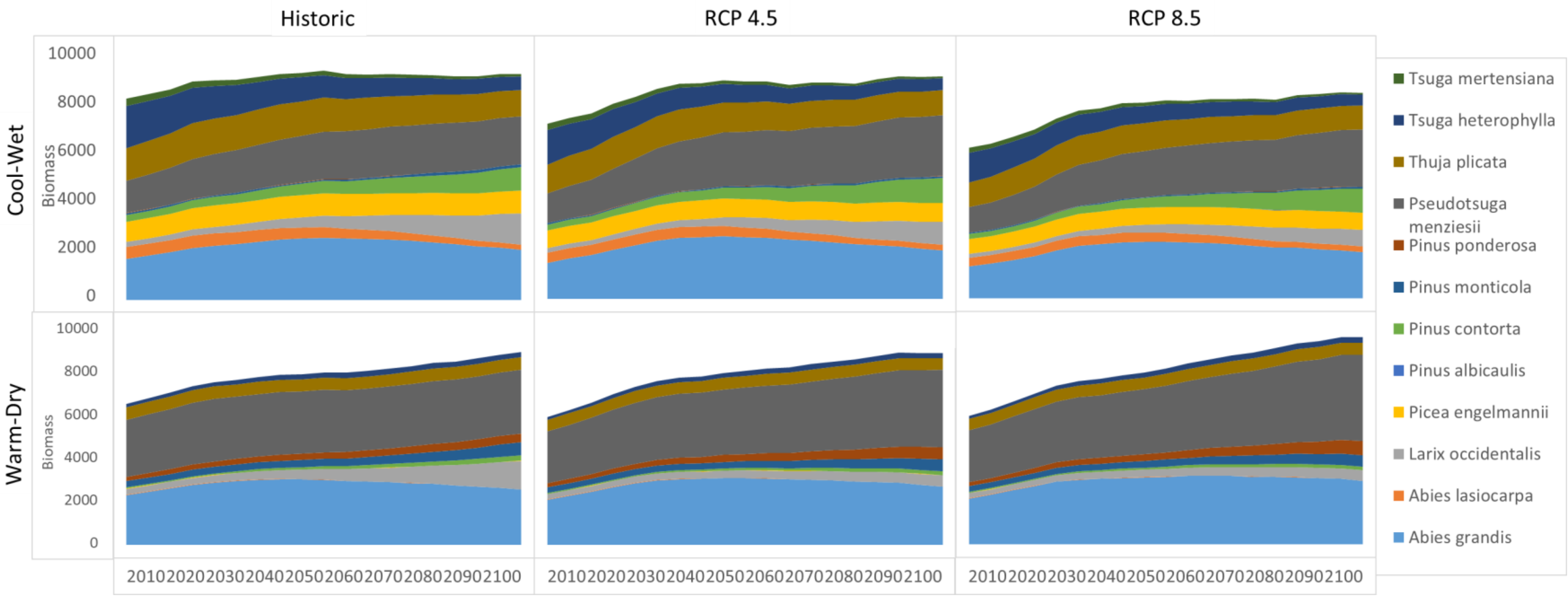


Figure 3.11. The modeled AGB (g/m^2) of each species under historic climate conditions and warming scenarios RCP 4.5 and 8.5 with fire interacting.

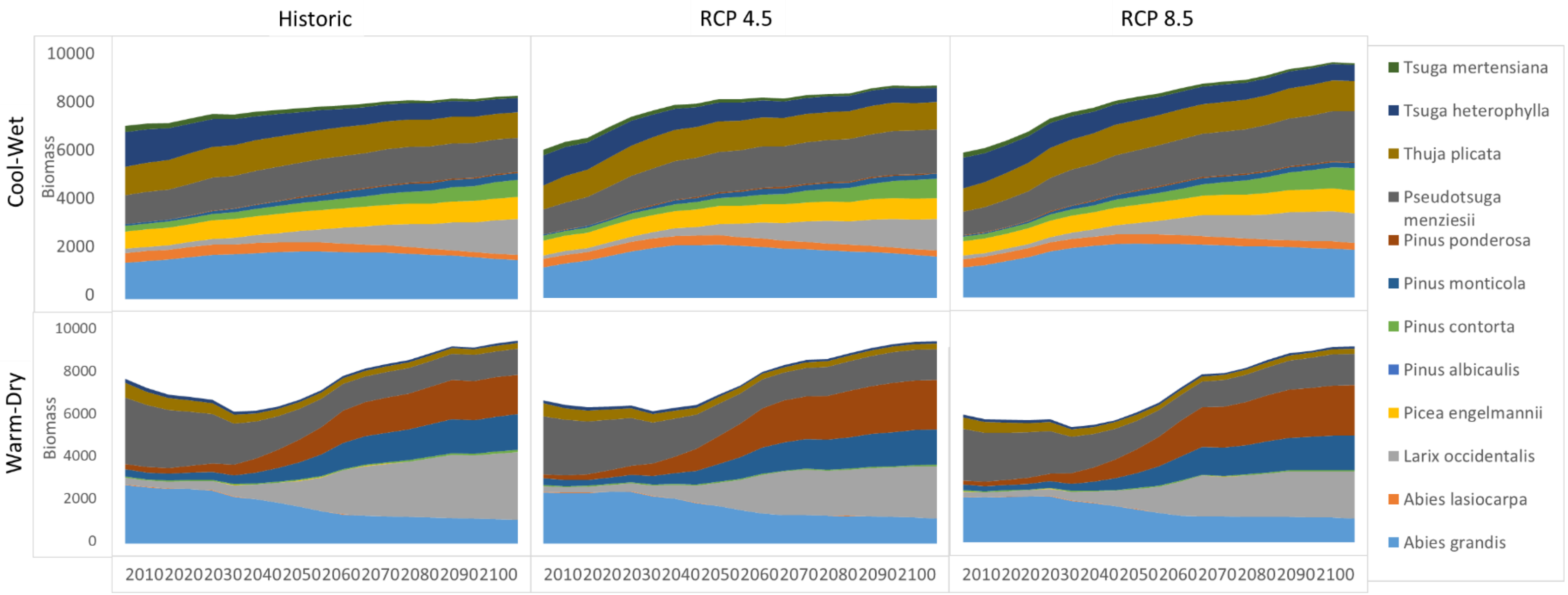
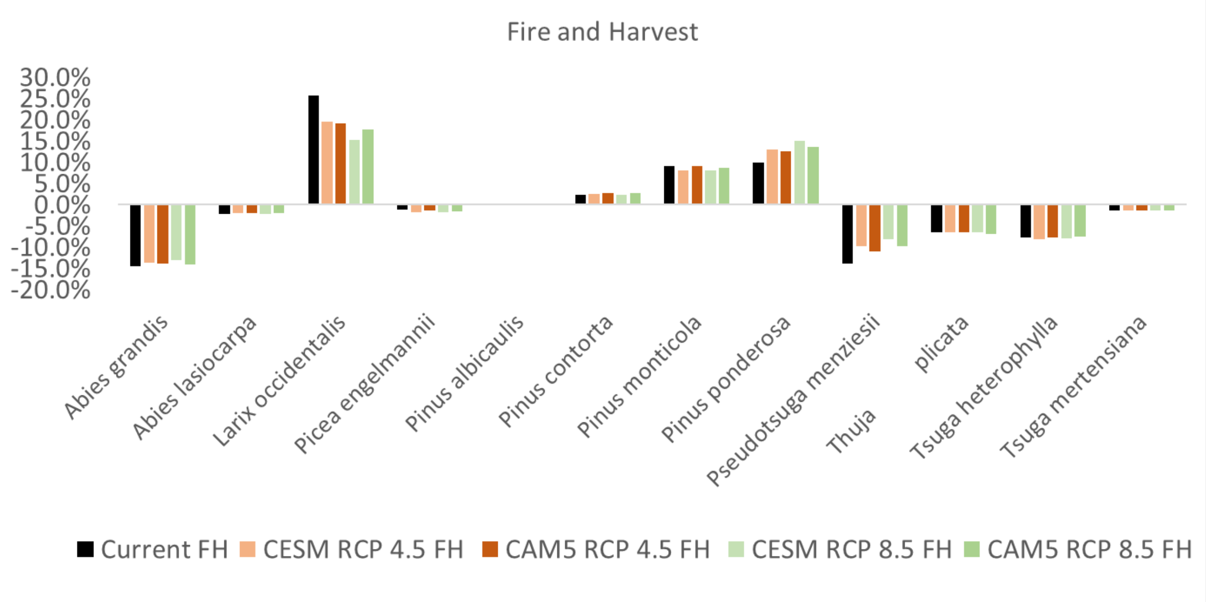
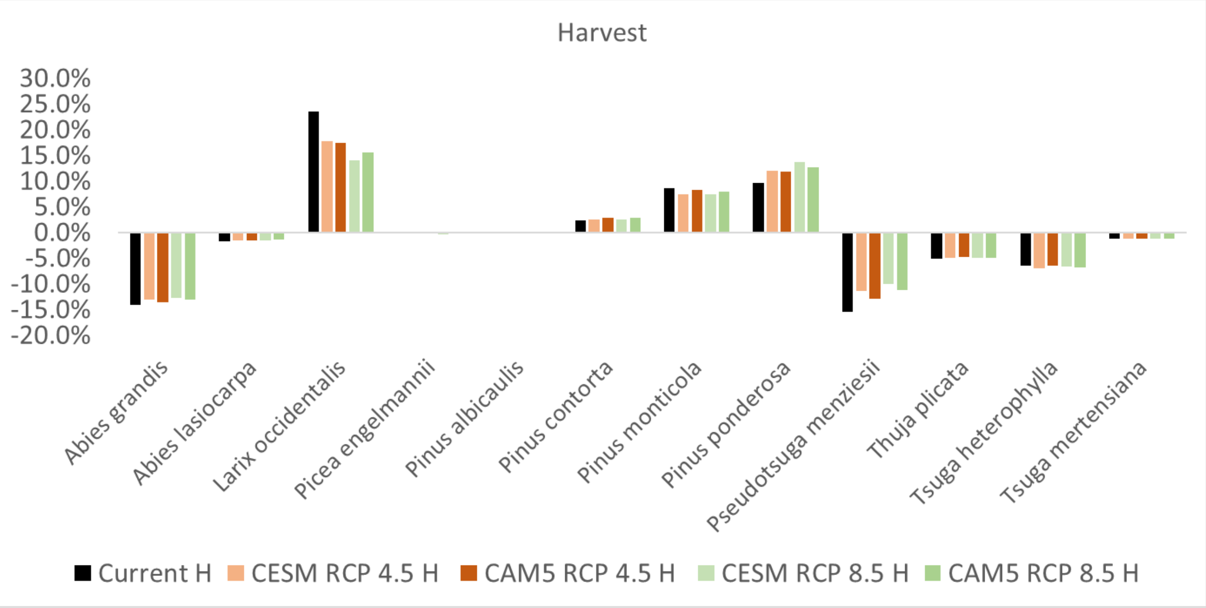


Figure 3.12. The modeled AGB (g/m^2) of each species under historic climate conditions and warming scenarios RCP 4.5 and 8.5 with harvest interacting.


Fire and Harvest
30.0%
25.0%
20.0%
15.0%
10.0%
5.0%
0.0%
-5.0%
-10.0%
-15.0%
-20.0%
Abies grandis
Abies lasiocarpa
Larix occidentalis
Picea engelmannii
Pinus albicaulis
Pinus contorta
Pinus monticola
Pinus ponderosa
Pseudotsuga menziesii
Thuja plicata
Tsuga heterophylla
Tsuga mertensiana
Current FH
CESM RCP 4.5 FH
CAM5 RCP 4.5 FH
CESM RCP 8.5 FH
CAM5 RCP 8.5 FH


Harvest
30.0%
25.0%
20.0%
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-10.0%
-15.0%
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Abies grandis
Abies lasiocarpa
Larix occidentalis
Picea engelmannii
Pinus albicaulis
Pinus contorta
Pinus monticola
Pinus ponderosa
Pseudotsuga menziesii
Thuja plicata
Tsuga heterophylla
Tsuga mertensiana
Current H
CESM RCP 4.5 H
CAM5 RCP 4.5 H
CESM RCP 8.5 H
CAM5 RCP 8.5 H

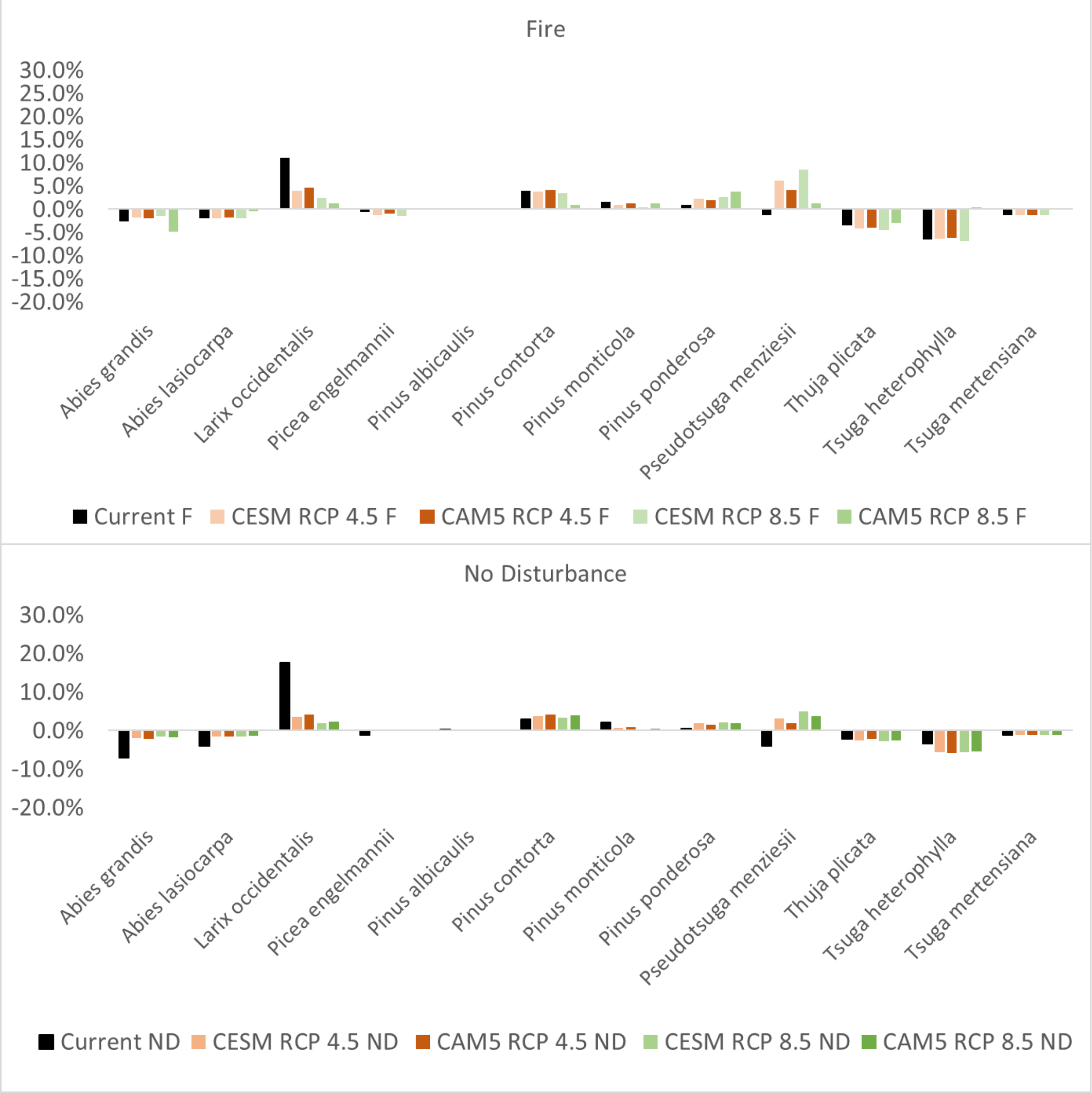


Figure 3.13. The change in species % composition among climate scenarios.

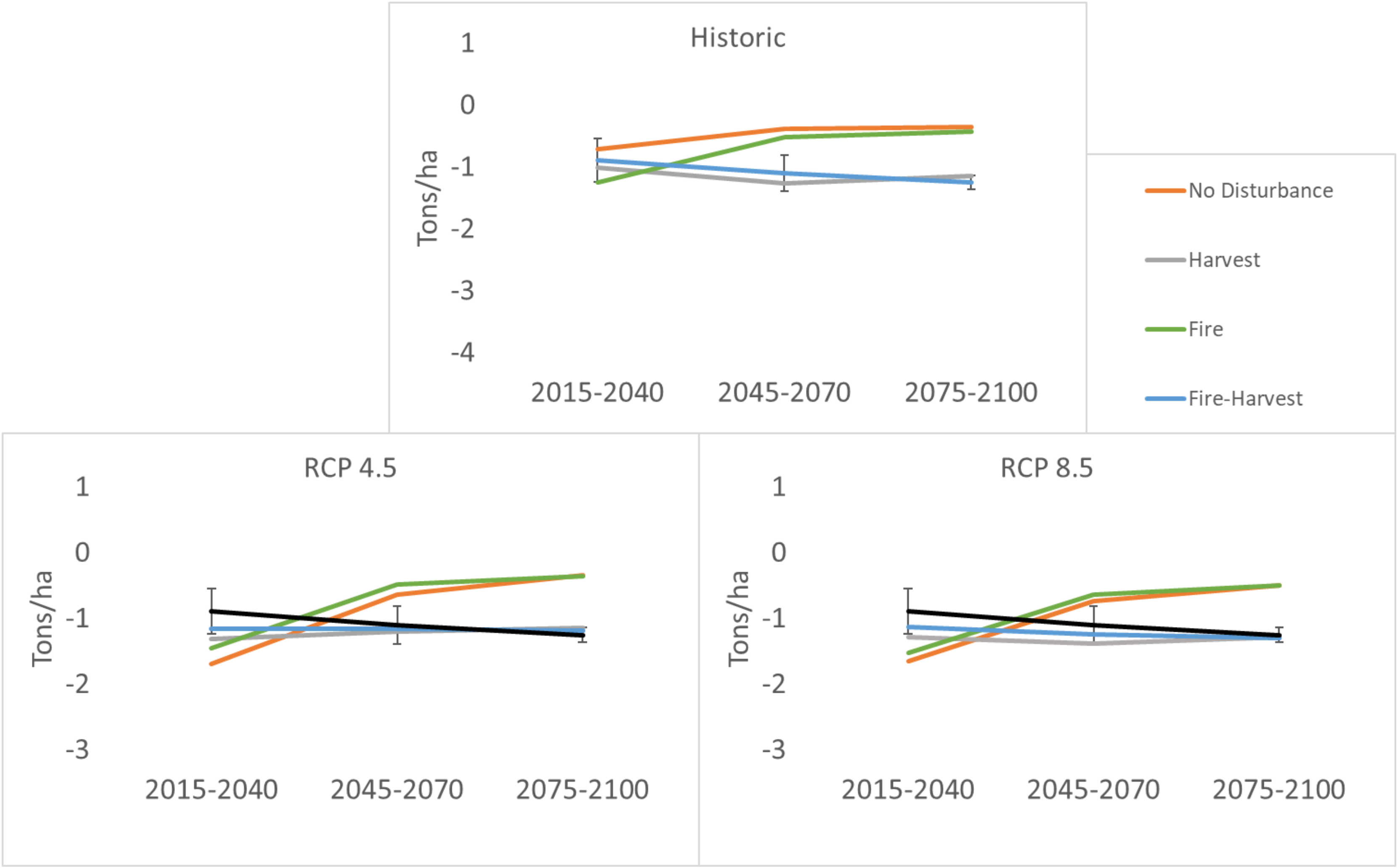


Figure 3.14. The net ecosystem exchange for all climate scenarios, RCP 4.5 and 8.5 are the mean of the two GCMs. The black line is the fire-harvest historic climate trajectory with the replicate simulation standard deviation bars.

Figure 3.15. The aboveground NPP with the historic fire-harvest interaction simulation overlaid (blue solid) with replicate simulation standard deviation bars. Dotted lines are CanESM and dashed are CAM5 GCMs.

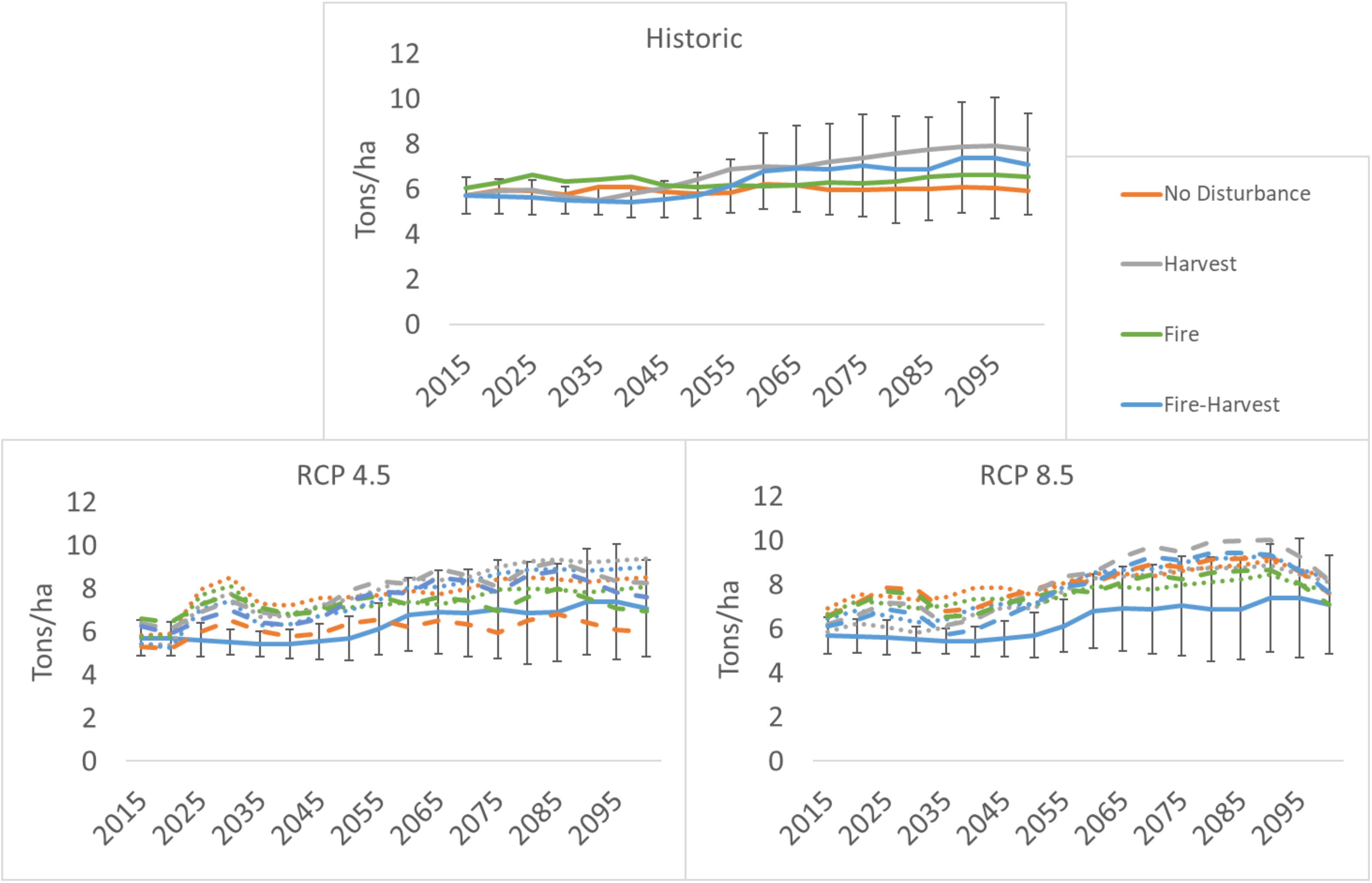


Figure 3.16. Total NPP with the historic fire-harvest interaction simulation overlaid (blue solid) with replicate simulation standard deviation bars. Dotted lines are CanESM and dashed are CAM5 GCMs.

Figure 3.17. Ecosystem NEP with the historic fire-harvest interaction simulation overlaid (blue solid) with multi-simulation standard deviation bars. Dotted lines are CanESM and dashed are CAM5 GCMs.

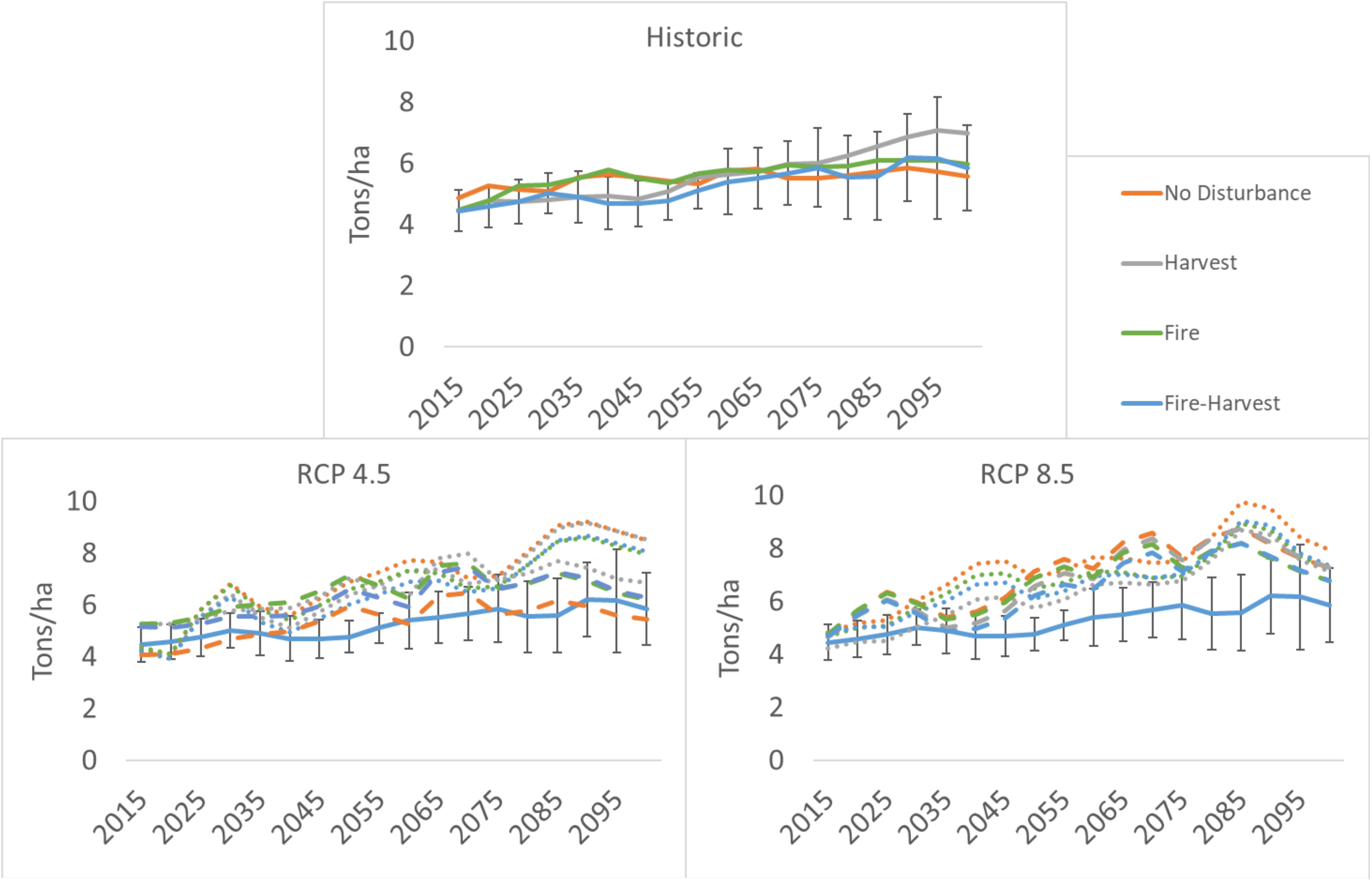


Figure 3.18. Ecosystem respiration with the historic fire-harvest interaction simulation overlaid (blue solid) with multi-simulation standard deviation bars. Dotted lines are CanESM and dashed are CAM5 GCMs.

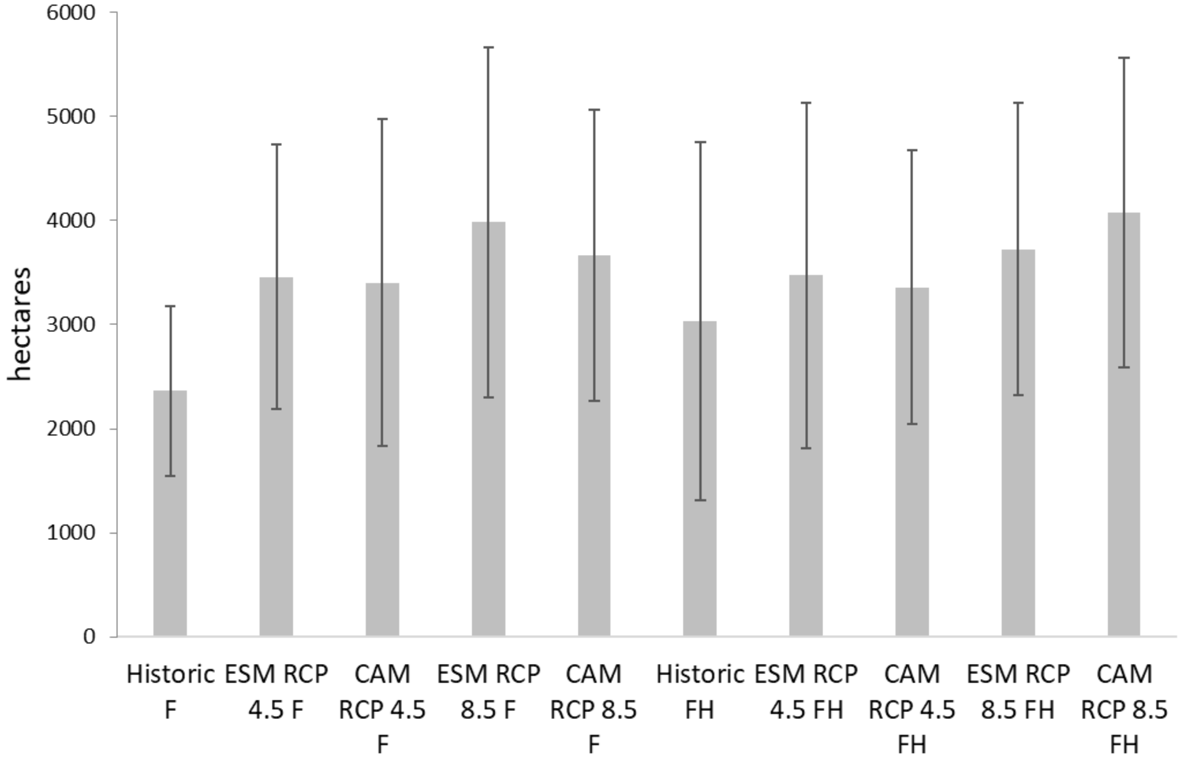


Figure 3.19. The mean annual burned area among all scenarios for the entire simulations with standard error bars of the replications and the mean percent of the total area burned per year (triangles).

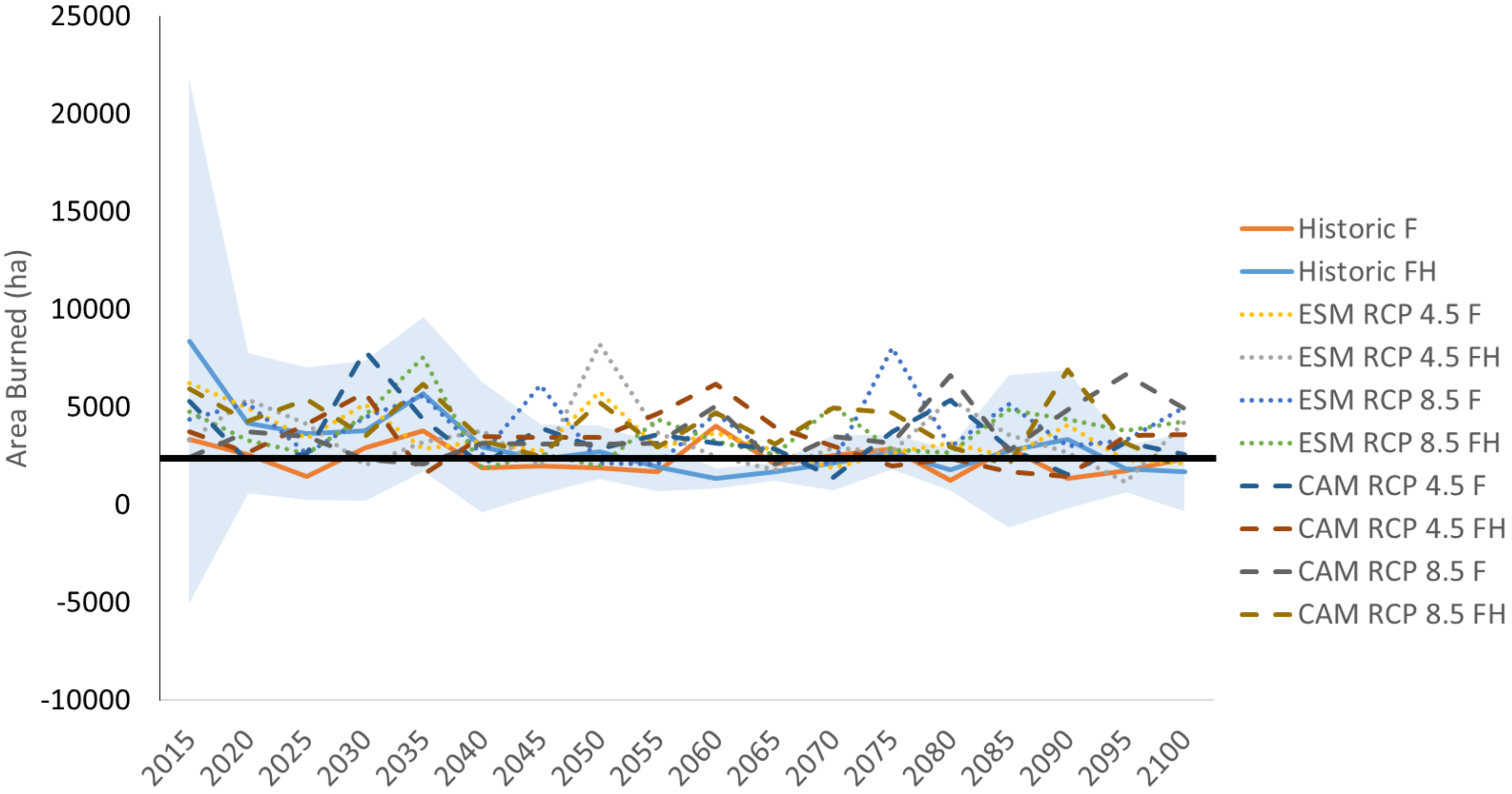


Figure 3.20. The simulated mean area burned per year with the standard deviation envelop of the replication simulations of historic climate with fire-harvest interacting.

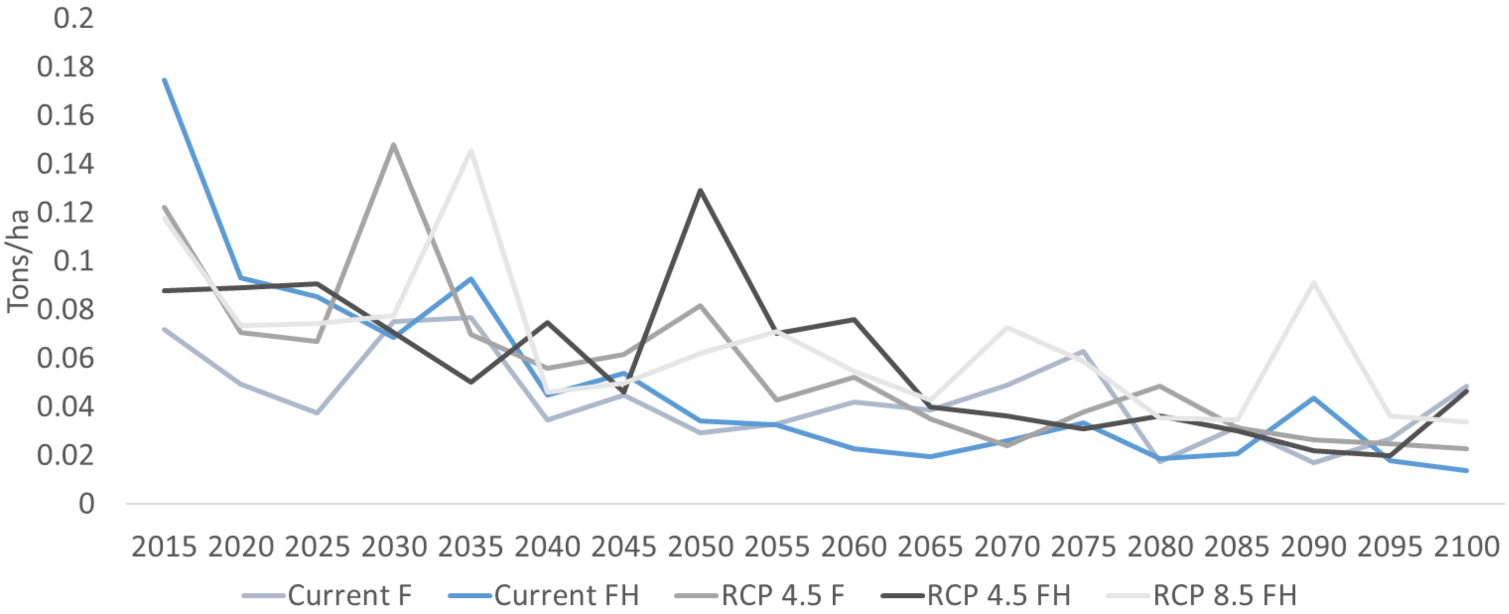


Figure 3.21. The carbon emissions of each simulated fire climate scenario.

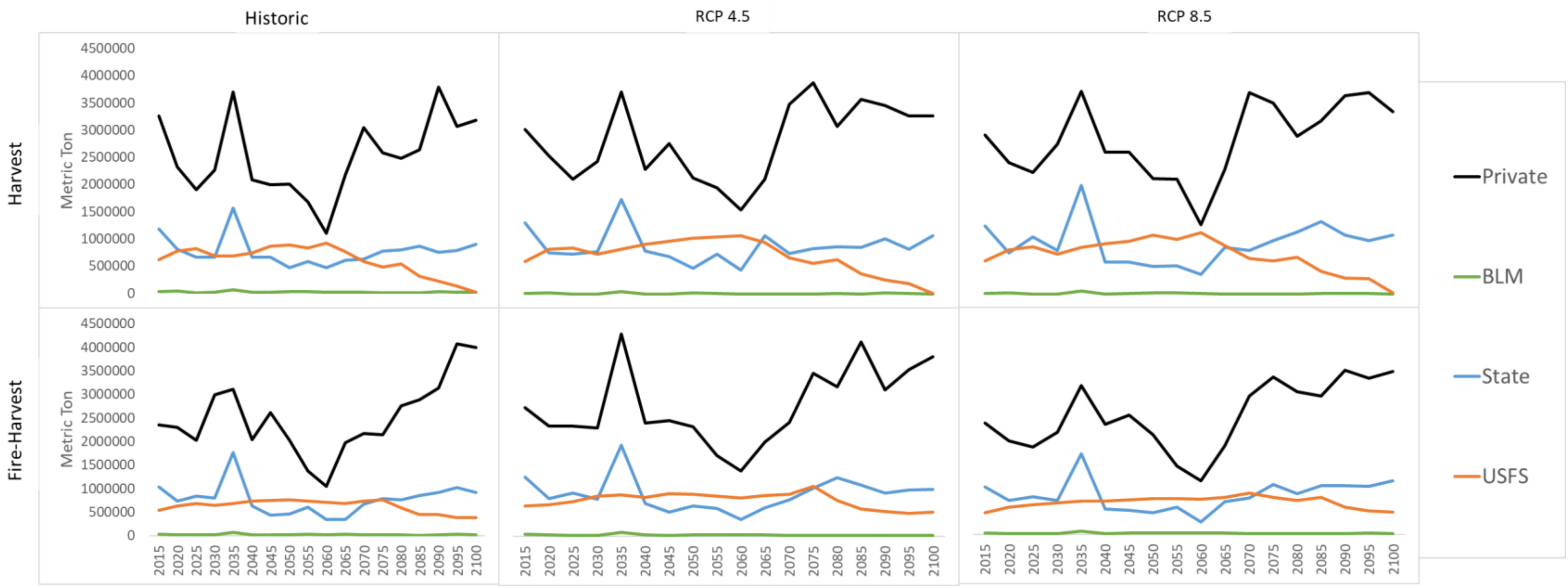


Figure 3.22. The harvest projections among all scenarios. The climate change scenarios are the mean of the two GCMs.

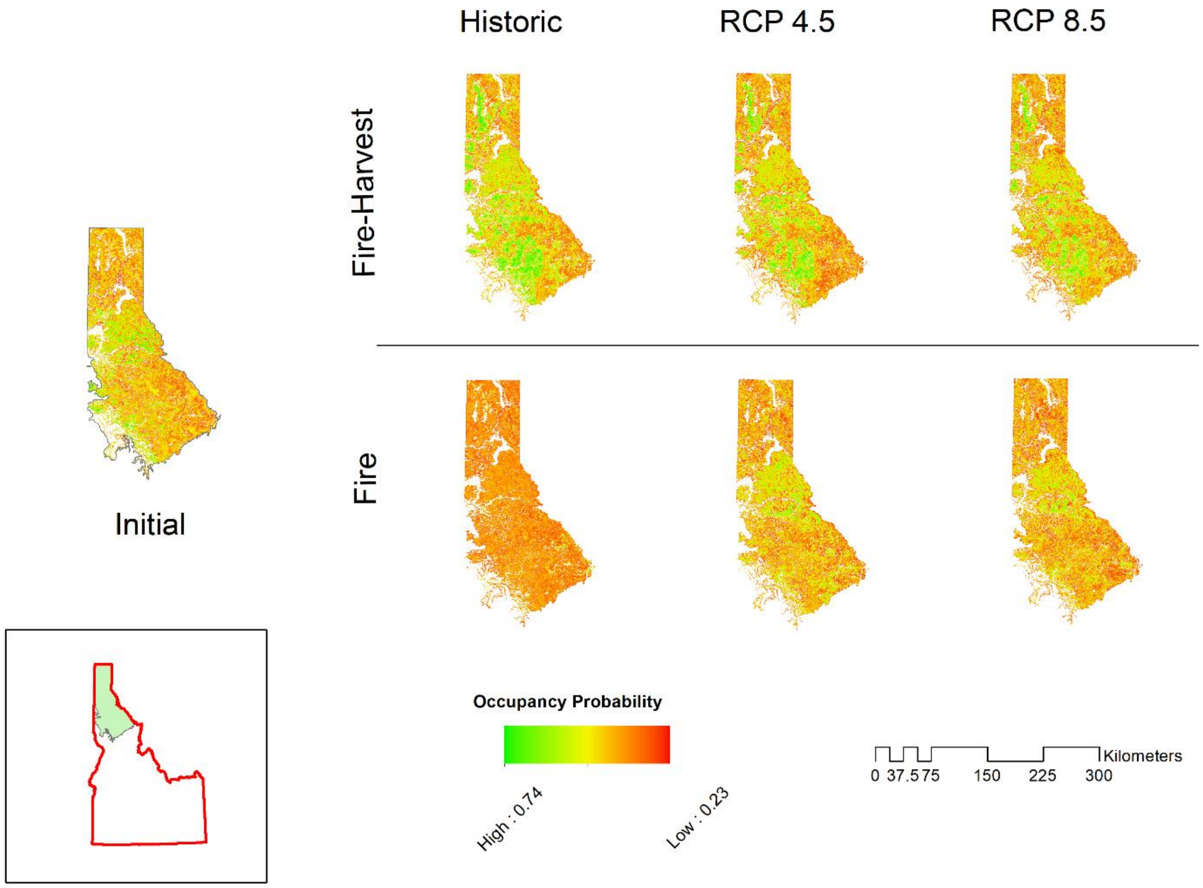


Figure 3.23. The Flammulated Owl habitat suitability maps at the end of the century.

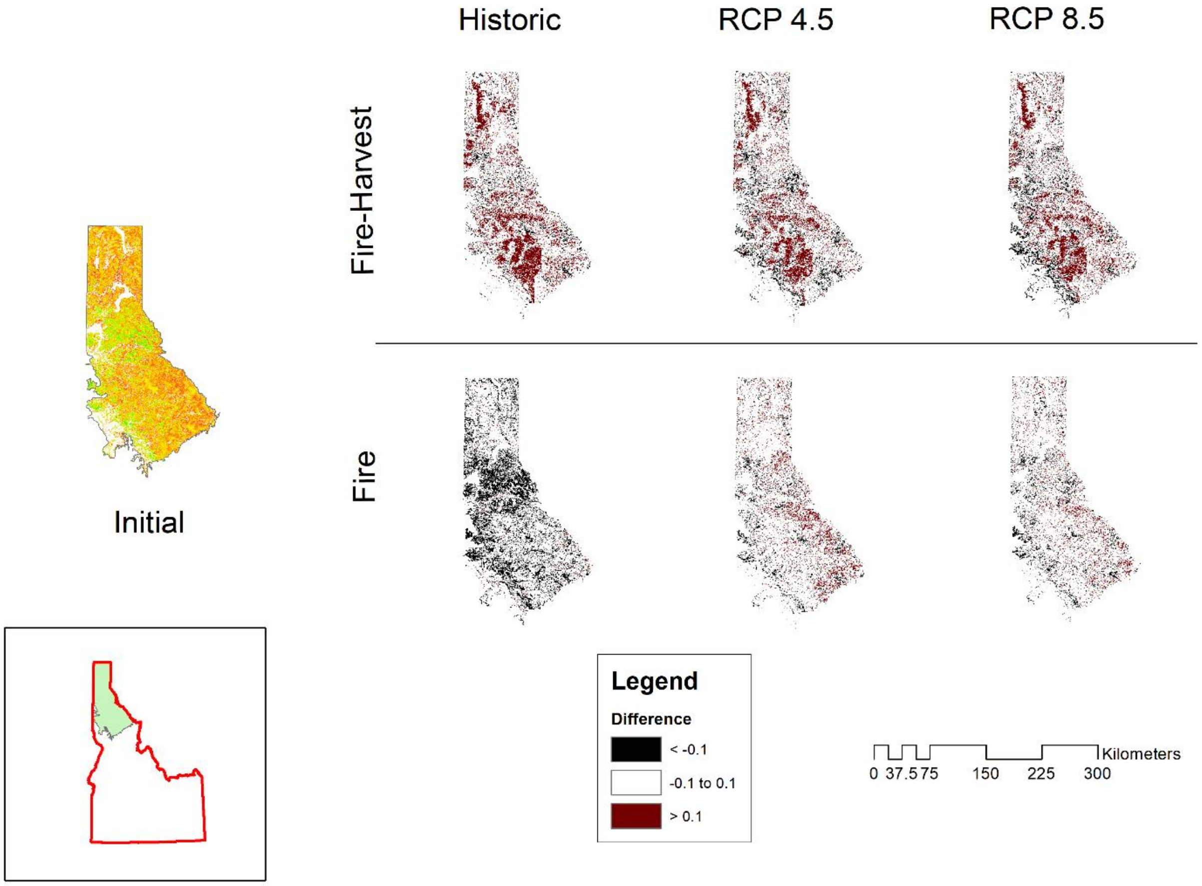


Figure 3.24. The Flammulated Owl difference in habitat suitability maps at the end of the century compared with the beginning.

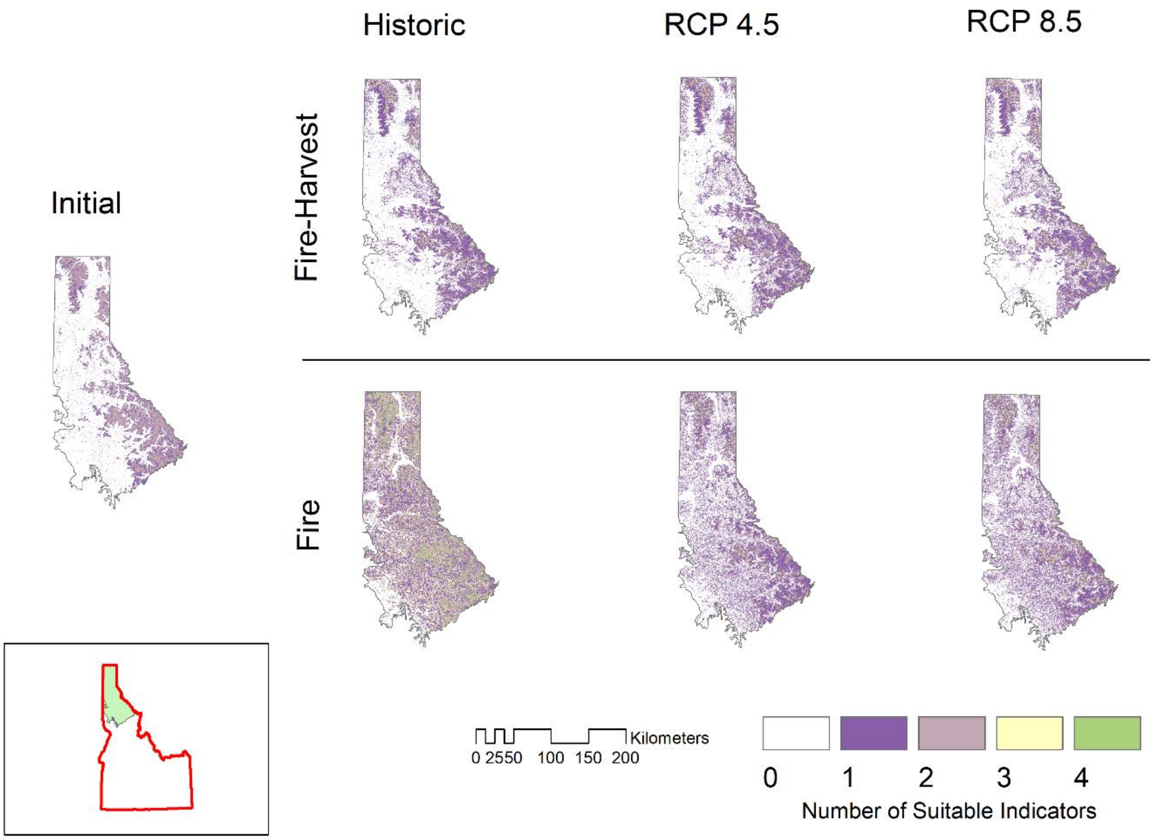


Figure 3.25. The American Three-toed Woodpecker potential niche predictions for the fire alone and fire-harvest interactions scenarios.

Appendix A: Supplemental information for Chapter 1

Appendix A.1. Supplemental results

High Emissions (Breeding Distribution Change by 2020 relative to 2000)	Low Emissions (Breeding Distribution Change by 2020 relative to 2000)	Hi Emissions (Wintering Distribution Change by 2020 relative to 2000)	Low Emissions (Wintering Distribution Change by 2020 relative to 2000)	High Emissions (Breeding Distribution Change by 2080 relative to 2000)	Low Emissions (Breeding Distribution change by 2080 relative to 2000)	High Emissions (Wintering Distribution) Change by 2080 relative to 2000)	Low Emissions (Wintering Distribution change by 2080 relative to 2000)	Audubon Climate Sensitivity Rank	Change in Productivity relative to year 2000 RCP 2.6	Change in Productivity relative to year 2000 RCP 4.5	Change in Productivity relative to year 2000 RCP 8.5	Sensitivity	Unadaptability	Exposure	Overall Vulnerability
36.6%	25.2%	29.8%	26.1%	-11.5%	-5.2%	23.7%	13.3%	STABLE				H	L	L	L
-70.1%	-72.8%	-40.9%	-43.8%	-73.3%	-79.3%	-44.3%	-52.7%	ENDANGERED				H	U	L	L
NA	NA	295.9%	242.1%	NA	NA	149.7%	173.8%	STABLE				H	L	H	L
NA	NA	0.9%	9.4%	NA	NA	6.7%	-2.9%	THREATENED	81%	89%	92%	H	L	L	L
14.8%	17.7%	-1.9%	-0.5%	50.7%	58.3%	1.0%	4.0%	STABLE				H	L	L	L
228.6%	263.7%	200.6%	175.9%	708.9%	595.0%	824.6%	453.7%	THREATENED				H	L	H	L
212.4%	183.4%	239.5%	251.9%	1559.5%	918.3%	1285.8%	931.2%	THREATENED				H	L	H	L
-29.2%	-5.1%	-25.5%	-27.1%	134.5%	77.9%	-20.4%	-53.0%	THREATENED				L	L	H	L
-7.6%	-3.4%	-6.9%	-4.9%	-18.9%	8.0%	-21.7%	-11.6%	THREATENED				H	L	H	L
49.2%	55.8%	32.9%	40.5%	153.2%	84.1%	161.5%	96.9%	STABLE				H	L	H	L
-15.8%	-10.8%	56.7%	56.7%	-89.9%	-70.1%	94.3%	70.8%	THREATENED				H	L	H	L
-4.5%	-16.7%	7.5%	7.5%	-51.2%	-51.8%	32.9%	26.6%	STABLE				H	L	L	L
-2.8%	-7.2%	11.5%	10.9%	-4.5%	-16.4%	17.6%	25.3%	STABLE				H	L	L	L
24.9%	26.6%	7.5%	9.1%	-7.3%	21.4%	4.5%	23.3%	STABLE				H	H	L	L
14.6%	14.9%	16.0%	18.2%	54.5%	45.8%	72.6%	58.9%	STABLE				H	L	L	L
-5.1%	-17.6%	17.4%	9.5%	5.4%	-6.2%	24.2%	17.2%	THREATENED				H	L	L	L
NA	NA	70.4%	94.4%	NA	NA	32.3%	50.8%	THREATENED				H	H	L	L
7.4%	7.9%	8.8%	8.4%	49.3%	50.5%	59.0%	50.1%	STABLE				H	L	L	L
8.1%	-16.9%	58.1%	65.5%	-62.2%	-57.2%	174.7%	140.0%	ENDANGERED				H	L	H	L
-27.3%	-33.5%	-6.1%	-23.5%	-98.1%	-82.0%	-68.9%	-48.9%	ENDANGERED				H	L	L	L
55.3%	-7.5%	92.8%	37.3%	-92.9%	-90.4%	-45.9%	-68.0%	ENDANGERED				H	H	L	L
44.4%	62.0%	21.4%	24.9%	-30.7%	53.0%	64.5%	60.8%	THREATENED				H	H	L	L

Species	Hi Emissions (GCM Avg) (Breeding Abundance % change)	Low Emissions (GCM Avg) (Breeding Abundance % change)	Hi Emissions (GCM Avg) (Breeding Abundance % change)	Low Emissions (GCM Avg) (Breeding Abundance % change)	Hi Emissions (GCM Avg) (Breeding Distribution) % Change	Low Emissions (GCM Avg) (Breeding Distribution % change)	High Emissions % Breeding Area Change	Low Emissions % Breeding Area Change	High Emissions Breeding Centroid Shift (km)	Low Emissions Breeding Centroid Shift (km)	Breeding Habitat Climate Response
Acorn Woodpecker											
American Three-toed Woodpecker							**46.8**	**29.6**	**909.8**	**532**	
Arizona Woodpecker											
Balck-backed Woodpecker							**18**	**25.2**	**931.2**	**1160**	
Downy woodpecker	-11.4	-11.4	3	6.6	0	0					
Gila Woodpecker											
Gilded Flicker											
Golden-fronted Woodpecker											
Hairy Woodpecker											
Ladder-backed Woodpecker											
Lewis's Woodpecker											
Northern Flicker											
Nuttall's Woodpecker											
Pileated woodpecker	2.5	3.6	50.5	26.1	0.6	0.6					
Red-bellied Woodpecker	14.3	14.3	200	145.5	44.1	32.1					
Red-breasted Sapsucker											
Red-cockaded Woodpecker											null
Red-headed Woodpecker	10.9	9.3	200	200	62.2	33.2					
Red-naped Sapsucker											
White-headed Woodpecker											
Williamson's Sapsucker											
Yellowbellied sapsucker	-77.2	-58.2	-70.6	-49.8	-34.5	-30					

Forecasted values represent the end of the century 2080-2100, unless otherwise noted

Bancroft et al. 2016
Foden et al. 2013
Langham et al. 2015
Matthews et al. 2011
Ralston and Kirchman 2013
Rodenhouse et al. 2008
Tremblay et al. 2018

Table A.1.1 The summarized woodpecker responses of the prediction studies reviewed. Only studies with reportable data are included.

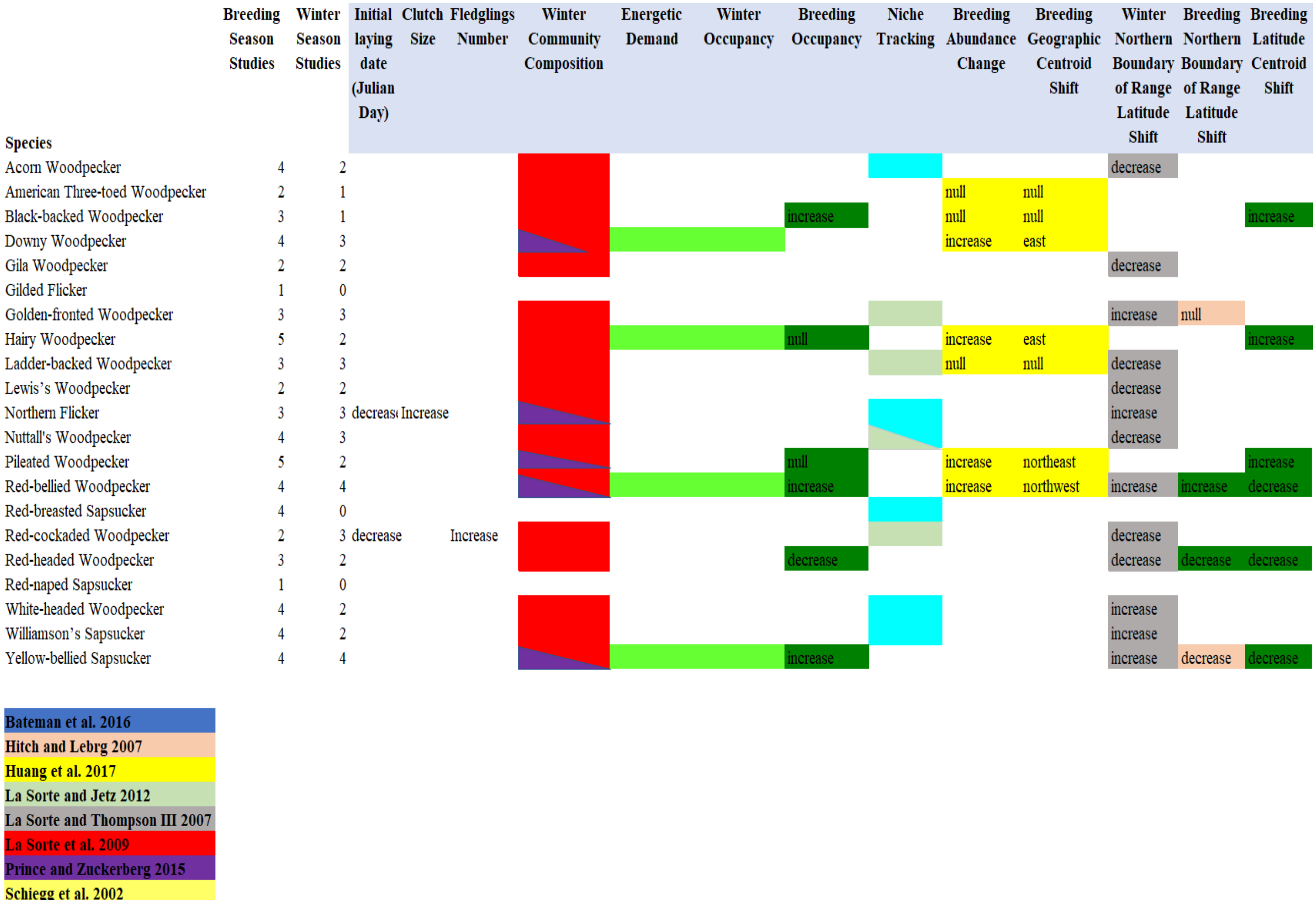
Paper	Year	Season	Temperature	Precipitation	Climate Averages	Climate Extremes/ Anomalies	Bioclimatic Variable (Aggregates)	Elevation	Latitude	Tree Species	Plant Functional Types	Land use change	Land Use/ cover	Trait Based Climate Sensitivit	Survey Effort	Forest Stand Characteristic
Bancroft et al.	2016	B		X							X	X				
Foden et al.	2013		X	X	X									X		
Langham et al.	2015	W,B					X									
Matthews et al.	2011	B	X	X	X			X		X						
Ralston and Kirchman	2013	B	X	X	X	X										
Rodenhouse et al.	2008	B	X	X	X			X		X						
Tremblay et al.	2018	B														X

Paper	Year	Season	Climatic Suitable Habitat/Range Distribution	Species Richness	Niche Flexibility	Abundance Response	Demographic Responses	Dispersal Response	Niche Temperature Gradient	Climate Sensitivity	Climate Exposure	Adaptive Capacity	Productivity
Bancroft et al.	2016	B					X	X					
Foden et al.	2013									X	X	X	
Langham et al.	2015	W,B	X										
Matthews et al.	2011	B	X										
Ralston and Kirchman	2013	B	X										
Rodenhouse et al.	2008	B	X			X							
Tremblay et al.	2018	B											X

Independent Variable
Response Variable
B, breeding season
W, wintering season

Table A.1.2. The summarized explanatory and response variables of the prediction studies reviewed.

Winter Latitude Centroid Shift (occurrence)	Winter Latitude Centroid Shift (abundance)	Breeding Southern Boundary of Range Latitude Shift	Direction of Breeding Distribution Shift	Breeding Geographic area change	Breeding Upper Elevation Range Limit Shifts	Breeding Elevation Centroid Shift	Breeding Lower Elevation Range Limit Shifts	Climate Suitability Trend (positive) (Value:number of	Climate Suitability Trend (negative) (Value:number of
decrease	decrease		east	expanding	downslope		null	1	3
									4
		decrease				downslope	upslope		11
			west	expanding	upslope		downslope	6	42
increase	decrease		northwest	expanding				1	
								1	
decrease	decrease		west	no change				1	
			east	no change	downslope	upslope	upslope	6	42
decrease	decrease		west	contracting				4	1
decrease	decrease		north	no change				7	2
increase	increase				null		downslope		
decrease	decrease		north	no change	null		null	1	
			northeast	expanding	null	downslope	downslope	24	15
increase	increase		northwest	expanding	upslope	upslope		27	4
			north	no change	null		upslope	2	1
decrease	decrease							4	2
increase	decrease		southwest	contracting	downslope	downslope		6	29
								9	
decrease	increase		north	no change	mixed		mixed	2	1
increase	increase		northeast	contracting	null		null	7	2
increase	increase	decrease	east	expanding		downslope	downslope	1	10



Species	Breeding Season Studies	Winter Season Studies	Initial laying date (Julian Day)	Clutch Size	Fledglings Number	Winter Community Composition	Energetic Demand	Winter Occupancy	Breeding Occupancy	Niche Tracking	Breeding Abundance Change	Breeding Geographic Centroid Shift	Winter Northern Boundary of Range Latitude Shift	Breeding Northern Boundary of Range Latitude Shift	Breeding Latitude Centroid Shift
Acorn Woodpecker	4	2				🟥				🟦			decrease		
American Three-toed Woodpecker	2	1				🟥					null	null			
Black-backed Woodpecker	3	1				🟥			increase		null	null			increase
Downy Woodpecker	4	3				🟥🟪	🟩	🟩			increase	east			
Gila Woodpecker	2	2				🟥							decrease		
Gilded Flicker	1	0													
Golden-fronted Woodpecker	3	3				🟥				▨			increase	null	
Hairy Woodpecker	5	2				🟥	🟩	🟩	null		increase	east			increase
Ladder-backed Woodpecker	3	3				🟥				▨	null	null	decrease		
Lewis's Woodpecker	2	2				🟥							decrease		
Northern Flicker	3	3	decreas	Increase		🟥🟪				🟦			increase		
Nuttall's Woodpecker	4	3				🟥				🟦▨			decrease		
Pileated Woodpecker	5	2				🟥🟪			null		increase	northeast			increase
Red-bellied Woodpecker	4	4				🟥🟪	🟩	🟩	increase		increase	northwest	increase	increase	decrease
Red-breasted Sapsucker	4	0								🟦					
Red-cockaded Woodpecker	2	3	decrease		Increase	🟥				▨			decrease		
Red-headed Woodpecker	3	2				🟥			decrease				decrease	decrease	decrease
Red-naped Sapsucker	1	0													
White-headed Woodpecker	4	2				🟥				🟦			increase		
Williamson's Sapsucker	4	2				🟥				🟦			increase		
Yellow-bellied Sapsucker	4	4				🟥🟪	🟩	🟩	increase				increase	decrease	decrease

Bateman et al. 2016
Hitch and Lebrg 2007
Huang et al. 2017
La Sorte and Jetz 2012
La Sorte and Thompson III 2007
La Sorte et al. 2009
Prince and Zuckerberg 2015
Schiegg et al. 2002

Table A.1.3. The summarized woodpecker responses of the observation studies reviewed.

Paper	Year	Temperature	Precipitation	Bioclimatic	Climatic Average	Climatic extreme/anomaly/ min/max	Ratio of Actual to Potential Evapo-transpiration	Snow depth	Individual Age	Individual Condition	Individual Breeding Experience	Migratory Strategy	Body Mass	Territory Type	Mean Home Range	Mean Clutch Size	Diet Bredth	Inbreeding Condition	Land use/ cover	Scale Dependent	Climatic Response was Considered Impliciety
Bateman et al.	2016	x	x	x	x	x													x		
Hitch and Lebrg	2007																				
Huang et al.	2017	x	x	x	x	x															
La Sorte and Jetz	2012	x				x															
La Sorte and Thompson III	2007																				x
La Sorte et al.	2009	x			x														x		
Prince and Zuckerberg	2015	x				x						x	x								
Schiegg et al.	2002	x	x		x	x			x		x							x			
Stephens et al.	2016	x	x		x	x	x														
Tingley et al.	2009																				x
Tingley et al.	2012	x	x		x							x	x	x	x	x	x				
Wiebe and Gerstmar	2010	x							x	x										x	
Zuckerberg et al.	2009																				x
Zuckerberg et al.	2011	x	x			x		x													

Table A.1.4. The summarized explanatory variables of the observation studies reviewed.

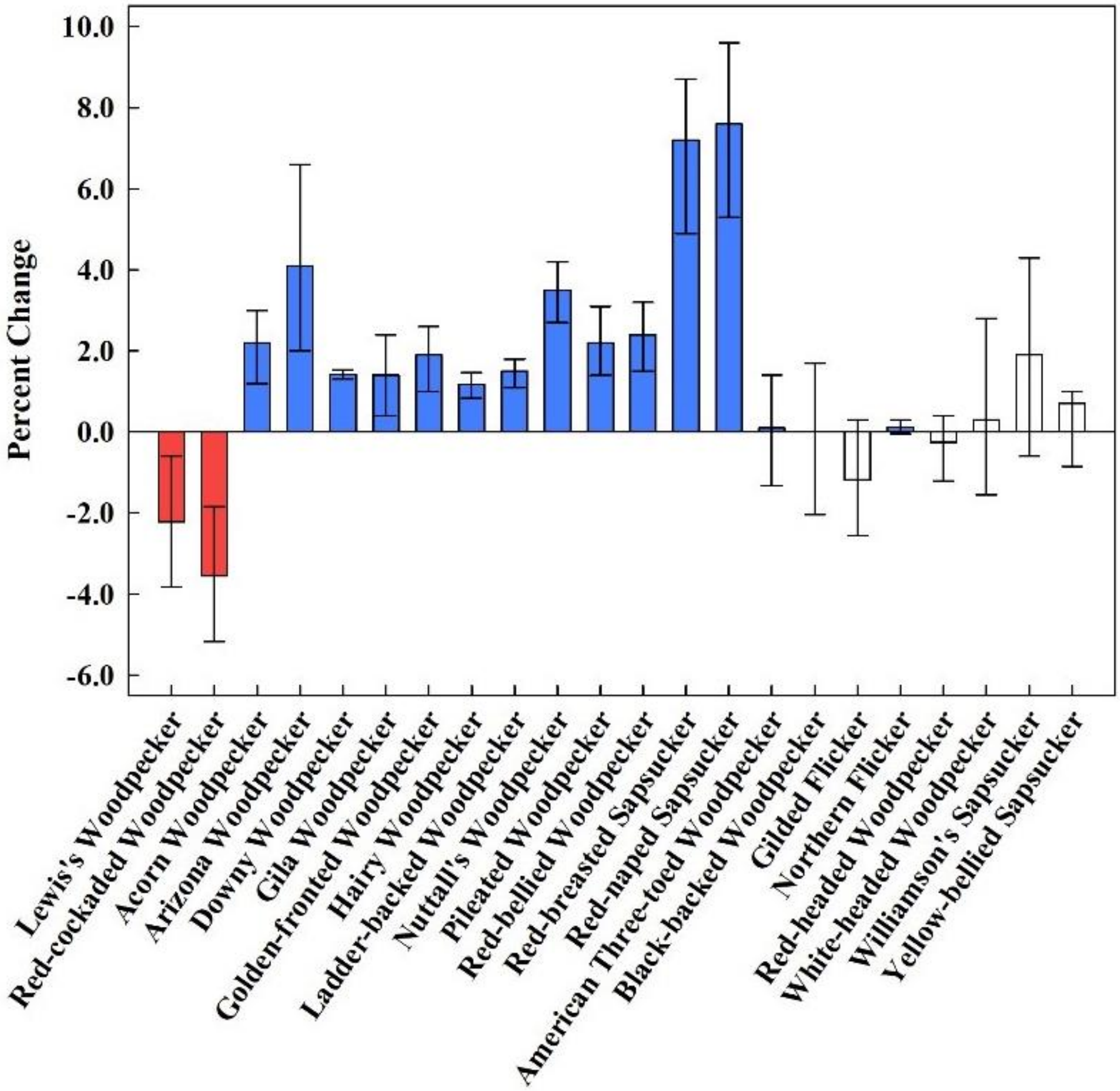


Figure A.1.1. The median percent abundance change per year of North American woodpecker winter populations from 1966 to 2013 with 95% CI. Red and blue bars represent species with significant declines and increases, respectively. Data from Soykan et al. (2016).

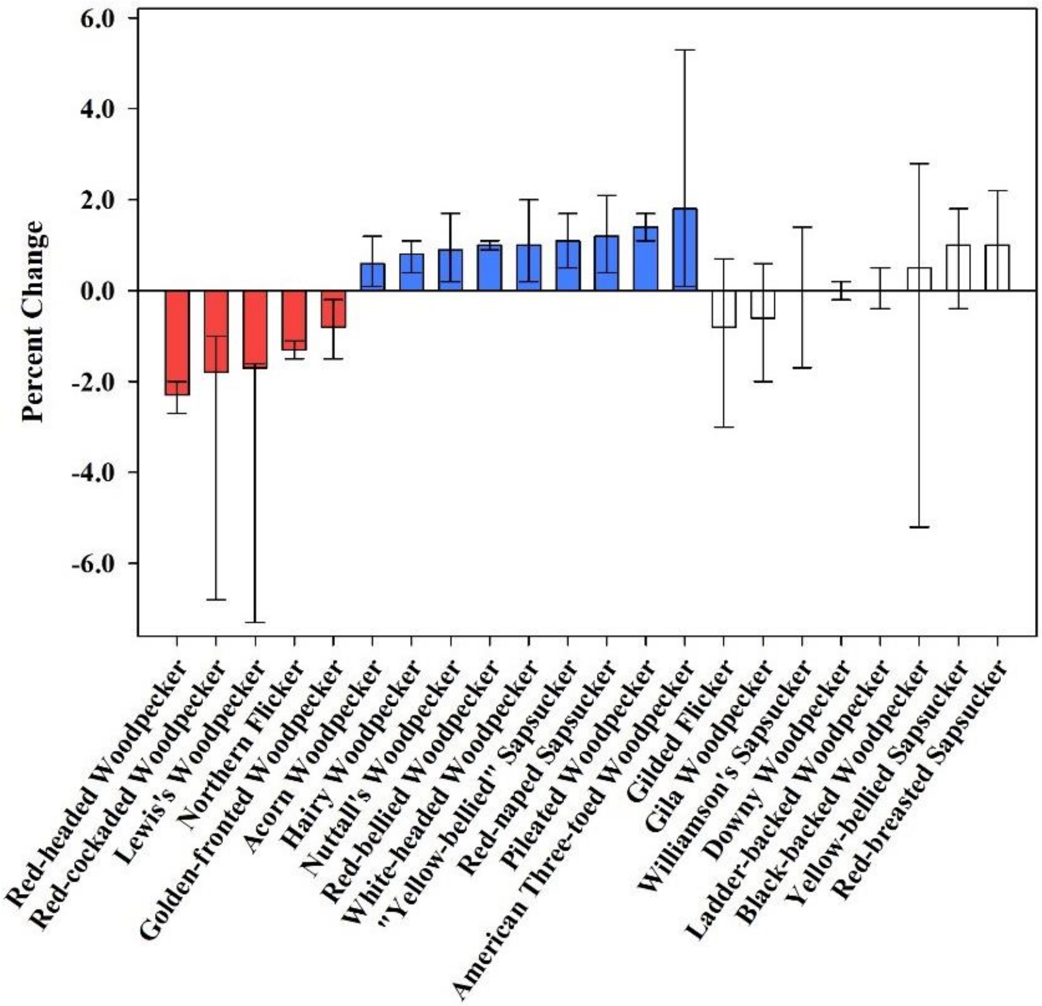


Figure A.1.2. The precision weighted mean percent change of North American woodpecker breeding populations from 1966 to 2015 with 97.5% CI. Red and blue bars represent species with significant declines and increases, respectively. The “Yellow-bellied Sapsucker” is representative of the Yellow-bellied Sapsucker and Red-naped Sapsucker prior to being considered distinct species. Data from Sauer et al. (2017), Cavity Nesting Species Group survey wide results of the Breeding Bird Survey.

Appendix B: Supplemental information for Chapter 2

Appendix B.1.1 Supplemental methods

General Random Forest implementation

We conducted three Random Forest (RF) (1) classification analyses to predict the level of canopy cover (Flammulated Owl), the forest cover type (Flammulated Owl and American Three-toed Woodpecker), and the snag presence (American Three-toed Woodpecker) of forested grid cells across the study area for the respective studies. The RF was implemented in Rstudio (2) with R (v. 3.5.1) (3) using the *randomForest* package (4). The algorithm is optimized via three parameters *ntree, mtry*, and *nodesize* (Table B1.3.1). The parameter *ntree* is the number of trees grown from a bootstrapped sample and was determined based on a stabilized prediction error; *mtry* is the number of predictors randomly tested at each node, which was determined using the randomForest's *tuneRF* function; *nodesize* is the minimal size (i.e., cases) of the terminal node. The *nodesize* was set to values >1 to improve model computation given the large sample size, which has minimal effect on accuracy for large datasets (1). Random Forest produces an unbiased error estimate (out-of-box (OOB) error), enabling model validation without an independent dataset (1,5).

Canopy cover analysis

We used a RF classification analysis to predict the level of canopy cover of each forested grid cell across the study area. There were four canopy cover classes corresponding to the parameterization described in (6). We trained the model using 200 m gridded data of the Contiguous U.S. Biomass Map (biomass) (7), elevation (8), aspect, slope, and landform class (a derivative of topographic position index) as predictor variables with the LANDFIRE 2008 Forest Canopy Cover (9) data as the dependent variable. Aspect, slope, elevation, and landform index were included because of their associations with ecosystem characteristics (10,11). Landform index is a classification system based on the topographic position index (12,13) (derived from elevation and slope), which indicates the type of terrain (e.g., canyon, mid slope, or ridge) present in each grid cell. The response variable canopy cover class was derived from the LANDFIRE aggregated into four canopy cover classes (1 = 0-10%, 2 = 11-40%, 3 = 41-70%, and 4 = 71-100%) with the category's midpoint value assigned to a grid cell (6). The canopy cover RF model OOB error was 45.1% with the most accurately predicted class being *medium* and least being *high* (Table B1.2.3). The strongest predictor of canopy cover class was biomass (Fig B1.2.1).

Forest cover type analysis

We used a RF classification analysis to predict the 11 cover classes corresponding to the parameterization described in (6). We trained the model using 200 m gridded data of elevation (8), aspect, slope, landform class, soil parameters (field capacity, available water, and wilting point) (14), and tree species biomass totals as predictor variables with the LANDFIRE Existing Vegetation Type data (15) as the dependent variable. Elevation, aspect, slope, and landform have been used in similar modeling approaches (16,17). Soil characteristic were included because of their association with forest cover types of northern Idaho from initial modeling (data not shown) and association with biomass (18). The tree species biomass totals were estimated from the LANDIS-II spin-up models. These data were included because they are outputs of LANDIS-II allowing for model inclusion in future scenario runs. However, unlike the canopy cover model that trained on a dataset independent of LANDIS-II outputs, there was no alternative dataset that provided the same level of species-biomass totals per grid cell. However, these data were directly informed from Forest Inventory Analysis data (19) using a landscape "seeding" process (20) and were verified. The final land cover map used in the Flammulated Owl model was based on only three land cover types (Douglas fir, ponderosa pine, and vegetative non-forest) (6), therefore we were most concerned with the prediction of these cover types. The land cover RF model OOB error was 9.4% with the (Table B1.2.4). The strongest predictors of land cover type were Douglas fir (Dfir), grand fir (Gfir), and elevation (DEM) (Fig B1.2.2).

Snag presence analyses

We used a RF classification analysis to predict the snag presence. Each data point in the RF training set represented a Forest Inventory Analysis (FIA) plot within the study area coded as the appropriate snag density being present/absent. The covariate data associated with each data point included elevation (8), aspect, slope, average forest age, and total aboveground live biomass (AGB). The forest age and AGB were derived from the FIA plot data. The snag RF model OOB error was 25.7% with the (Table B1.2.5). The strongest predictors of land cover type were AGB (AboveLiveB) and forest age (AGE) (Fig B1.2.3). A RF model with aboveground dead biomass (an alternative to live biomass) may have provided a better fit, however the LANDIS-II succession extension we implemented did not output spatially explicit maps of aboveground dead biomass.

Appendix B.1.2. Supplemental figures and tables

Table B.1.2.1. Random Forest parameters used to optimize performance

Parameter	**Canopy Cover**	**Forest Cover**	**Snag Presence**
ntree	1000	1000	10000
mtry	2		1
nodesize	5		1

Table B.1.2.2. Explanatory variables for the canopy cover Random Forest model

Variable	**Rational**	**Value**
aspect	niche differentiation	degrees
elevation	niche differentiation	elevation in meters
slope	niche differentiation	degrees
biomass	proxy for tree density and Leaf Area Index	grams/m^2
landform	niche differentiation	index value

Table B.1.2.3. The confusion matrix of the Random Forest canopy cover classification model

	High	**Low**	**Medium**	**Medium-Low**	**Class Error**
High	9886	289	18739	1577	0.68
Low	199	8361	4199	7395	0.59
Medium	6860	2149	62336	11714	0.25
Medium-Low	892	5311	21885	18208	0.61

Table B.1.2.4. The confusion matrix of the Random Forest land cover classification model

	Anthro-pogenic	Non-Forest	Riparian	Aspen	Douglas-fir	Lodgepole	Ponderosa Pine	Larch	Mix-conifer	Spruce-Fir	Barren	Class Error
Anthropogenic	8953	1833	524	0	0	57	149	0	0	1	0	0.22
Non-forest	1711	18081	1818	2	0	430	238	1	0	1098	0	0.23
Riparian	463	1924	4343	2	0	37	61	2	0	0	0	0.36
Aspen	2	29	2	7	0	0	0	0	0	0	0	0.83
Douglas-fir	15	38	4	0	44739	10	123	0	1108	246	0	0.03
Lodgepole	42	767	106	0	0	1492	11	0	0	483	0	0.49
Ponderosa Pine	226	474	237	0	450	6	1918	0	38	3	0	0.43
Larch	6	58	9	0	0	0	0	2	0	4	0	0.97
Mix-conifer	5	55	4	0	865	1	10	0	56447	316	0	0.02
Spruce-Fir	4	255	0	0	125	10	0	0	306	27120	0	0.03
Barren	1	75	11	0	0	1	0	0	0	5	1	0.99

Table B.1.2.5. The confusion matrix of the Random Forest snag classification model

	No Snags	**Snags**	**Error Rate**
No Snags	681	152	18.2%
Snags	216	374	36.6%

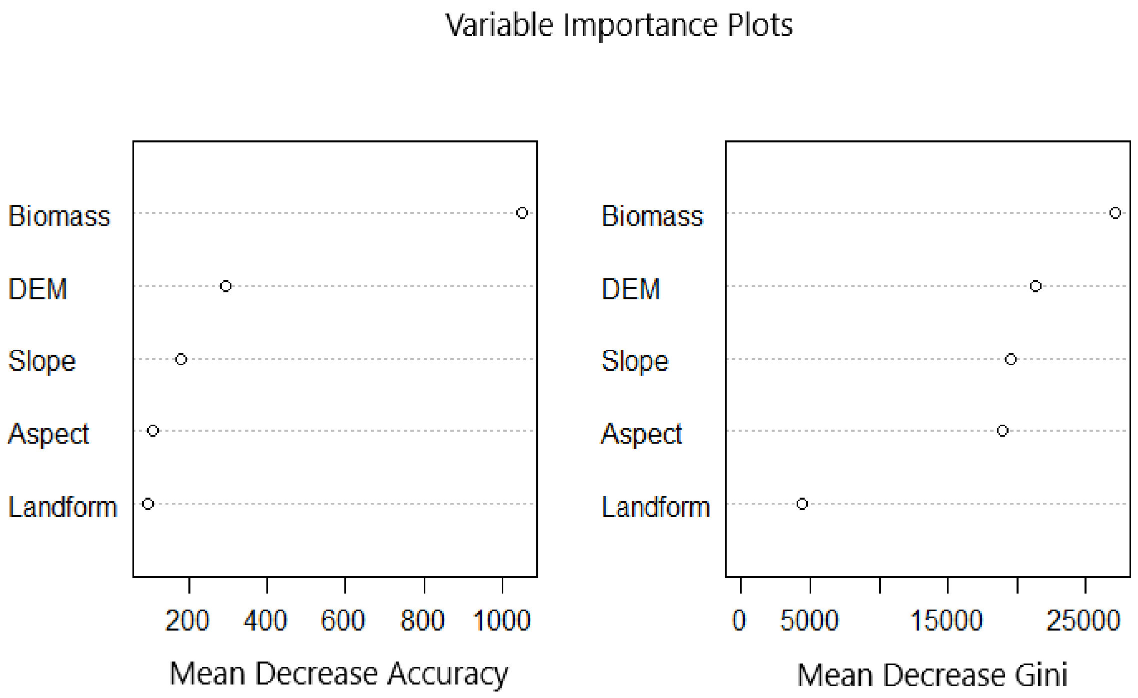


Figure B.1.2.1. The variable importance plots for the canopy cover Random Forest analysis

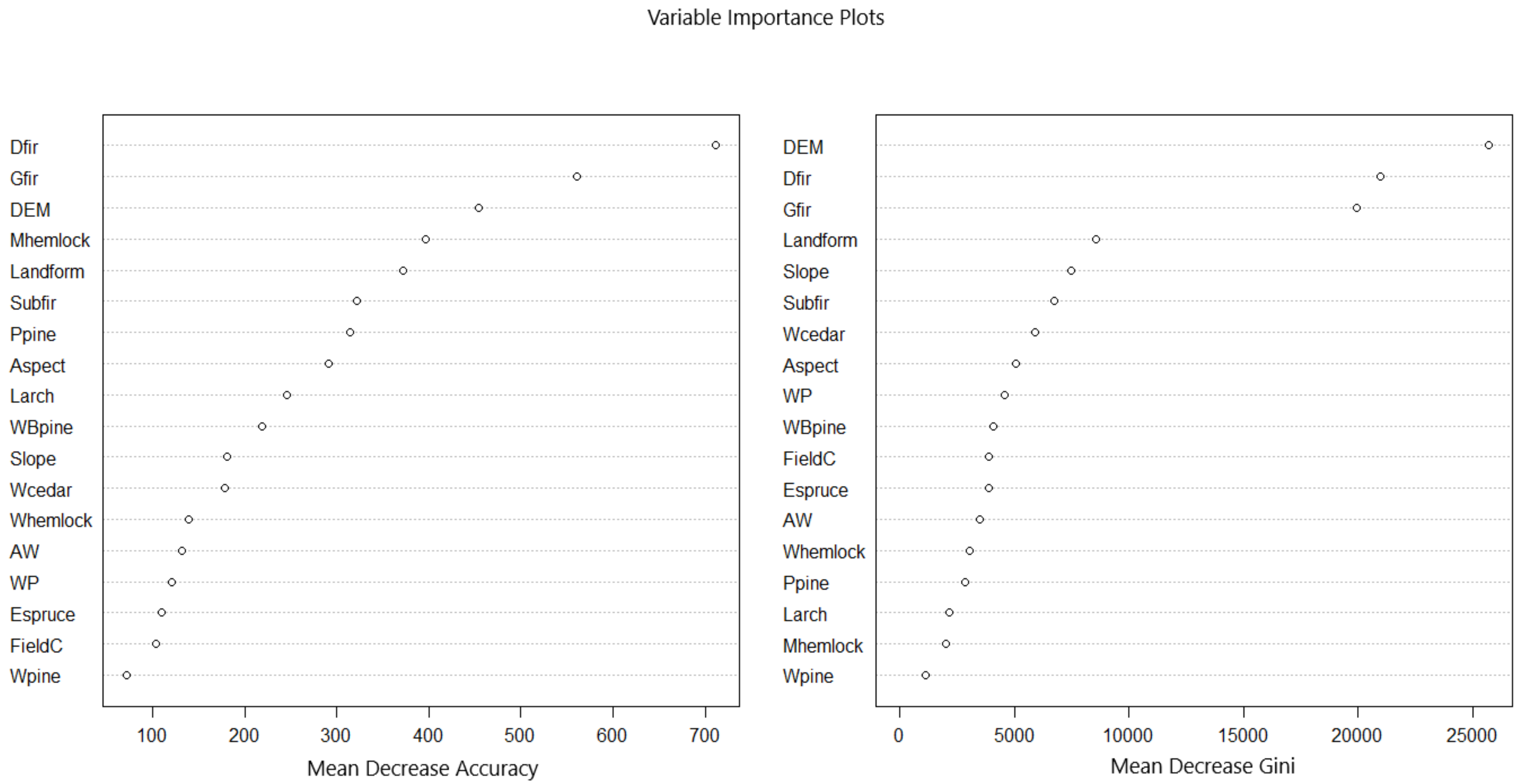


Figure B.1.2.2. The variable importance plots for the land cover Random Forest analysis. AW= available water (soil), DEM=Digital Elevation Model, *Dfir= *Pseudotsuga menziesii*, *Espruce= *Picea engelmannii*, FieldC= field capacity (soil), *Gfir= *Abies grandis*, Landform= topographic position index, *Larch= *Larix occidentalis*, *Mhemlock= *Tsuga mertensiana*, *Ppine= *Pinus ponderosa*, *Subfir= *Abies lasiocarpa*, *WBpine= *Pinus albicaulis*, *Wcedar= *Thuja plicata*, *Whemlock= *Tsuga heterophylla*, WP= wilting point (soil), *Wpine= *Pinus albicaulis*. *variables that are outputs of LANDIS-II

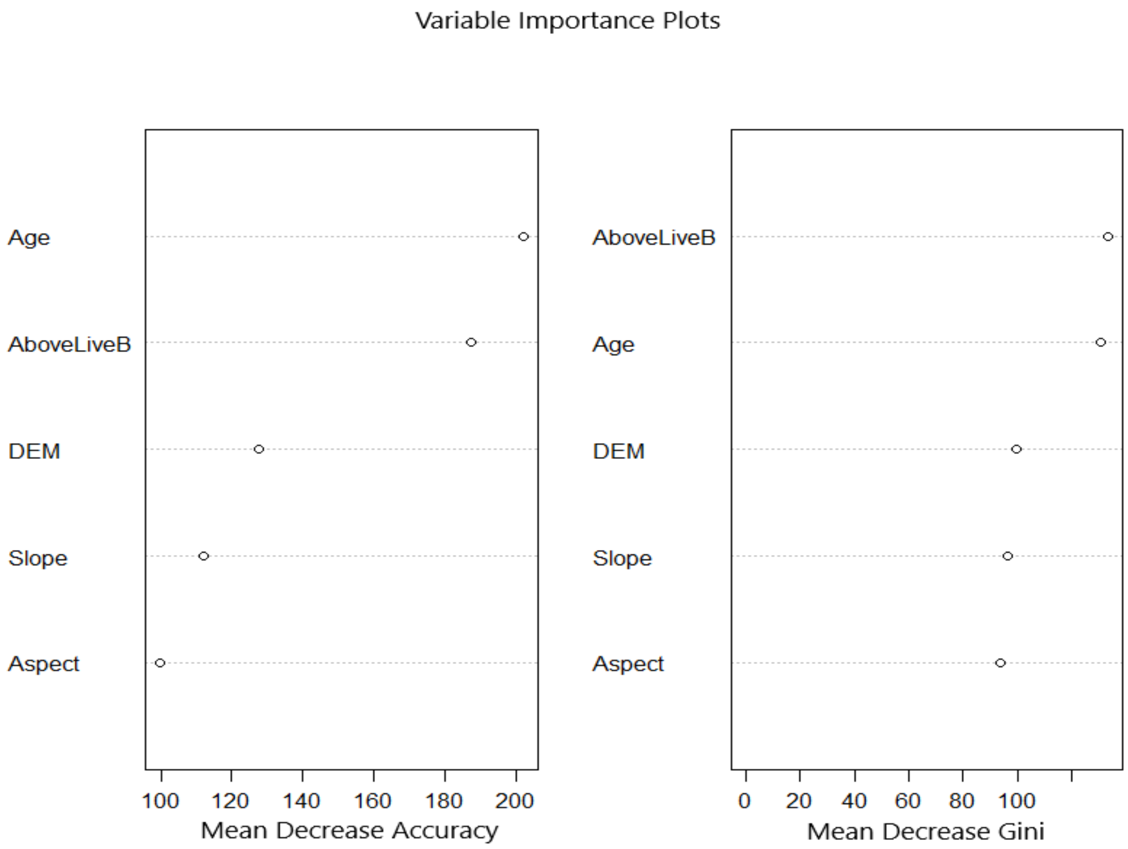


Figure B.1.2.3. The variable importance plots for the snag Random Forest analysis

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Appendix B.2. Supplemental figures and tables

Table B.2.1. The summary statistics of the base model and LANDIS-II Flammulated Owl occupancy predictions of the study area.

Statistic	Base Model	LANDIS-II
Mean	43%	43%
Minimum	23%	23%
Maximum	74%	74%

Table B.2.2 The summary niche model occupancy values associated with the observed Flammulated Owl locations.

Statistic	Base Model	LANDIS-II	LANDIS-II Buffers
Mean	47%	46%	44%
Minimum	34%	33%	37%
Maximum	62%	62%	51%
Count	28	28	28

Table B.2.3 The percent distribution of forested area among the different American Three-toed Woodpecker indicators for the *very good* and *good* suitability levels.

Indicator	Percent of Landscape Very Good	Percent of Landscape Good
Timber	3.5	3.5
Elevation	31.0	31.0
Fire	12.9	12.9
Snags	4.4	4.4
Stand Age	1.4	6.9
Forest Type	18.0	84.0
Continuous Forest	0.0	0.0

Table B.2.4. The percent distribution of forested area among the total number of indicators associated with the suitability level *very good* and *good*.

Number of Indicators	Percent of area very good	Percent of area good
0	61.2%	12.6%
1	15.7%	50.4%
2	15.1%	23.4%
3	6.8%	10.1%
4	0.8%	2.3%
5	0.2%	1.0%
6	0.1%	0.2%

Table B.2.5. The area (ha) of the landscape associated with each indicator code depending on the suitability criteria (*very good* or *good*).

Indicator Code	Area Very Good	Index Very Good	Area Good	Index Good
0	1681652	0	347200	0
20	2788	1	1303504	1
300			3016	1
320			30720	2
4000	32804	1	2788	1
4020	408	2	23748	2
4300			172	2
4320			6504	3
50000	107544	1	948	1
50020	548	2	105328	2
50300			32	2
50320			1784	3
54000	2720	2	8	2
54020	112	3	2288	3
54320			536	4

600000	267048	1	74132	1
600020	295120	2	471772	2
600300			24	2
600320			16240	3
604000	7368	2	3464	2
604020	20224	3	9172	3
604320			14956	4
650000	72996	2	4452	2
650020	145136	3	205760	3
650300			28	3
650320			7892	4
654000	1440	3	208	3
654020	10276	4	3332	4
654320			8176	5
7000000	21436	1		
7000020	28	2		
7000300	16112	2	2528	2
7000320	12	3	35060	3
7004000	14360	2		
7004020	56	3		
7004300	9944	3	980	3
7004320	48	4	23428	4
7050000	1300	2		
7050020	12	3		
7050300	740	3	12	3
7050320	4	4	2044	4
7054000	1268	3		
7054020	16	4		
7054300	452	4	12	4
7054320	4	5	1728	5
7600000	3388	2		
7600020	3888	3		
7600300	1704	3	40	3
7600320	1228	4	10168	4
7604000	2016	3		
7604020	6884	4		
7604300	1020	4	12	4
7604320	2700	5	12608	5
7650000	1108	3		
7650020	1820	4		
7650300	700	4	12	4
7650320	556	5	4172	5

7654000	664	4		
7654020	3044	5		
7654300	364	5	4	5
7654320	1476	6	5544	6

Table B.2.6. The number of observation point buffers of each habitat suitability level that is dominated by the specified number of indicators.

Number of Indicators	Very Good	Good
0	31	4
1	4	26
2	7	12
3	0	0
4	0	0
5	0	0
6	0	0
7	0	0

Table B.2.7. The number of observation buffers of each habitat suitability level that contain a minimum of one grid cell with the number of indicators.

Number of Indicators	Very Good	Good
0	8	0
1	9	7
2	14	5
3	6	14
4	5	9
5	0	7
6	0	0
7	0	0

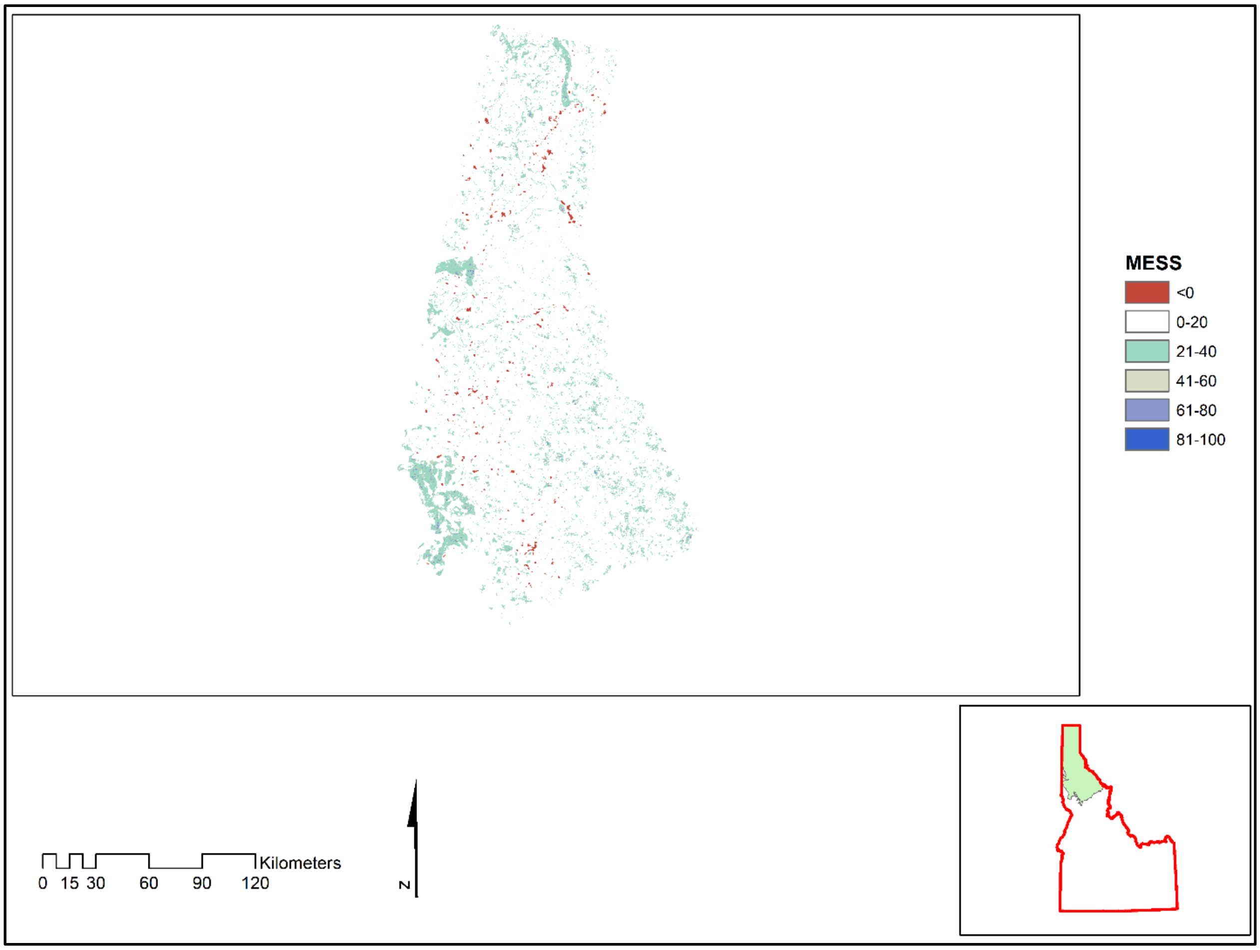

Figure B.2.1. The multivariate environmental similarity surface of the study area. Values <0 indicate locations that are novel and not present in the original region used to inform the niche suitability model. As a location approaches 1 the application predictor values are all equal to the median value in the training area.

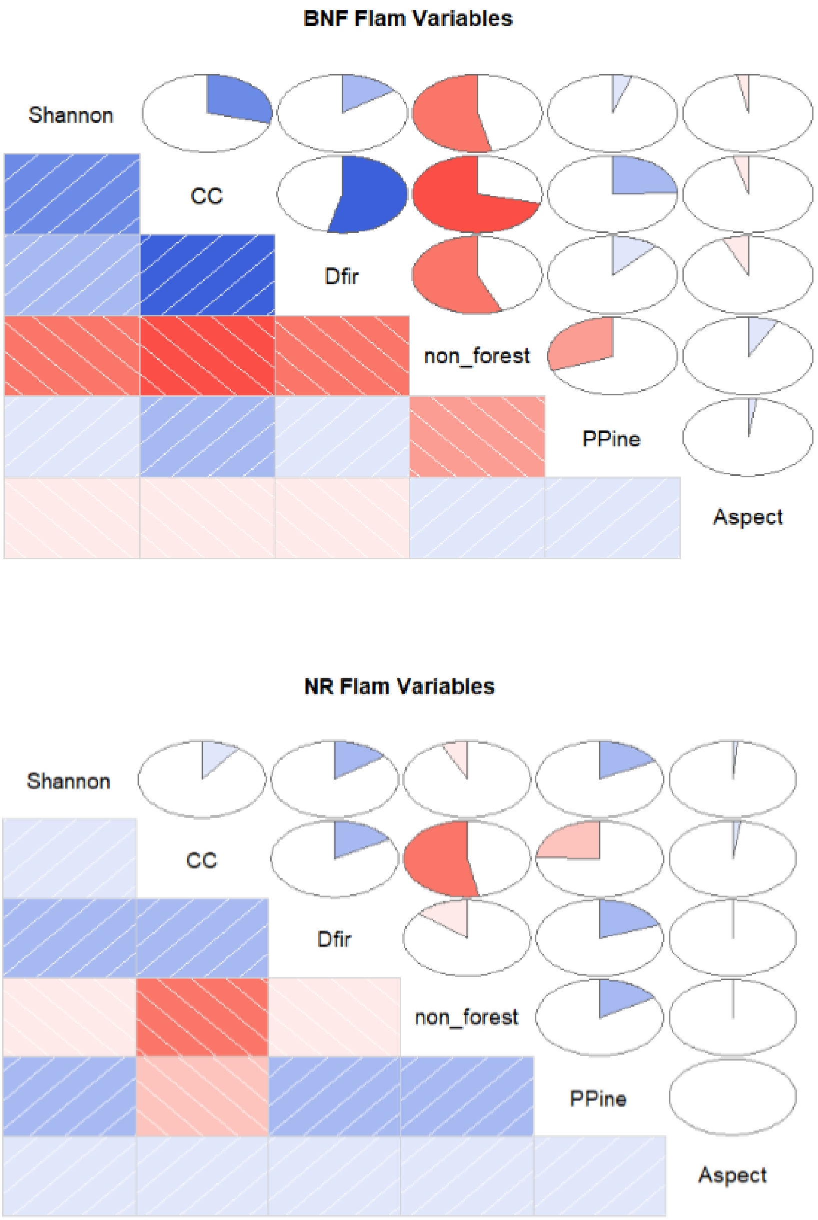

Figure B.2.2. The covarience structure of the Flammulated Owl realized niche model explanatory variables in the training and application region. Intensity of the color or size of the pie indicate strength while red and blue indicate negative or positive relationships, respectively.

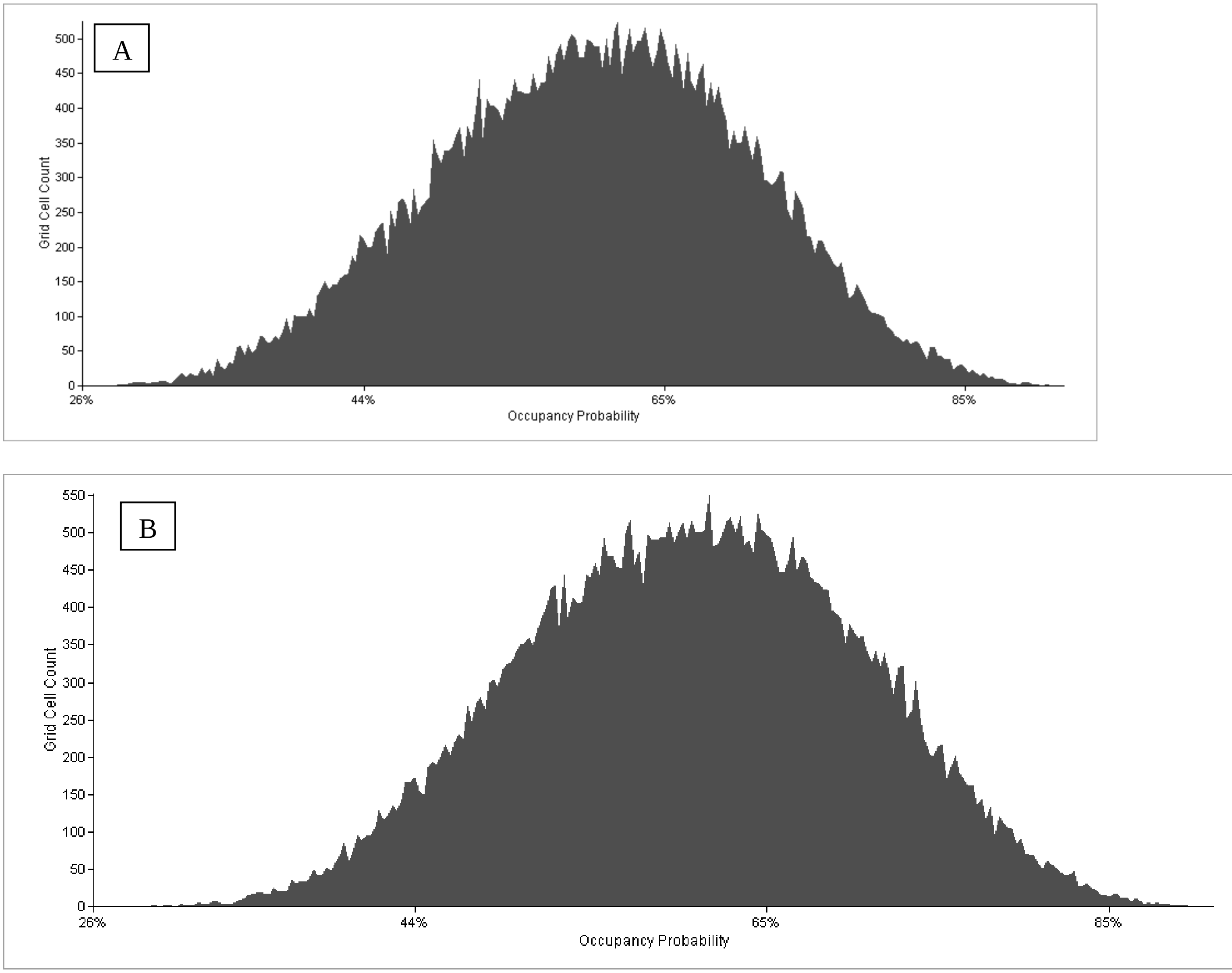

Figure B.2.3. Histogram of predicted occupancy probability values: A) Base model B) LANDIS-II model

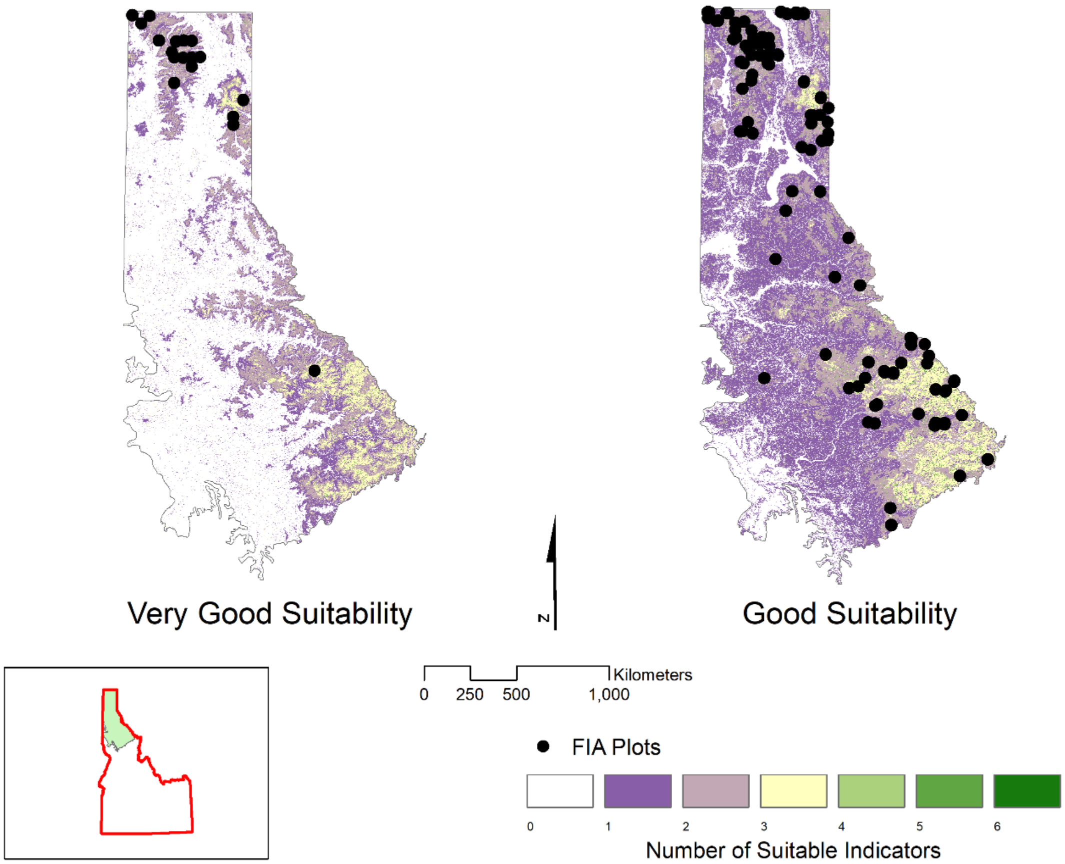

Figure B.2.4. The American Three-toed Woodpecker habitat suitability map with the corresponding FIA plots that meet the criteria of *very good* and *good* suitability.

Appendix C: Supplemental information for Chapter 3

Table C.1.1. The basic LANDIS-II parameters of the tree species.

Species	Longevity	Sexual Maturity	Shade Tolerance	Fire Tolerance	Seed Dispersal Effective	Seed Dispersal Maximum	Vegetative Reproduction Probability	Sprout Age Minimum	Sprout Age Maximum	Post-fire Regeneration
Abies grandis	230	20	4	3	50	244	0	0	0	none
Abies lasiocarpa	140	20	4	1	30	80	0.05	0	0	none
Larix occidentalis	320	20	1	5	122	250	0	0	0	none
Picea engelmannii	500	25	3	2	100	244	0	0	0	none
Pinus albicaulis	500	20	3	3	2	22000	0	0	0	none
Pinus contorta	400	10	1	4	61	244	0	0	0	serotiny
Pinus monticola	500	7	2	3	50	800	0	0	0	none
Pinus ponderosa	380	7	2	5	40	200	0	0	0	none
Pseudotsuga menziesii	650	13	2	4	80	244	0	0	0	none
Thuja plicata	330	6	4	3	30	122	0.6	5	300	none
Tsuga heterophylla	350	25	5	2	120	1158	0.05	5	10	none
Tsuga mertensiana	200	20	5	1	38	120	0.05	10	180	none

Table C.1.2. The LANDIS-II Net Ecosystem Carbon Nitrogen extension species parameter table.

Species	Functional Type	Nitrogen Fixer	GDD Min	GDD Max	Minimum January Temperature	Max Drought	Leaf Longevity	Epicormic Repro-duction	Leaf Lignin %	Fine Root Lignin %	Wood Lignin %	Coarse Root Lignin	Leaf C/N ratio	Fine Root C/N ratio	Wood C/N ratio	Coarse Root C/N ratio	Litter C/N ratio
Abies grandis	2	N	390	2915	-10	0.7	7	N	0.25	0.22	0.3	0.21	42 58	50	0	200	93
Abies lasiocarpa	1	N	105	3100	-29	0.5	7	N	0.25	0.198	0.28	0.21	42	80.6	500	200	87.3
Larix occidentalis	1	N	445	2000	-12	0.5	1	N	0.12	0.22	0.27	0.21	29.1	58	500	200	93
Picea engelmannii	1	N	105	2375	-14	0.5	6	N	0.25	0.19	0.28	0.21	42	68.4	500	200	88.5
Pinus albicaulis	1	N	110	3170	-13	0.5	8	N	0.25	0.22	0.3	0.21	45.4	58	500	200	94
Pinus contorta	1	N	110	3080	-29	0.7	8	N	0.16	0.21	0.26	0.21	41.7	90.9	500	200	100
Pinus monticola	2	N	345	6905	-12	0.9	6	N	0.25	0.22	0.26	0.21	42	58	500	200	77.1
Pinus ponderosa	1	N	110	3170	-13	0.5	8	N	0.25	0.22	0.3	0.21	45.4	58	500	200	94
Pseudotsuga menziesii	2	N	105	6800	-14	0.7	7	N	0.25	0.22	0.27	0.21	43.3	80.6	500	200	68.9
Thuja plicata	2	N	205	2725	-14	0.5	9	N	0.25	0.22	0.32	0.21	42	58	500	200	100
Tsuga heterophylla	1	N	205	2770	-13	0.5	7	N	0.25	0.22	0.29	0.21	50	58	500	200	84
Tsuga mertensiana	1	N	205	2135	-12	0.5	7	N	0.25	0.22	0.27	0.21	41.7	58	500	200	93

Table C.1.3. The LANDIS-II Net Ecosystem Carbon Nitrogen extension species functional groupings parameter table.

Name	Index Code	PPDF1 T-Mean	PPDF2 T-Max	PPDF3 T-shape	PPDF4 T-shape	PCFRAC Leaf	BTOLAI	KLAI	MAXLAI	PPRPTS2	PPRPTS2	Wood Decay Rate	Monthly Wood Mortality	Age Mortality Shape	Leaf Drop Month	Coarse Root Fraction	Fine Root Fraction
Con1	1	15.5	36.3	1	5	0.3	-0.9	18000	12	0.4	0.4	0.09	0.005	15	10	0.3	0.6
Con2	2	25	45	1	3.8	0.3	-0.9	26000	12	0.2	0.3	0.09	0.005	15	10	0.3	0.6

Table C1.4. The LANDIS-II Net Ecosystem Carbon Nitrogen extension species soils parameter table. CW: cool-wet; WD: warm-drv

Ecoregion	**SOM1 C surface**	**SOM1 N surface**	**SOM1 C soil**	**SOM1 N soil**	**SOM2 C**	**SOM2 N**	**SOM3 C**	**SOM3 N**	**Mineral N**
CW	119	12	186.7	18.7	5507.5	314.7	3547.2	417.3	22.5
WD	102.2	10.2	171.1	17.1	5048	288.5	3251.2	382.5	22.5

Table C.1.5. The LANDIS-II Net Ecosystem Carbon Nitrogen extension ecoregions parameter table. CW: cool-wet; WD: warm-dry

Ecoregion	Soil Depth (cm)	% clay	% sand	Field Capacity	Wilt point	StormF	BaseF	Drain	Atmosphere N slope	Atmosphere N intercept	Latitude	Decay rate surface	Decay rate SOM1	Decay rate SOM2	Decay rate SOM3	Denitrification slope
CW	100	0.06	0.51	0.08	0.02	0.006	0.01	0.6	0.0025	0.05	47	1.15	1.4	0.045	0.00007	0.0011
WD	100	0.11	0.4	0.14	0.05	0.006	0.01	0.6	0.0025	0.05	47	0.89	1.29	0.039	0.00007	0.0011

Table C.1.6. The LANDIS-II Net Ecosystem Carbon Nitrogen extension max monthly NPP and max biomass of the cool-wet (CW) and warm-dry (WD) ecoregions.

	Monthly Max NPP (g/m^2)		**Max Biomass (g/m^2)**	
Species	**CW**	**WD**	**CW**	**WD**
Abies grandis	850	550	131564	220202
Abies lasiocarpa	255	80	72195	1480
Larix occidentalis	299	250	48647	65805
Picea engelmannii	275	80	63607	4440
Pinus albicaulis	589	189	310	91
Pinus contorta	225	100	87613	28666
Pinus monticola	480	560	6787	35315
Pinus ponderosa	589	189	6787	35315
Pseudotsuga menziesii	810	550	137453	234057
Thuja plicata	870	650	58365	88043
Tsuga heterophylla	800	190	65095	33319
Tsuga mertensiana	890	140	114551	167

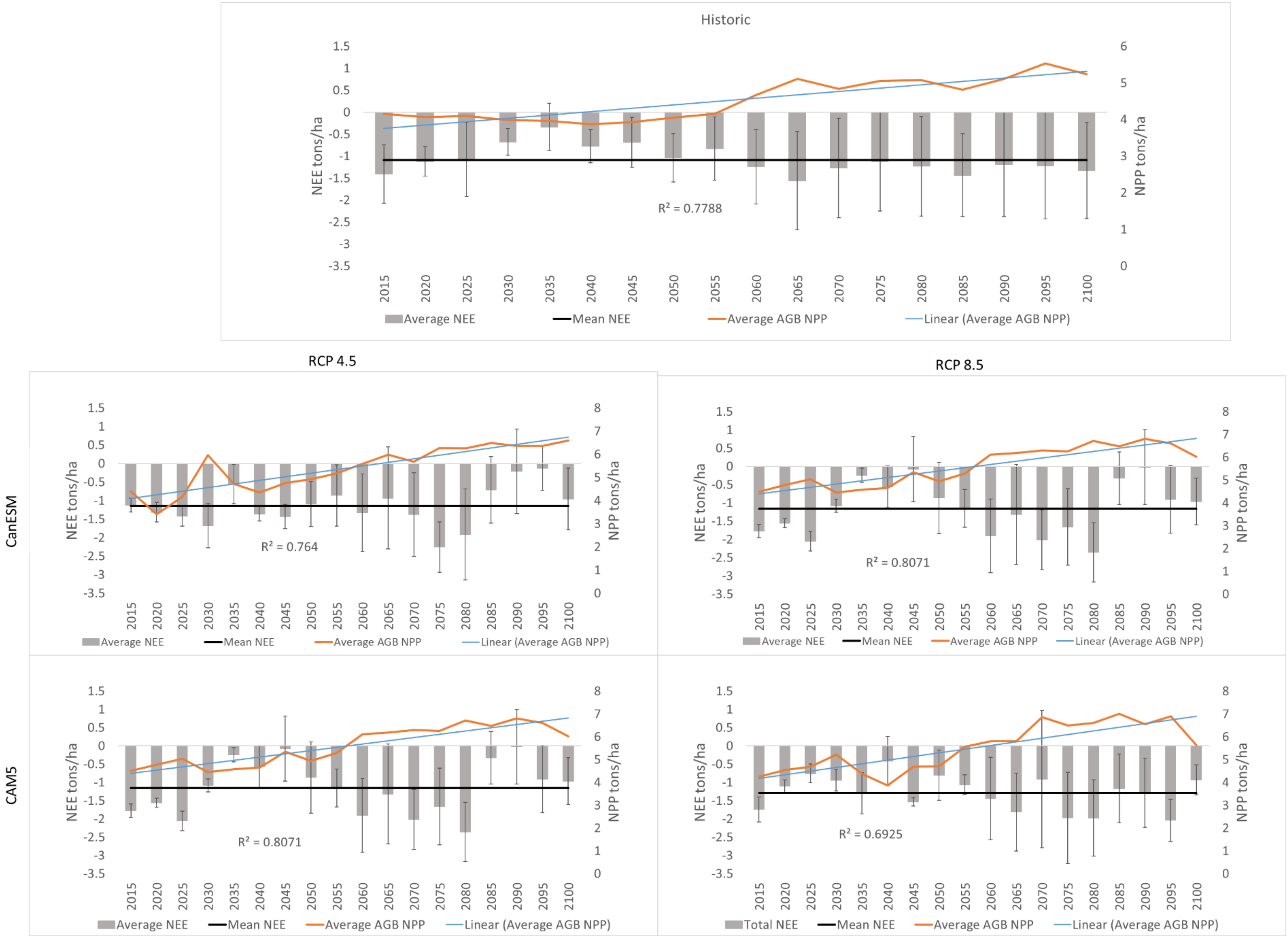

Figure C.1.1. The NEE and NPP of the GCMs and climate scenarios.