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Climate change mitigation through adaptation: the effectiveness of forest diversification by novel tree planting regimes

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Abstract. Climate change is projected to have negative implications for forest ecosystems and their dependent communities and industries. Adaptation studies of forestry practices have focused on maintaining the provisioning of ecosystem services; however, those practices may have implications for climate change mitigation as well by increasing biological sinks or reducing emissions. Assessments of the effectiveness of adaptation strategies to mitigate climate change are therefore needed; however, they have not been done for the world's northern coniferous forests. Diversifying the forest by planting tree species more likely suited to a future climate is a potential adaptation strategy to increase resilience. The efficacy of this strategy to reduce the risks of climate change is uncertain, and other ecosystem services provided by the forest are also likely to be affected. We used a spatially explicit forest landscape modeling framework (LANDIS-II) to simulate the effects of planting a range of native tree species in colder areas than where they are currently planted in a managed temperate coniferous forest landscape in British Columbia, Canada. We investigated impacts on carbon pools, fluxes, tree species diversity, and harvest levels under different climate scenarios for 100 yr (2015–2115) and found that the capacity of our forest landscape to sequester carbon would largely depend on the precipitation rates in the future, rather than on temperature. We further found that, irrespective of the climate prediction model, current planting standards led to relatively low levels of resilience as indicated by carbon fluxes and stocks, net primary productivity (NPP), and species diversity. In contrast, planting a mix of alternative tree species was generally superior in increasing the resilience indicators: carbon stocks and fluxes, NPP, and tree species diversity, but not harvest rates. The second best novel planting regime involved adding *Pinus contorta* to the stocking standard in three ecoregions; however, that species is susceptible to a high number of insects and pathogens. We conclude that although the capacity of temperate coniferous forest landscapes to sequester carbon in the future is largely dependent on the precipitation regime, negative effects may be counteracted to some extent by increasing resilience through tree species diversity in forests.

Key words: assisted migration; boreal forest; carbon stocks; climate change; ecosystem services; forestry; modeling; temperate forest.

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Introduction

Climate change, forestry, and their interaction can be important drivers of changes in forest dynamics and provision of related ecosystem services (Sykes and Prentice 1996, Hanski 2000, Scheller and Mladenoff 2005). For example, trees may grow faster or slower under changing climatic conditions which may affect the availability of forest products that can provide bioenergy among other things (Körner 2017). However, boosted growth rates of trees may still be offset by deforestation for development (Thompson et al. 2011). Different climatic conditions will, however, not only affect the distribution and growth rate of tree species, but will likely also have an impact on disturbances such as pest infestations (Klapwijk et al. 2013) and the frequency of forest fires (Stocks et al. 1998). Various treatment and management options, such as insecticides, sanitation harvest, and thinning, can lower the risk of pest outbreaks (Fettig et al. 2014) and strategically placed fuel treatments may reduce the risk of wildfire as well as increase the resiliency of forests to fire, and thus benefit long-term carbon management (Loudermilk et al. 2014). There is increasing awareness of the opportunity and necessity to use such and other forest management practices to increase uptake of carbon by the vegetation (Fares et al. 2015), or to reduce emissions associated with natural disturbances (Noss 2001, Millar and Stephenson 2015), thus reducing the risk of positive feedback.

Forest management practices have already been assessed for the potential to mitigate climate change in several ways. Thinning practices have shown to promote high carbon sequestration rates and enhance structural and compositional complexity in forests (D'Amato et al. 2011). Uneven- instead of even-aged management and prescribed fire regimes have also been suggested as mitigation measures (Millar et al. 2007). However, such adaptations may, like direct effects of climate change, negatively affect some ecosystem services (Noss 2001, Jackson et al. 2005, Lindenmayer et al. 2012) and positively affect others, such as species diversity (Imai et al. 2009), timber supply (Bright et al. 2014), and water quality (Ford et al. 2011). We therefore need careful and thorough assessments of the various effects adaptation strategies may have on ecosystems, addressing not only economic aspects but also environmental and social effects, while collaborating with important factors involved (Keenan 2015).

One of the frequently mentioned forest management strategies to mitigate climate change effects and manage for future uncertainty is to increase the resilience of forests by diversifying it and thus reducing the dependence of ecological services on our ability to predict the future climate (Noss 2001, Temperli et al. 2012, Dymond et al. 2014, 2015*b*). It has been hypothesized that the most resilient forest contains several specialist tree species in which species respond differently to a given future, so despite the future being unpredictable, there will be species present that would likely be able to exploit the climatic niche that occurs (Crowe and Parker 2008). Planting alternative tree species, genotypes, or provenances additional to the species already planted under current forest management is a way to adapt the managed forest to a changing climate. Such adaptations have frequently been proposed in scientific literature as well as by forest agencies (Kellomäki et al. 2005, Aitken et al. 2008, Gray and Hamann 2011). They entail planting tree species/genotypes/provenances that currently either do not occur or are less common in a region but may potentially be valuable for the forest industry, or for other ecosystem services, now and in the future. Species that would qualify are those with climate niches that are not common in the region now but are predicted to become common in the future. Such a strategy is ecologically justified since natural shifts in the composition of tree species have already occurred in the past due to changes in climatic conditions and are suggested to occur in the near future as well (Searle and Chen 2017).

There are some clear benefits to planting alternative or novel species. As already mentioned, planting novel species will increase species diversity and natural selection will lead to a species population that is better adapted to changing climatic conditions (Kolström et al. 2011 and references therein). Also, it may be sensible to manage the uncertainty of the severity of climate change and its feedback to, for example, potential increased risk of extreme weather events (Schlyter et al. 2006) and outbreaks of pest and pathogens (Klapwijk et al. 2013), by spreading the risk and thus by planting a mix of species (Crowe and Parker 2008, Meason and Mason 2014). Indeed,

various studies exist that provide evidence that planting alternative species can help increase the resilience of forests to climate change; for example, the planting of *Eucalyptus fastigata* was predicted to be more attractive in New Zealand under increased hazards (drought, pathogens, and insects) and elevated CO_2 concentrations than the planting of conventionally planted species. In Scotland, Scots pine (*Picea abies*) may also become more attractive to plant than the conventionally planted Sitka spruce (*Picea sitchensis*) under climate change (Meason and Mason 2014). There are, however, also several potential difficulties to and problems associated with planting novel species, one being the risk that the novel species are less marketable, which may mean an economic loss for those forest owners that chose to plant them (Meason and Mason 2014). Another possible problem is that potential new pathogens and pests may be attracted to the system by the novel species (Burdon 2001). Furthermore, the novel species may have a lower productivity in the new ecosystem than expected. Also, there may be some negative effects on wildlife dependent on the current species composition, especially if functionality is not retained.

Few studies have thus far investigated the potential effects of planting novel tree species on forest carbon dynamics. Ravenscroft et al. (2010) simulated the interaction between climate change and, among others, forest restoration practices in which four uncommon species were planted, on a forest ecosystem in Minnesota. Buma and Wessman (2013) studied the effects of planting the most climatically suitable species, including local and non-local species, to and in the southern Rocky Mountains in Colorado, USA, on carbon stocks. Duveneck and Scheller (2015) investigated moving deciduous species northward in Minnesota and Michigan. Seidl et al. (2008, 2014) have assessed more complex adaptation strategies in Austrian spruce/deciduous forests. None, as far as we are aware, have investigated the potential impact on the forest carbon pools in temperate or boreal coniferous forests. However, an alteration in the species composition due to the introduction of novel species or the increase in formerly less common species may turn carbon sinks into carbon sources or the other way around. Assessing the potential impacts of planting novel tree species as adaptation strategies to mitigate negative effects of climate change is therefore highly relevant.

We hypothesize that the choice of planting regime, that is, which novel tree species are planted, may significantly affect the carbon stocks in the forest. Other ecosystem services, like timber production and species diversity, will also be affected by the tree species chosen. The direction and extent of the impacts will, however, likely depend as well on the climate and environmental conditions experienced. Due to the potential large number of impacts the choice of planting regime may have on ecosystem services, we expect the best strategy to be a regime in which a number of novel tree species are planted rather than a regime in which a single novel tree species is planted. We therefore simulated the impacts of planting several species native to British Columbia, Canada, into colder ecoregions than where they are currently planted. We simulated planting of (1) Douglas-fir (*Pseudotsuga menziesii*), (2) ponderosa pine (*Pinus ponderosa*), (3) western larch (*Larix occidentalis*), and (4) lodgepole pine (*Pinus contorta*). We chose to limit our studies to species native to British Columbia and mostly those that were either already used or planned to be used for planting in the warmer parts of the study region. The likelihood that stakeholders will adopt the proposed regimes is larger than the probability that they would adopt regimes that plant tree species that are currently absent from the region (Hajjar et al. 2014) and larger uncertainty about their performance in the new region. We did, however, also simulate the effect of planting ponderosa pine, which is currently not used in forestry in the study region. This species is nevertheless already present in gardens and parks in the region (*personal observation*). In addition to four regimes in which only one of the above-mentioned novel species was planted, a fifth added up to four species to maximize the potential diversity. We compared these five planting regimes against the current regulated standard. Large parts of the study region have not been managed and are over 100 yr in age; we therefore also included a so-called no management regime in the simulations to understand the effect of climate change alone on the biological system. We concurrently analyzed the impacts of these different planting regimes on various indicators of resilience: carbon stocks,

fluxes, species diversity, and harvest rates under four climate scenarios.

Methods

The study site

We simulated the forest dynamics of a 734-km^2 large forested mountain valley called Copper–Pine Creek near the town of Smithers in northwestern British Columbia, Canada (latitude 54.782, longitude 127.168; Fig. 1). This study region is an ideal example that represents a range of forest ecosystems with naturally varying climate envelopes, tree species composition, management activities, and natural disturbance rates within an area small enough to be simulated at a detail consistent with operational activities. The landscape is dominated by coniferous forests that are largely unharvested and mostly over 100 yr in age, but several forest companies now manage the forest and currently unharvested areas will likely be harvested in the future. The area is climatologically interesting since it is located in the transition zone where coastal and continental climates meet. Winters are generally cold and snowy, while summers are mild and dry. The mean annual temperature ranges from 0.5° to 3.1°C, and the mean annual precipitation ranges from 500 to 1600 mm (Table 1). This study builds on the work of Dymond et al. (2016) that identified both positive and negative climate change effects on the tree productivity and carbon dynamics of the study area by (1) assessing the impacts of different planting regimes, (2) modeling several climate scenarios rather than that of an ensemble of climate scenarios, and (3) including pest outbreaks.

Forest dynamics simulation

We used a spatially explicit forest landscape modeling framework (Landis-II, Scheller and Mladenoff 2004) that integrates ecosystem processes, management, and disturbances to simulate the effect of the planting regimes on the forest dynamics in the study region from 2015 to 2115, with a time step of one year and on a one-hectare

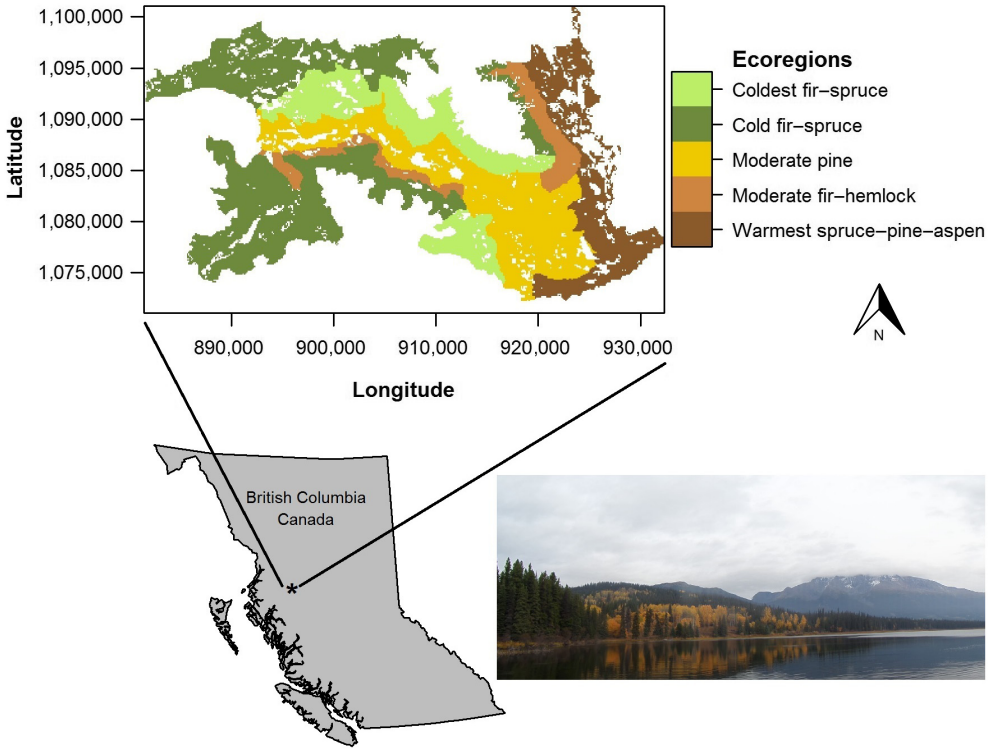


Fig. 1. The study region showing the different ecoregions. See Table 1. The photograph looking west across part of the study region. Elevation increases from east to west and from the yellow colors to the green.

Table 1. Characteristics of the ecoregions in the study region.

Ecoregion	Characteristics	Mean current NPP ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	MAT (°C)	MAP (mm)	FRI (yr)
Coldest fir–spruce	Moist relative to the cold fir–spruce ecoregion. Dominant species: subalpine fir (42%), lodgepole pine (33%), interior spruce (24%)	118	1.4	1081	700
Cold fir–spruce	Wet relative to the coldest fir–spruce ecoregion. Dominant species: subalpine fir (86%), lodgepole pine (10%), interior spruce (4%)	314	1.6	1291	700
Moderate pine	Moist relative to the warmest spruce–pine–aspen ecoregion. Dominant species: lodgepole pine (46%), interior spruce (27%), subalpine fir (20%)	595	2.2	851	400
Moderate fir–hemlock	Dominant species: subalpine fir (50%), western hemlock (15%), lodgepole pine (15%), interior spruce (15%)	497	2.3	899	400
Warmest spruce–pine–aspen	Dry relative to the moderate pine ecoregion. Dominant species: trembling aspen (44%), interior spruce (23%), lodgepole pine (22%)	669	3.1	521	200

Note: NPP, net primary productivity; MAT, mean annual temperature (source: BC Environment [1995]); MAP, mean annual precipitation (source: PCIC [2012]); FRI, fire return interval.

scale, while accounting for climate change, fire, and disturbances caused by mountain pine beetle outbreaks (*Dendroctonus ponderosae*). The model allows for the simulation of forest dynamics over large spatial scales and long timescales, incorporating individual tree species, biomass accumulation and decomposition, carbon sequestration, seed dispersal, climate change, harvesting, and disturbances (Scheller and Mladenoff 2004, Scheller et al. 2007). LANDIS-II has been extensively validated and used in forest ecosystems across North America (Scheller and Mladenoff 2005, Shinneman et al. 2010, Steenberg et al. 2011). It is built on the original LANDIS model (Mladenoff et al. 1996, Mladenoff and He 1999), which has a long use in assessing the effects of climate change on forest dynamics (Gustafson et al. 2010, Steenberg et al. 2011, Thompson et al. 2011). LANDIS-II has further been used to assess the effects of climate change on forest carbon storage (Dymond et al. 2016).

LANDIS-II is the core model to which various optional extensions can be linked to incorporate the above-mentioned ecological processes (Scheller and Domingo 2011). To obtain a realistic baseline, we used, in addition to the core of LANDIS-II, the Base Fire v.3.0 extension to simulate the effect of forest fires (Scheller and Domingo 2012), the Biological Disturbance Agent v.3.0 to account for the disturbance caused by outbreaks of the mountain pine beetle (Sturtevant et al. 2015), the Base Harvest extension v.2.2 to simulate the effect of different harvest and planting regimes (Scheller et al. 2015), and the Forest Carbon Succession Extension v.2.0 (ForCS, Dymond et al. 2016) to assess the effect of different management and harvest strategies on the forest dynamics and carbon pools.

The initial forest community that forms the basis of the simulations and is needed for the core of the model was taken from the spatial forest inventory dataset from the Government of British Columbia. The species and age composition of each polygon in the forest inventory was assigned to the spatially overlapping 1-ha grid cells for input to LANDIS-II. That initial community map is comprised of 380 unique forest types with varying tree species compositions and age cohorts. At present, the most dominant tree species are subalpine fir (*Abies lasiocarpa*, the dominant species in 56% of the area) and lodgepole pine (the dominant species in 29% of the area, Fig. 2). Although processes happen across borders, we specified ecoregions to account for differences in local climate, available moisture, and soil type, which all affect tree growth. In British Columbia, different regions have been identified throughout the province by the Biogeoclimatic Ecosystem Classification (BEC) Program (https://www.for.gov.bc.ca/hre/becweb/index.html). Data on prevailing vegetation, soils, and topography are used to identify geographic areas that have relatively uniform conditions. In our study region, five zones that support closed-canopy forests were identified and formed the ecoregions in the simulations. In order from the coldest to warmest ecoregion, there are

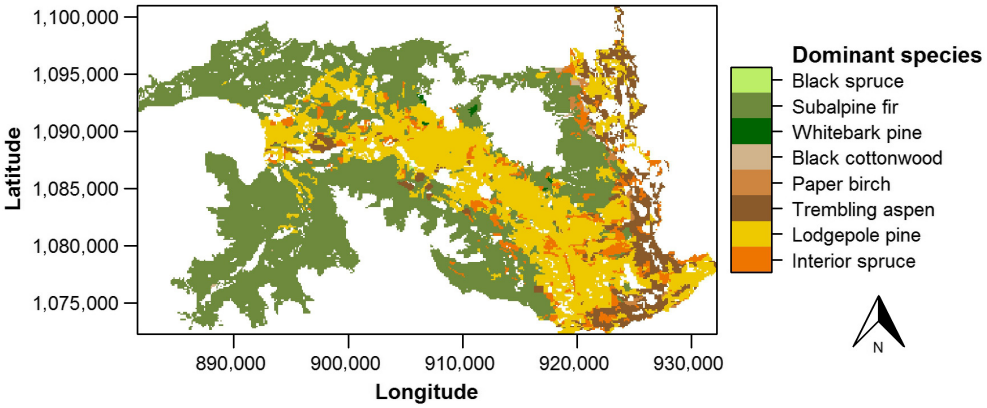


Fig. 2. The dominant tree species in the landscape at present (shown in the North American geodetic datum NAD83).

two ecoregions mostly dominated by subalpine fir and hybrid spruce (*Picea engelmannii* × *Picea glauca*) at higher elevations on mountain slopes and valley bottoms which we called "coldest fir–spruce" and "cold fir–spruce"; on the lower-elevation slopes, there is an ecoregion dominated by lodgepole pine which we called "moderate pine" and there is an ecoregion dominated by subalpine fir and western hemlock (*Tsuga heterophylla*), which we called "moderate fir–hemlock"; along the valley bottoms at lower elevations, there is an ecoregion characterized by a mix of species including hybrid spruce, lodgepole pine, and trembling aspen (*Populus tremuloides*), which we called "warmest spruce–pine–aspen" (Table 1). See Fig. 1 for the distribution of the different ecoregions.

Species parameters required in the model include longevity, sexual maturity, shade tolerance, fire tolerance, effective seed dispersal distance, maximum seed dispersal distance, vegetative reproduction probability, minimum sprout age, maximum sprout age, and post-fire regeneration. Values for each species were obtained from the literature (Burns and Honkala 1990, Klinka et al. 2000) and can be found in the supporting information (Appendix S1: Table S1). The Forest Carbon Succession extension calculates how cohorts reproduce, age, and die on an annual basis (Dymond et al. 2015*a*). From the output, it can be determined during each year of the simulation which species dominate per stand, how old trees are per stand, where clear-cuts are, how much biomass has been affected by pests, etc. Furthermore, changes in cohort biomass carbon, dead organic matter, and soil carbon are tracked over time. In addition to the carbon stocks for several pools, the extension reports the fluxes: turnover, net growth, net primary production, heterotrophic respiration, net ecosystem productivity, net biome productivity, transfers between pools, losses from the ecosystem due to logging, and carbon emissions due to decay or combustion. To account for climate change, the species' establishment probabilities, maximum aboveground net primary productivity (ANPP), and maximum biomass inputs required by the Forest Carbon Succession extension can be adjusted for each simulation year. We used the species' establishment, maximum ANPP, and maximum biomass inputs that were generated by Dymond et al. (2016) for each simulation year for each species and ecoregion in our study region (see Appendix S1: Table S2 for the current and future projected ANPP for each species in each ecoregion). Dymond et al. (2016) used the Tree and Climate Assessment Tool Establishment Model (TACA-EM) to estimate the establishment probability of each tree species in each ecoregion for each simulation year through natural regeneration based on soil and climatic conditions and a range of parameters including amount of growing degree days needed, tolerance to drought, frost, and shade, and onset of bud burst (Nitschke and Innes 2008, Nitschke et al. 2012). They used the Tree and Climate Assessment Tool Growth and Productivity model 10 (TACA-GAP) to estimate the maximum ANPP and maximum biomass for each species in each ecoregion for each simulation

year. While TACA-GAP uses the growth and response functions of the BRIND (Shugart and Noble 1981) and ZELIG++ (Burton and Cumming 1995) models, it is run at a daily time step to allow the incorporation of snow, soil moisture, and phenology components and natural history traits such as base temperature, bud burst, lethal temperature, minimum and maximum growing degree days, tolerance to drought, frost, shade, and wet soils, of TACA-EM (Nitschke et al. 2012). However, values were obtained separately for three climate scenarios derived from different global circulation models (GCMs) rather than as an ensemble, as Dymond et al. (2016) did, to be able to assess the effects of different planting regimes under different plausible futures. We selected three different GCMs under two emission scenarios that represented different plausible futures made available by the Pacific Climate Impacts Consortium (PCIC 2012). Data were available at the 300 arc-seconds scale (~10 km at the equator), which was detailed enough to generate averages for each of the ecoregions in our 734-km^2 large study region. First, we used the third version of the Canadian Centre for Climate Modeling and Analysis Coupled Global Climate Model (CGCM3) under the A2 emission scenario which is characterized by an increasing population, regionally oriented economic development, and relatively slow technological development (Nakicenovic et al. 2000). Secondly, we used the third version of the Hadley Centre Coupled Model (HADCM3) under the A1B emission scenario. The A1B emission scenario is characterized by very rapid economic growth, rapid introduction of new and more efficient technologies, an increasing global population until around 2050 after which it declines, and energy consumption that does not rely too heavily on one energy source (Nakicenovic et al. 2000). Lastly, we used the Hadley Centre Global Environment Model (HADGEM) as well under the A1B emission scenario. The predicted mean annual temperature is highest under the HADGEM climate scenario and lowest under the HADCM3 climate scenario, while the predicted future average precipitation is highest under the CGCM3 climate scenario and lowest under the HADGEM climate scenario (Fig. 3). Although newer climate scenarios are available, we chose to use the same climate scenarios as Dymond et al. (2016) for consistency. We, however, extended the simulation period used by Dymond et al. (2016) to 100 yr (2015–2115). Climatic data were available up to the period 2071–2100. After year 2100, we projected the climate trends into the future according to the slope of the trend during previous decades. Although data were available with inter-annual variation, this inter-annual variation is highly uncertain and not available after year 2100. As we were interested in trends rather than exact predictions based upon climate data fraught with inter-annual uncertainties, we decided to smoothen the inter-annual variation by using incremental changes based on data regarded as the current climatic conditions (1960–1990) and the future climatic conditions (2071–2100).

The Base Fire extension simulates the effect of forest fires by randomly creating fires according to user-defined values of the ignition probability and mean, minimum, and maximum size of events for the existing ecoregions (Scheller and Domingo 2012). These fires are applied spatially to the ecoregion they start in but may spread into neighboring regions. Tree species with higher fire tolerances as defined in the species traits file and older cohorts will be less likely to be killed than those with a lower tolerance for fires or younger cohorts. There is a low risk of fire in the region. Dependent on the ecoregion, fire return intervals range from about 200 to 700 yr and an ignition probability of between 0.0003 and 0.0004 (Table 1). The parameterization of the fire regimes is described by Dymond et al. (2016). As in that study, we did not alter the fire regimes following the climate scenarios since future changes to the fire regimes are predicted to be small (Haughian et al. 2012).

The Biological Disturbance Agent extension simulates the effect of user-specified pests on forest ecosystems by creating pest outbreaks based on user-defined likelihood of probabilities, and kills species stands or age cohorts, based on user-defined mortality (Sturtevant et al. 2015). We simulated the effect of the mountain pine beetle since it has shown to be capable of effecting forest ecosystems and carbon in British Columbia to a large extent (Taylor et al. 2006, Kurz et al. 2008) and is identified as one of the prime pests to cause future damage to forest ecosystems in Canada (Johnston et al. 2010). The extension was parameterized based on the findings in the literature (Safranyik et al. 1992, Alfaro et al. 2003, Safranyik and Wilson 2007). It has been

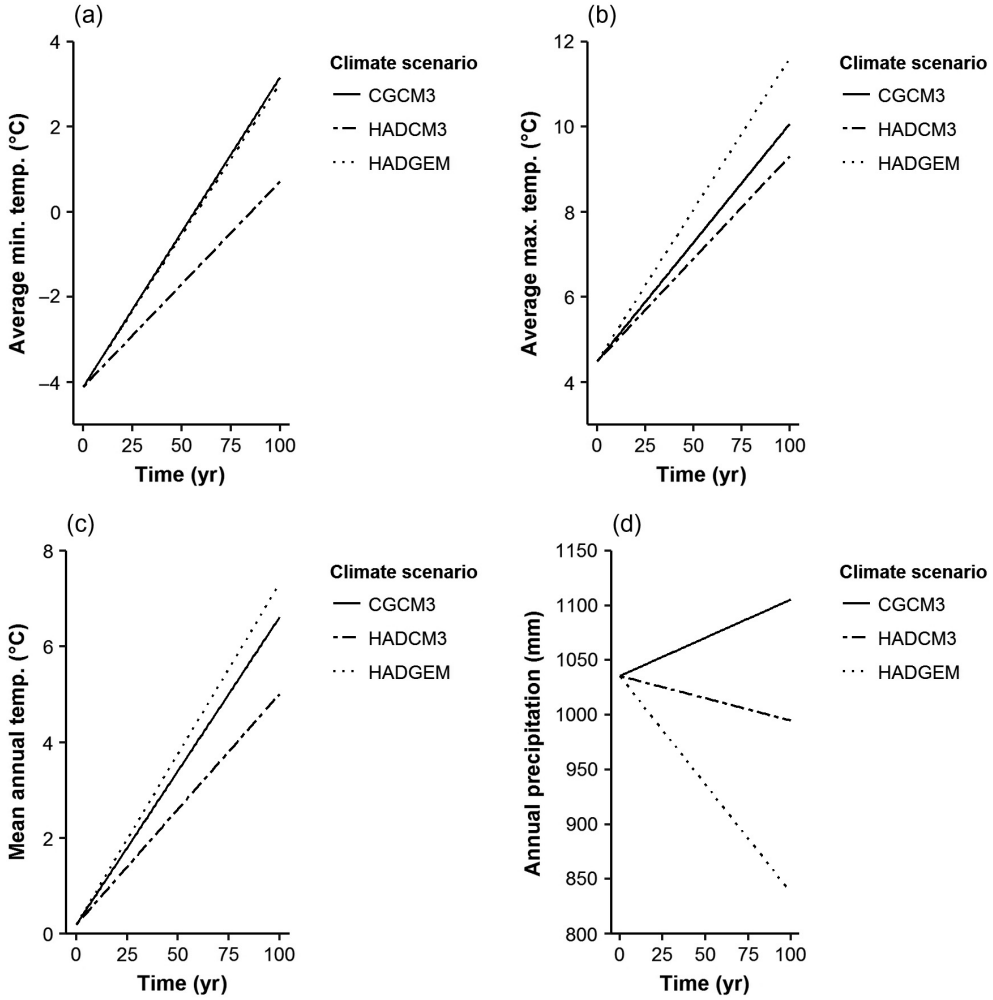


Fig. 3. The climate trends of the CGCM3, HADCM3, and HADGEM climate scenarios; (a) average minimum temperature, (b) average maximum temperature, (c) mean annual temperature, and (d) annual precipitation.

estimated that there have been three to five outbreaks prior to the current outbreak in British Columbia since the mid- to late 1700s (Hawkes et al. 2003, Alfaro et al. 2003, Hrinkevich and Lewis 2011). The duration and extent of the outbreaks and the mortality of trees varied based upon among others the climatic conditions, size and age of the stands, and the proportion of lodgepole pine in the region. Hrinkevich and Lewis (2011) found, for instance, that the mortality of pine in outbreak sites varied between 22% and 100%. Our study region is outside the area where historical mountain pine beetle populations and outbreaks have been large or frequent (Aukema et al. 2006), but it is expected that outbreaks will increasingly occur outside their historical range with ongoing climate change (Carroll et al. 2003, Safranyik et al. 2010). We therefore accounted for the occurrence of one to two short outbreaks, causing a total mortality of up to 6% of the lodgepole pine in our 100-yr simulation period as is consistent with historical data in this area. Total mortality was, however, dependent on the amount of viable pine in the region. Actively increasing the proportion of lodgepole pine in the region by planting will therefore increase the likelihood of outbreaks being simulated when newly planted lodgepole pine becomes vulnerable, thus accounting for feedbacks.

The harvest and planting regimes

The Base Harvest extension simulates harvesting and planting (Gustafson et al. 2000). The user can define the type and level of harvesting (percent area by time step), which species and species age cohorts can or should be harvested and which are forbidden to be harvested per management region of which multiple can exist in each ecoregion. As an example, the user can specify that in 1% of the area of a particular ecoregion, all lodgepole pine older than 60 yr should, if present, be harvested at each time step. Information about the location of current management regions and current management strategies, such as the average size of a clear-cut, average amount of forest that is being clear-cut, or thinned each year, was taken from the forest stewardship plans for the Wetzin'kwa Community Forest Corporation (2009) and the B.C. Timber Sales–Babine Business Area (2007). Local forest managers reviewed the modeling parameters and results of the baseline strategies during meetings. See Appendix S1: Table S3 for the baseline harvest strategies used in our study.

Following simulated harvest, the Base Harvest extension can plant new cohorts of species but only in equal proportions. The number of trees planted can also not be specified nor can the spatial pattern of the planted trees be specified. At each time step (a time step being one year in our study), species were planted in each grid cell (100 × 100 m) that was harvested. Other than proportions, the operational planting activities in the watershed follow the BC Government Stocking Standards for species and density; these already include some climate change adaptation provisions namely the planting of Douglas-fir and western larch in the warmest spruce–pine–aspen ecoregion (Table 2). In these standards, hybrid spruce is planted after harvest events in all ecoregions, subalpine fir in the coldest and cold fir–spruce ecoregions, and the moderate fir–hemlock ecoregion. Western hemlock is currently also planted in the latter. Lodgepole pine is currently planted in the moderate pine ecoregion and the warmest spruce–pine–aspen ecoregion but not in the other ecoregions.

In developing novel planting regimes to simulate, we felt it was important to consult local stakeholders. This would potentially increase the likelihood of acceptance of forest adaptation strategies by local stakeholders (Spathelf et al. 2014). We consulted local forest managers and staff of the Skeena Stikine Forest District (the district under which our study region falls) for their view on feasible and likely alternative adaptive planting regimes. Based on those consultations and the species-specific productivity modeling, we developed four planting regimes which each added a single species to the simulated planting

Table 2. The planting regimes per ecoregion.

Planting regime	Coldest and cold fir–spruce	Moderate pine	Moderate fir–hemlock	Warmest spruce–pine–aspen
Stocking standards†	Hybrid spruce, subalpine fir	Hybrid spruce, lodgepole pine	Hybrid spruce, western hemlock, subalpine fir	Hybrid spruce, lodgepole pine, *Douglas-fir, western larch*
Adding Douglas-fir	Stocking standards	Stocking standards and **Douglas-fir**	Stocking standards and **Douglas-fir**	Stocking standards
Adding lodgepole pine	Stocking standards and **lodgepole pine**	Stocking standards	Stocking standards and **lodgepole pine**	Stocking standards
Adding ponderosa pine	Stocking standards	Stocking standards and **ponderosa pine**	Stocking standards and **ponderosa pine**	Stocking standards and **ponderosa pine**
Adding western larch	Stocking standards	Stocking standards and **western larch**	Stocking standards and **western larch**	Stocking standards
Diversification	Stocking standards and **lodgepole pine, whitebark pine, Douglas-fir**	Stocking standards and **Douglas-fir, subalpine fir, western hemlock, black spruce**	Stocking standards and **western larch, lodgepole pine, Douglas-fir, western redcedar**	Stocking standards and **subalpine fir, black spruce**

Notes: Boldface indicates differences from the stocking standard. Italics indicates climate change adaptation provisions to the stocking standards.

† Source: MFR 2016.

mix (Table 2). In addition, we simulated a diversification planting regime based on existing plans for diversification benchmarks within the region developed through a stakeholder-consultation process (Mah and Astridge 2004). During this development, experts from multiple disciplines came together and choose tree species based on a synthesis of existing species information at a landscape scale. The benchmark "represents the desired proportion of tree species for managed stands at the landscape level that would maintain or increase tree species diversity in ecosystems and promote resilient landscapes," and its intended use is "to provide forest management direction from an ecological perspective within a BEC subzone/variant [ecoregions] for the next 10–15 years" (Mah and Astridge 2004). In the diversification regime, we simulated the planting of two to four more species than are in the stocking standard. They included species not used in the individual planting regimes: whitebark pine (*Pinus albicaulis*), black spruce (*Picea mariana*), and western redcedar (*Thuja plicata*).

Harvesting parameters were adapted per planting regime. Baseline harvesting regimes were in place for the first 80 yr after which the model could harvest the new species provided that they had a minimum age of 80 yr (50 for lodgepole pine). Since not all species have equal growth rates, it is likely that planting new species alters the amount of harvest that can occur and therefore also the amount of planting after each harvest event. However, we did not change the rate of harvest (annual percent of a management area). In addition to these different planting and harvesting regimes, we ran simulations without any anthropogenic management, harvest, nor planting.

Model validation and analyses

Landis-II, its extensions, and TACA-Gap have all been validated against independent forest data (Scheller and Mladenoff 2005, Mok et al. 2012, Dymond et al. 2016). Furthermore, at the beginning of each simulation, ForCS does a spin-up to calculate the carbon stock values estimated for each site. The ability of LANDIS-II to simulate the forest biomass dynamics in our study region was validated by Dymond et al. (2016). We ran a simulation for each combination of planting regime and climate scenario 20 times for 100 yr at a 1-ha resolution and a time step of one year. The 20 replicates were intended to capture the variability in carbon dynamics caused by the stochastic representation of wildfires and mountain pine beetle disturbances.

Because the modeling framework does not consider all factors that affect growth rates of the tree species, we conducted a sensitivity analysis assessment of the impact of reducing the input growth rate of lodgepole pine (the fastest growing species) in the adding lodgepole pine regime. This regime was of particular concern because local forest managers indicated various forest health risks to mature stands such as damage due to heavy snow loads. Since we were unable to simulate these particular risks to lodgepole pine, we chose to conduct a sensitivity analysis by reducing the pine growth to 50% and 75% of the original levels.

We used R version 3.2.2 (R Development Core Team 2015) including the packages "Raster" (Hijmans et al. 2016) and "ggplot2" (Wickham and Winston 2009) for the analyses and graphical representation. We used the Shannon diversity index, as calculated by the package "Vegan" (Oksanen et al. 2017), to represent tree species diversity based on the woody biomass present per species. We used the Wilcoxon signed rank test in R to assess whether there were significant differences between carbon stocks and fluxes over time between planting regimes and the stocking standards and between climate scenarios. To clarify, we used the Wilcoxon signed rank test to assess whether there were significant differences between the mean net primary productivity (NPP) time-series of the 20 replicates for the stocking standards under baseline conditions and the mean NPP time-series of the 20 replicates for the diversification regime under baseline conditions. To detect trends in carbon stocks and fluxes over time, we used the Mann-Kendall test and prewhitened the data to reduce possible errors caused by autocorrelation, using the package "zyp" (Bronaugh and Werner 2013), following recommendations by Bayazit and Önöz (2007). Since the 20 replicates were used to represent the sample variability, the statistical tests only evaluated whether the difference between indicators was greater than the inter-annual variability created by disturbances. Furthermore, the ecoregions are not treated as equivalents, and they are represented by the sum of their cells, so landscape averages are therefore area-weighted.

Results

Effects on carbon stocks and fluxes

Landscape-wide, the average carbon stocks stored in aboveground biomass are predicted to significantly increase in the future under the stocking standards, irrespective of climate scenario (Mann-Kendall test, all $P < 0.001$, Fig. 4a). Carbon stocks in aboveground biomass are projected to increase significantly more under the CGCM3 climate scenario than under the baseline scenario in 2115 (Wilcoxon signed ranks test $V = 3$, $P < 0.001$). Under the HADCM3 climate scenario, carbon stocks in the aboveground

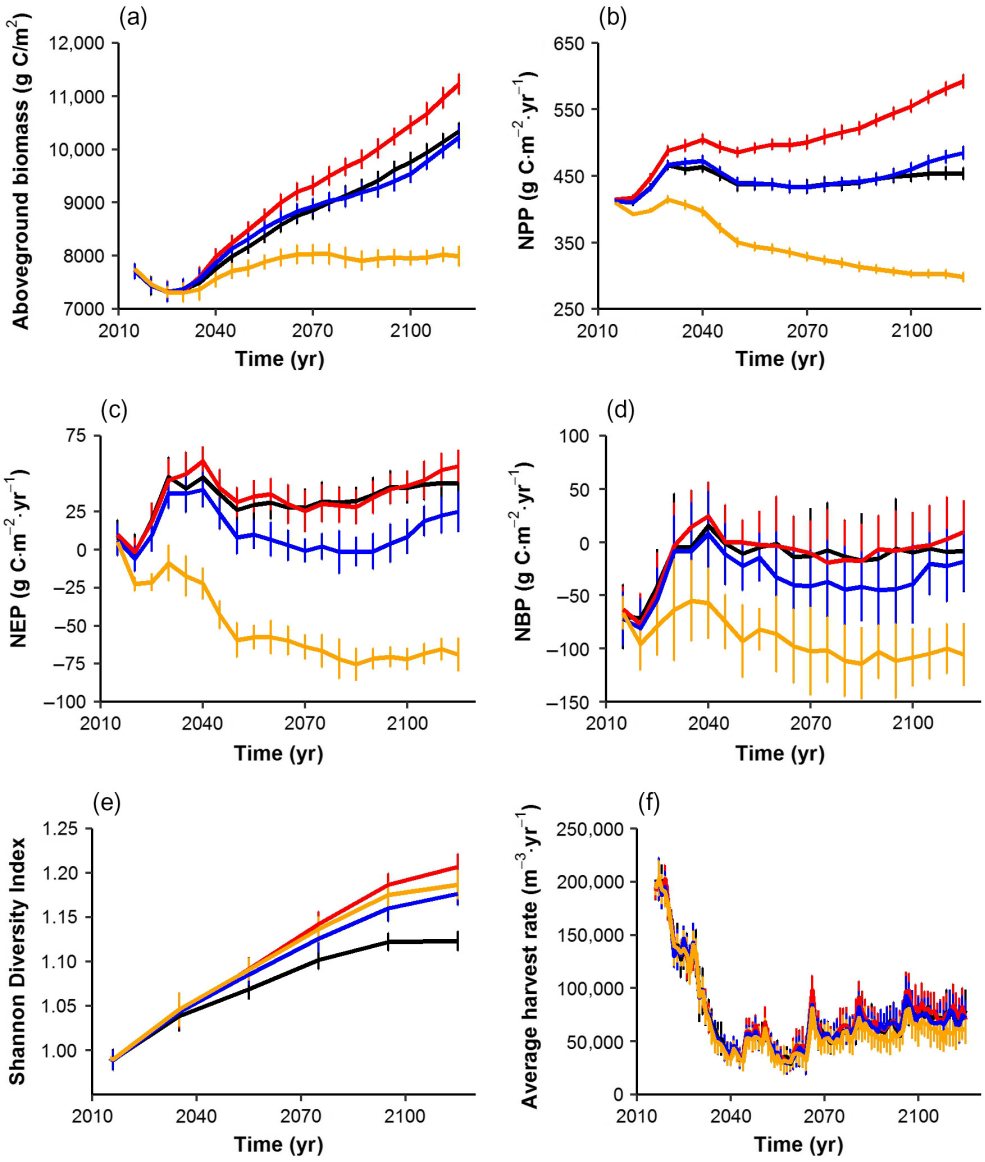


Fig. 4. The means of the indicators of forest resilience assessed over time under the stocking standards per climate scenario for the entire study region, under (a) the aboveground biomass, (b) the net primary productivity, (c) the net ecosystem productivity, (d) the net biome productivity, (e) Shannon diversity index, and (f) harvest rate. Error bars show the standard deviation over the 20 replicates. Black lines show the baseline climate scenario, red lines show the CGCM3 climate scenario, blue lines show the HADCM3 climate scenario, and yellow lines show the HADGEM climate scenario.

biomass are projected to be the same as in the baseline scenario (Wilcoxon signed ranks test $V = 123$, $P = 0.812$). However, under the HADGEM climate scenario, carbon stocks are projected to increase significantly less (Wilcoxon signed ranks test $V = 226$, $P < 0.001$). This future increase in carbon stocks stored in aboveground biomass holds true for all planting regimes except for the no management regime under the HADGEM climate scenario (Fig. 5). Under this scenario, the aboveground biomass carbon stock is predicted to decrease over time when no management is in place. The level of the increase/decrease did depend on the planting regime chosen. Under all planting regimes, but for the no management regime, the average carbon stocks stored in aboveground biomass were significantly larger compared to the stocking standards (Wilcoxon signed ranks test, all $P < 0.001$). This held true irrespective of the climate scenario experienced (Wilcoxon signed ranks test, all $P < 0.001$). The no management regime consistently resulted in the smallest aboveground biomass stocks irrespective of the climate scenario (Fig. 5). Landscape-wide,

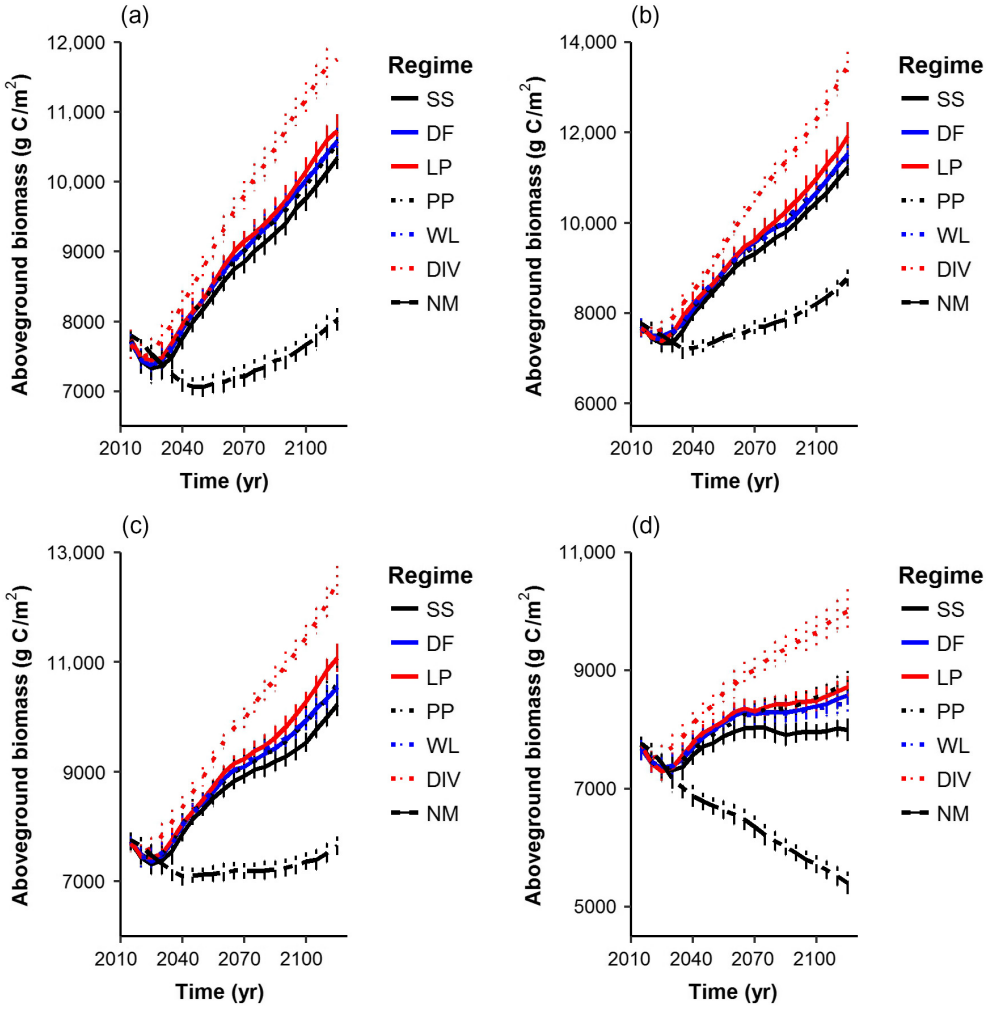


Fig. 5. The mean aboveground biomass stocks over time per planting regime for the entire study region, under (a) the baseline scenario, (b) the CGCM3 climate scenario, (c) the HADCM3 climate scenario, and (d) the HADGEM climate scenario. Error bars show the standard deviation over the 20 replicates. Note the different *y*-scales. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification; NM, no management or planting.

the diversification regime resulted in the highest aboveground biomass stocks (Fig. 5). This was also the case in most ecoregions under all climate scenarios, but for in the warmest spruce–pine–aspen ecoregion where adding ponderosa pine led to the highest aboveground biomass stocks, especially under the HADGEM climate scenario (Appendix S2: Figs. S1–S4). The highest stocks were generally found in the moderate fir–hemlock ecoregion (Appendix S2: Figs. S1–S4). In this ecoregion, all adaptive planting regimes significantly increased biomass stocks over the stocking standard regime (Wilcoxon signed ranks test, all $P < 0.001$, Appendix S1: Table S4). However, in the warmest spruce–pine–aspen ecoregion, there were no significant differences between most planting regimes except higher stocks under the adding ponderosa pine regime and lower stocks under the no management regime in all climate scenarios. The diversification regime also led to higher stocks but only under the baseline and the HADGEM climate scenario.

The landscape-wide NPP under the stocking standards is projected to increase over time under the baseline scenario as well as under the CGCM3 and the HADCM3 climate scenarios (Mann-Kendall test, baseline $\tau = 0.505$, $P = 0.002$, CGCM3 $\tau = 0.926$, $P < 0.001$, HADCM3 $\tau = 0.632$, $P < 0.001$, Fig. 4b). This projected increase is significantly greater under the CGCM3 and HADCM3 climate scenarios than under the baseline scenario (Wilcoxon signed ranks test CGCM3: $V = 0$, $P < 0.001$, HADCM3: $V = 31$, $P = 0.002$). Under the HADGEM climate scenario on the other hand, the NPP is projected to decrease over time under the stocking standards (Mann-Kendall test, $\tau = -0.947$, $P < 0.001$). The magnitude and even the direction of the change in NPP also depend on the planting regime chosen (Fig. 6). Compared to the stocking standards, NPP increased significantly more under most planting regimes under baseline climatic conditions, the CGCM3 climate scenario, and the HADCM3 climate scenario (Wilcoxon signed ranks test, all $P < 0.050$). However, the adding ponderosa pine and no management scenarios were inconsistent. Under the HADGEM climate scenario, the NPP is projected to decrease under all but the diversification regime (Mann-Kendall test, diversification: $\tau = 0.316$, $P = 0.056$, the others: $P < 0.001$, Fig. 6). Net primary productivity decreased significantly less under all novel planting regimes compared to the stocking standards (Wilcoxon signed ranks test, all $P < 0.050$). The projected decrease was, however, significantly greater under no management (Wilcoxon signed ranks test, $V = 9$, $P < 0.001$). At the end of the 100-yr simulation period, the NPP was often, but not always, highest in either the no management, the diversification regime, or the adding lodgepole pine regime (see Appendix S1: Table S5 and Appendix S2: Figs. S5–S8). The sensitivity analysis of the reduction in lodgepole pine growth to 50% and to 75% of the original level resulted in significantly lower landscape-scale NPP (Wilcoxon signed rank test 50%: $V = 231$, $P < 0.001$, 75%: $V = 231$, $P < 0.001$, Appendix S2: Fig. S9).

Patterns were not always clear on an ecoregion level. Growth rates generally increased in the coldest and cold fir–spruce ecoregions and in the moderate fir–hemlock ecoregion, decreased in the moderate pine ecoregion, and were more erratic in the warmest spruce–pine–aspen ecoregion. The highest growth rates were generally found in the moderate fir–hemlock ecoregion, while the lowest were generally found in the coldest fir–spruce ecoregion, the coldest ecoregion in the study region.

The net ecosystem productivity (NEP; NPP minus heterotrophic restoration) under stocking standards is projected to significantly increase as carbon sinks in the future under baseline climatic conditions (Mann-Kendall test, $\tau = 0.537$, $P = 0.001$, Fig. 4c) and under the CGCM3 climate scenario (Mann-Kendall test, $\tau = 0.484$, $P = 0.003$), but not change significantly under the HADCM3 climate scenario (Mann-Kendall test, $\tau = 0.053$, $P = 0.770$). Under the HADGEM climate scenario, NEP is projected to significantly decrease, that is, greater net emissions, in the future (Mann-Kendall test, $\tau = -0.842$, $P < 0.001$). The projected increase in NEP is significantly greater under the CGCM3 climate scenario compared to the baseline (Wilcoxon signed ranks test $V = 57$, $P = 0.042$). The trend in NEP over time also significantly differs from the baseline conditions under the HADCM3 and HADGEM climate scenarios (Wilcoxon signed ranks test HADCM3: $V = 231$, $P < 0.001$, HADGEM: $V = 231$, $P < 0.001$).

Under the baseline conditions, the NEP is projected to increase in the future under all planting regimes (Mann-Kendall test, all $P < 0.050$, Fig. 7)

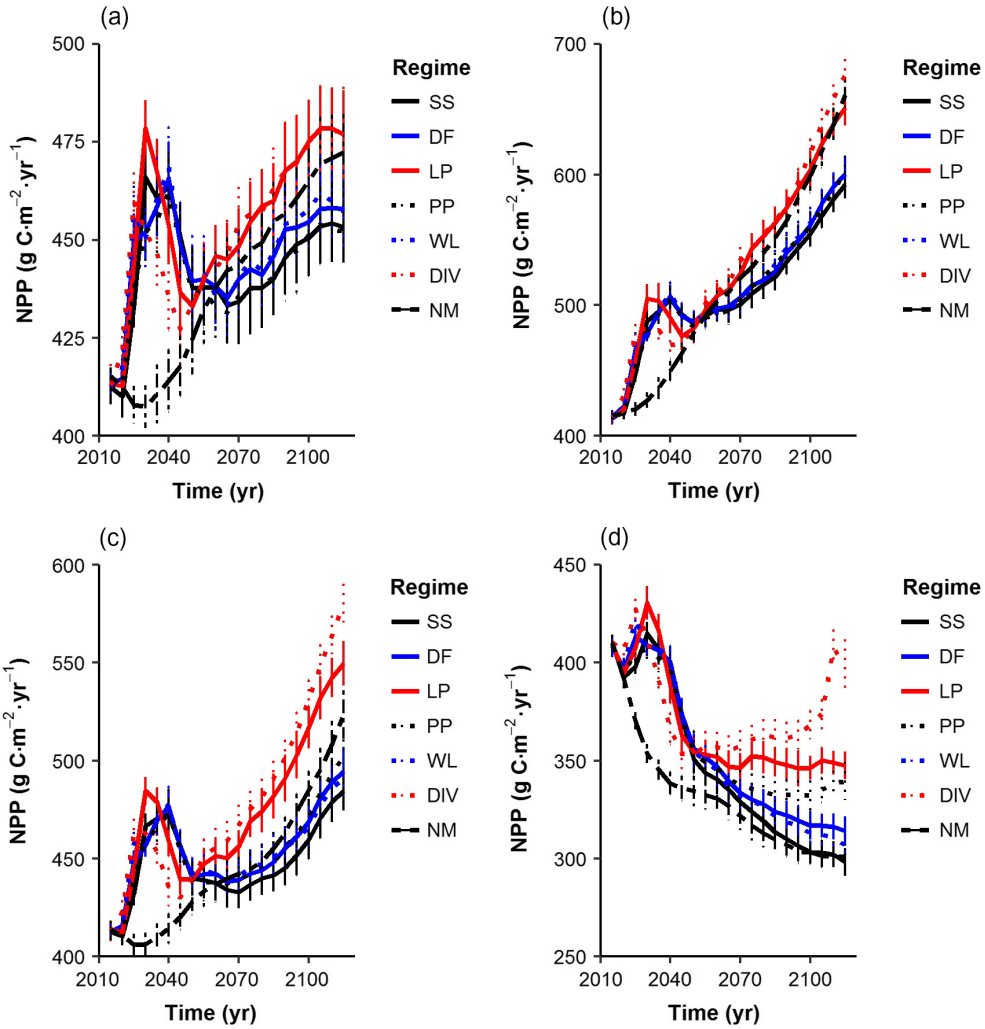


Fig. 6. The mean net primary production over time per planting regime for the entire study region, under (a) the baseline scenario, (b) the CGCM3 climate scenario, (c) the HADCM3 climate scenario, and (d) the HADGEM climate scenario. Error bars show the standard deviation over the 20 replicates. Note the different *y*-scales. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification; NM, no management or planting.

but for under the adding western larch regime (Mann-Kendall test, $\tau = 0.316$, $P = 0.056$). It is also projected to increase under the CGCM3 climate scenario under all planting regimes (Mann-Kendall test, all $P < 0.050$). Under the HADCM3 climate scenario, there was only an increasing trend under the diversification regime (Mann-Kendall test, $\tau = 0.757$, $P < 0.001$), the adding lodgepole pine regime (Mann-Kendall test, $\tau = 0.589$, $P < 0.001$), and when no management occurred (Mann-Kendall test, $\tau = 0.968$, $P < 0.001$). Under the HADGEM climate scenario, the NEP is projected to decrease, under all planting regimes (Mann-Kendall test, all $P < 0.050$), but for under the diversification regime. Under this regime, the NEP is projected to increase, although the landscape is still a net emitter (Mann-Kendall test, $\tau = 0.368$, $P = 0.025$).

Under stocking standards, the net biome productivity (NBP; NPP minus heterotrophic restoration and losses from the ecosystem due to disturbances such as harvest) in our study region is projected to remain stable and close to net zero flux over time under the baseline conditions

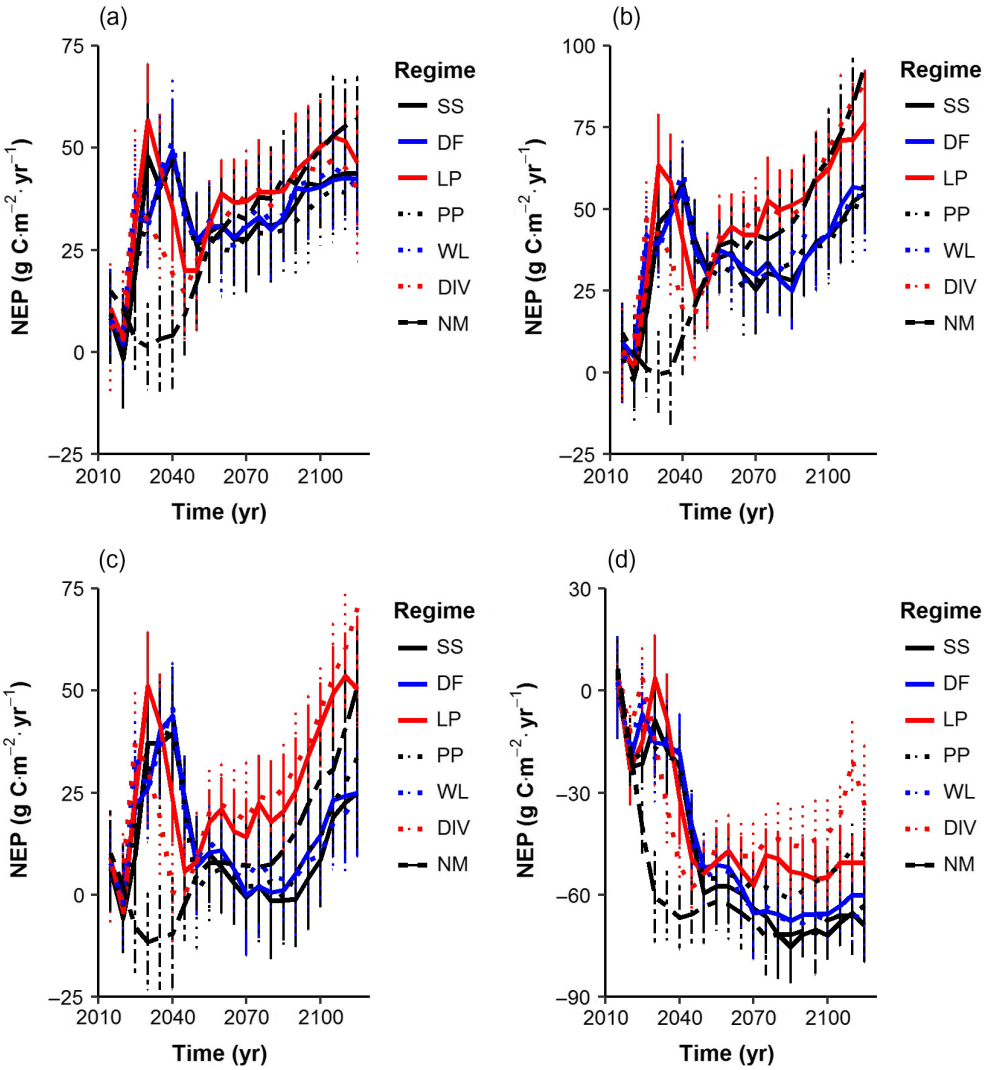


Fig. 7. The mean net ecosystem productivity over time per planting regime for the entire study region, under (a) the baseline scenario, (b) the CGCM3 climate scenario, (c) the HADCM3 climate scenario, and (d) the HADGEM climate scenario. Error bars show the standard deviation over the 20 replicates. Note the different *y*-scales. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification; NM, no management or planting.

(Mann-Kendall test, $\tau = -0.021$, $P = 0.922$) as well as under the CGCM3 (Mann-Kendall test, $\tau = 0.158$, $P = 0.347$) and the HADCM3 climate scenarios (Mann-Kendall test, $\tau = 0.011$, $P = 0.974$; Fig. 4d). However, it is projected to decrease under the HADGEM climate scenario and be a net source of emissions, similar to the NEP result (Mann-Kendall test, $\tau = -0.642$, $P < 0.001$). Furthermore, NBP sinks are smaller or emissions are larger under the stocking standards under both the HADCM3 (Wilcoxon signed ranks test $V = 231$, $P < 0.001$) and HADGEM (Wilcoxon signed ranks test $V = 230$, $P < 0.001$) climate scenario compared to the baseline. Emissions are, however, projected to be the same under the CGCM3 climate scenario and under the baseline conditions (Wilcoxon signed ranks test $V = 60$, $P = 0.055$).

The magnitude of the change in emissions depends on the planting regime chosen. Under baseline conditions and compared to the stocking

standards, the NBP is projected to remain similar under all but the adding ponderosa pine planting regime, which leads to somewhat greater emissions (Wilcoxon signed ranks test $V = 189$, $P = 0.009$, Fig. 8), and under no management, which leads to greater sequestration (Wilcoxon signed ranks test $V = 24$, $P < 0.001$). Under CGCM3 conditions, sinks are greater under diversification or no management compared to the stocking standards (Wilcoxon signed ranks test $V = 28$, $P = 0.001$, diversification: $V = 53$, $P = 0.029$). Whereas under the lodgepole pine planting regime the landscape is still a net emitter, but at a lower rate (Wilcoxon signed ranks test lodgepole pine: $V = 137$, $P = 0.016$). Under HADCM3 conditions, emissions are projected to be smaller and sinks larger under the same three planting regimes compared to the stocking standards (Wilcoxon

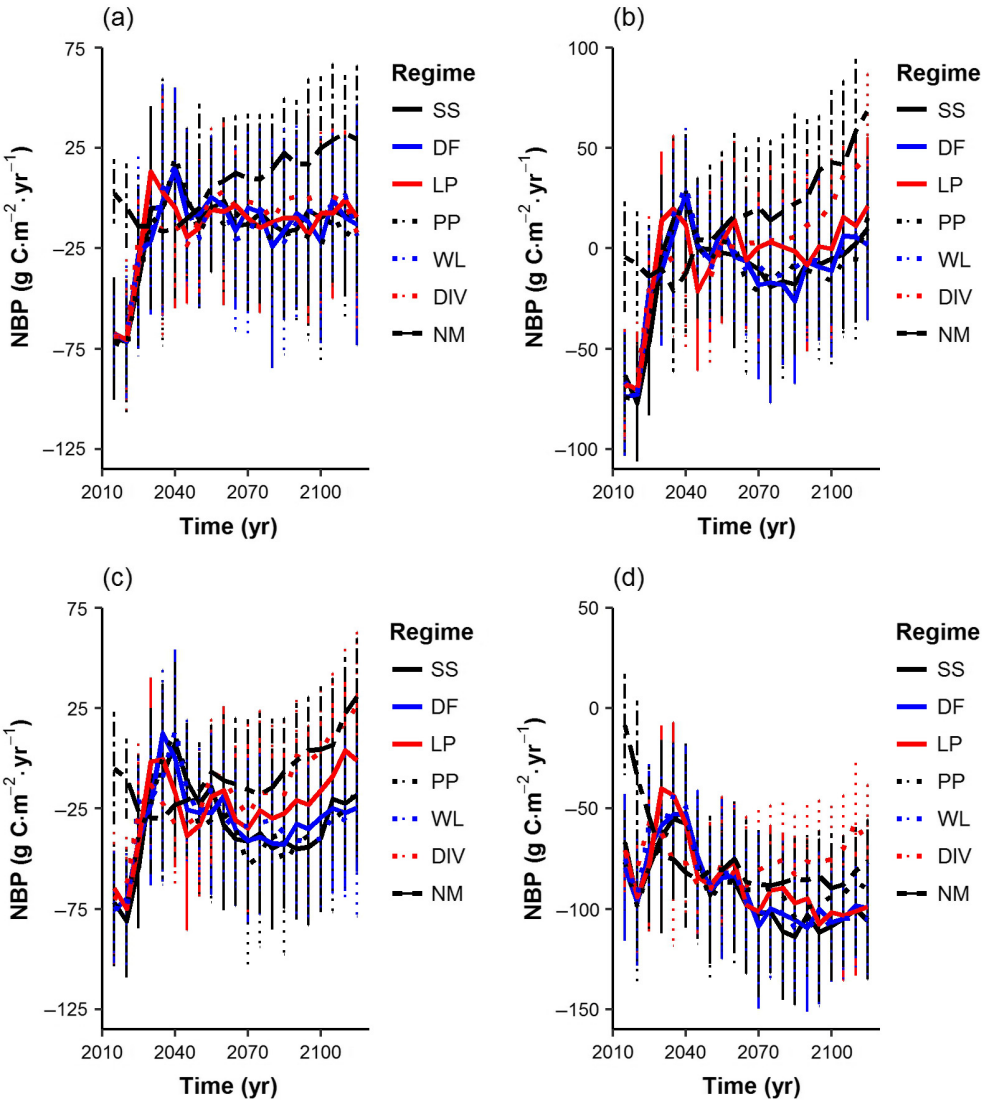


Fig. 8. The mean net biome productivity over time per planting regime for the entire study region, under (a) the baseline scenario, (b) the CGCM3 climate scenario, (c) the HADCM3 climate scenario, and (d) the HADGEM climate scenario. Error bars show the standard deviation over the 20 replicates. Note the different *y*-scales. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification; NM, no management or planting.

signed ranks test no management: $V = 27$, $P = 0.001$, lodgepole pine: $V = 49$, $P = 0.019$, diversification: $V = 38$, $P = 0.006$). Under the HADGEM climate scenario, emissions are projected to be smaller in the future under all novel planting except the adding Douglas-fir and adding western larch planting regimes (Wilcoxon signed ranks test no management: $V = 33$, $P = 0.003$, adding lodgepole pine: $V = 32$, $P = 0.002$, adding ponderosa pine: $V = 50$, $P = 0.021$, $P = 0.111$, diversification: $V = 31$, $P = 0.002$). However, no planting regimes led to net carbon sinks under the HADGEM climate scenario.

Effect on species diversity

Landscape-wide species diversity will increase in the future under the stocking standards which already include some climate change adaptation provisions; Douglas-fir and western larch are planted in the warmest spruce–pine–aspen ecoregion (Mann-Kendall test $\tau = 0.999$, $P = 0.009$, Table 2, Fig. 4e). This increase occurs under all the potential future conditions simulated but is significantly less under the baseline conditions than under the climate scenarios (Wilcoxon signed ranks test CGCM3: $V = 1$, $P = 0.031$, HADCM3: $V = 2$, $P = 0.047$, HADGEM: $V = 0$, $P = 0.016$). Tree species diversity varied significantly with the planting regime. All planting regimes, but for the no management regime under the baseline and the HADCM3 climate scenario, led to higher species diversity compared to the stocking standards (Wilcoxon signed ranks test $P < 0.001$, Fig. 9). The diversity resulting from the diversification regime was the highest under all climate scenarios. The stocking standards together with the no management regime led to relatively low species diversity (Fig. 9).

Effect on harvest rates

Harvesting levels and requirements were kept constant for the first 80 yr after which the newly planted species could also be harvested (see the method section). On a landscape level, harvest rates declined until approximately the year 2040 after which they slowly increased again (Fig. 4f). Harvest rates were generally significantly higher under the CGCM3 climate scenario than under the baseline scenario (Wilcoxon signed ranks test $V = 1459$, $P < 0.001$), but significantly lower under the HADGEM climate scenario compared to the baseline (Wilcoxon signed ranks test $V = 4729$, $P < 0.001$). Under the HADCM3 climate scenario, harvest rates were comparable to those under the baseline scenario (Wilcoxon signed ranks test $V = 2935$, $P < 0.159$).

As with other indicators, harvest rates significantly depended on the planting regime (Fig. 10). The adding Douglas-fir and adding lodgepole pine regimes resulted in significantly higher harvesting rates than the stocking standards under baseline climatic conditions (Wilcoxon signed ranks test adding Douglas-fir: $V = 1913$, $P = 0.036$, adding lodgepole pine: $V = 590$, $P < 0.001$). Harvesting rates under the adding ponderosa pine and adding western larch regimes were similar to those under the stocking standards (Wilcoxon signed ranks test adding ponderosa pine: $V = 2461$, $P = 0.827$, adding western larch: $V = 2328$, $P = 0.499$). However, harvesting rates under the diversification regimes were significantly lower than under the stocking standards (Wilcoxon signed ranks test $V = 3911$, $P < 0.001$).

Under the climate scenarios, the adding Douglas-fir and adding lodgepole pine planting regimes consistently resulted in higher harvesting rates than the stocking standards (Wilcoxon signed rank test, all $P < 0.001$). The diversification regime, on the other hand, consistently resulted in significantly lower harvesting rates (Wilcoxon signed ranks test, all $P < 0.001$). The adding ponderosa pine regime led either to higher (CGCM3 climate scenario: Wilcoxon signed ranks test $V = 1410$, $P < 0.001$, HADGEM climate scenario: Wilcoxon signed ranks test $V = 1422$, $P < 0.001$) or to similar (HADCM3 climate scenario: Wilcoxon signed ranks test $V = 1996$, $P = 0.069$) harvesting rates, as well as the adding western larch regime (CGCM3 climate scenario: Wilcoxon signed ranks test $V = 1872$, $P = 0.025$, HADCM3 climate scenario: Wilcoxon signed ranks test $V = 1953$, $P = 0.049$, HADGEM climate scenario: Wilcoxon signed ranks test $V = 2025$, $P = 0.086$).

On the ecoregion level, harvest rates were generally significantly higher under the adding lodgepole pine regime than under the stocking standards in the coldest and cold fir–spruce ecoregions and in the moderate fir–hemlock ecoregion (see Appendix S1: Table S6 and Appendix S2: Figs. S10–S13). In the moderate pine ecoregion, harvest rates were generally significantly higher under the adding Douglas-fir regime than under

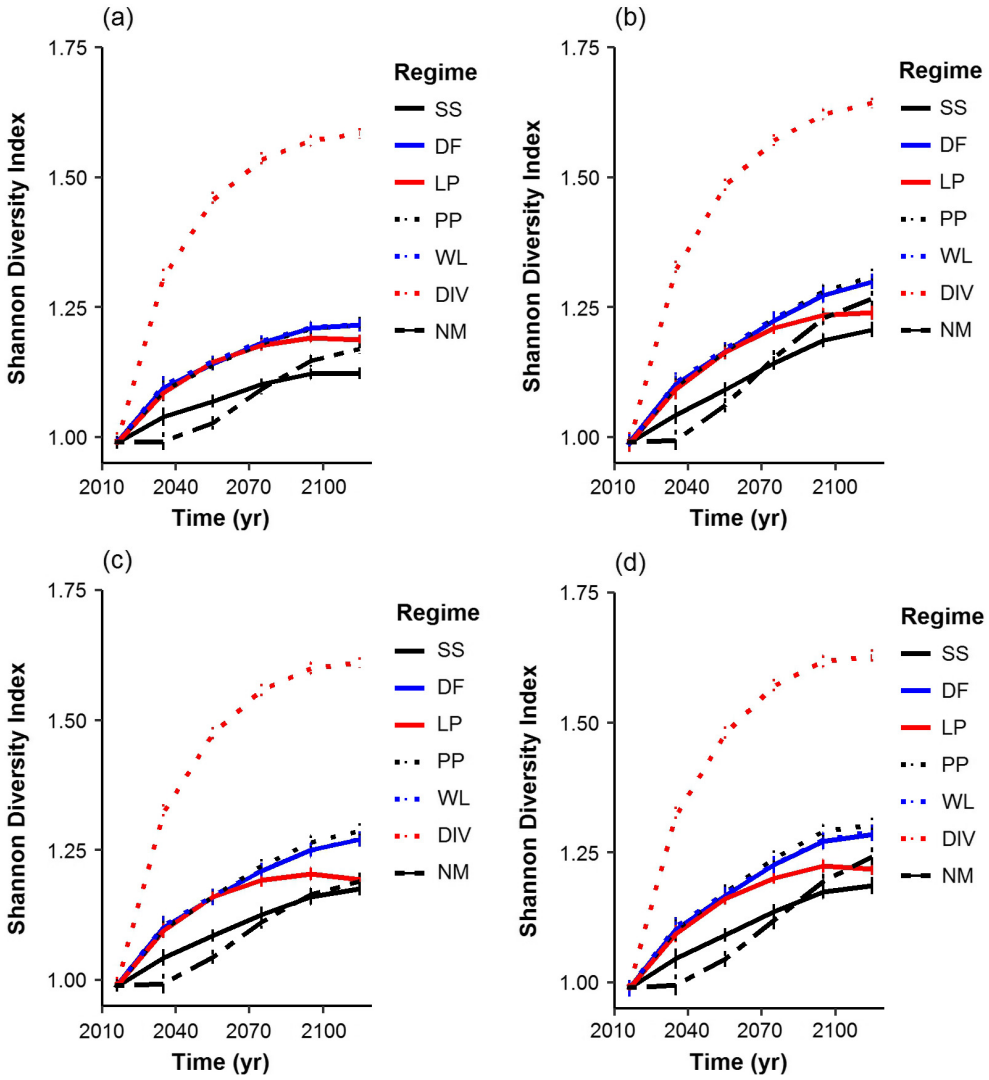


Fig. 9. The species diversity (based on the Shannon diversity index) over time per planting regime and climate scenario. Error bars show the standard deviation over the 20 replicates. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification; NM, no management or planting.

the stocking standards. Harvest rates were significantly lower under the diversification regime than under the stocking standards in all these ecoregions. There were no planting regimes that resulted in significantly higher or lower harvest rates than the stocking standards in the warmest spruce–pine–aspen ecoregion.

Effect on species composition

As mentioned before, the most dominant tree species (represented by the percentage of grid cells in which the aboveground biomass of the species is more abundant than that of other tree species) are currently subalpine fir and lodgepole pine (Fig. 2; Appendix S1: Table S7). Subalpine fir dominates at the higher-elevation and colder areas, while lodgepole pine leads in the valley bottom. Deciduous species become co-dominant with lodgepole pine and interior spruce on the eastern edge, which is the warmest and driest area. If the stocking standards remain in place and the climate remains unchanged, subalpine fir

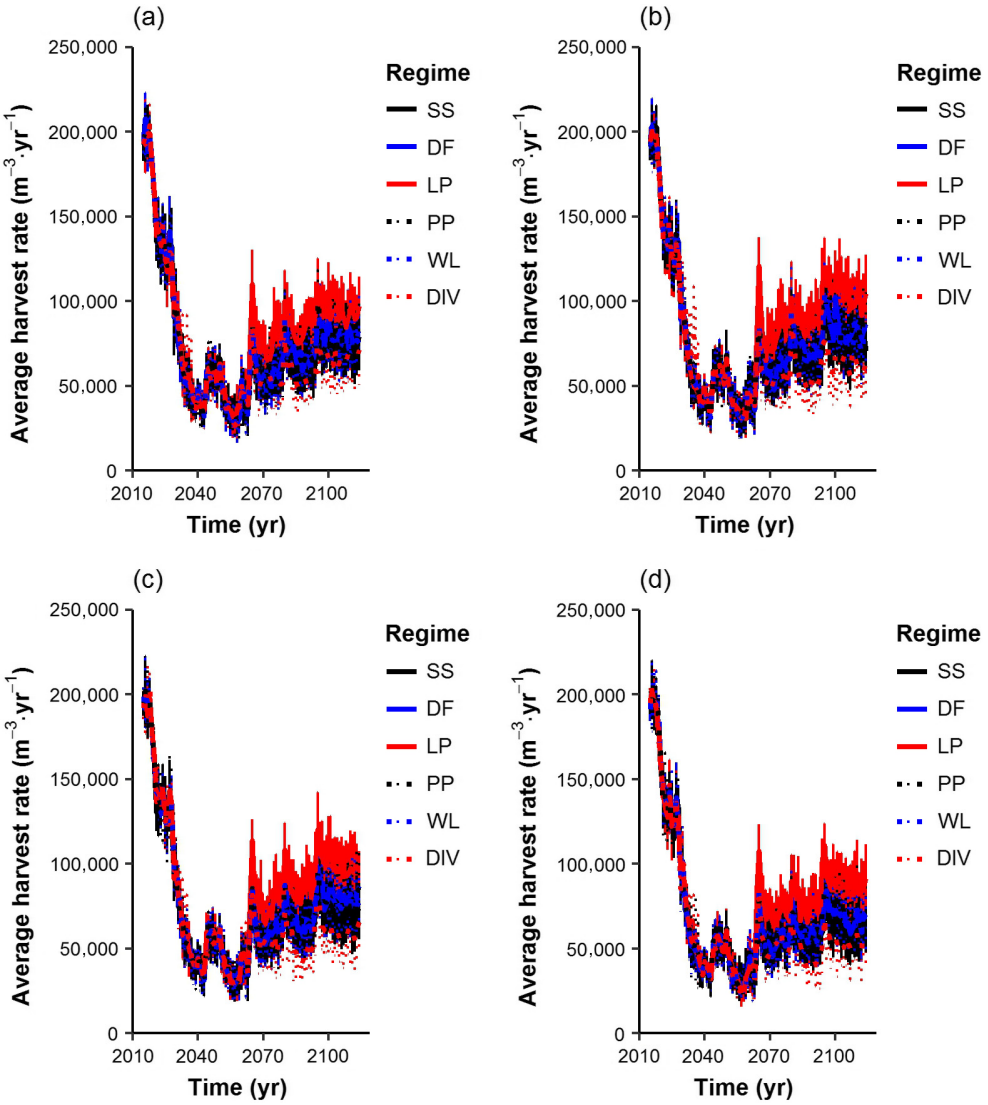


Fig. 10. The average harvest rate over time per planting regime and climate scenario. Error bars show the standard deviation over the 20 replicates. SS, stocking standards; DF, adding Douglas-fir; LP, adding lodgepole pine; PP, adding ponderosa pine; WL, adding western larch; DIV, diversification.

and lodgepole pine will continue to dominate the landscape but to a lesser degree (Fig. 11a; Appendix S1: Table S7). Hybrid spruce is increasingly the leading species, especially in the three warmer ecoregions in the center and east side of the study area, dominating 21% of the area under baseline climate conditions due to planting. These three species remain the most dominant in 2115 despite different planting regimes. Under the stocking standard, western larch and Douglas-fir are being planted by LANDIS-II in the warmest spruce–pine–aspen ecoregion. By 2115, western larch dominates 1.49% of the landscape, concentrated in the southeast corner, but Douglas-fir hardly occurs as a leading species (Fig. 11a). Adding Douglas-fir to the planting simulation in the moderate pine and moderate fir–hemlock ecoregions, which is being done in the adding Douglas-fir planting regime, is successful in that Douglas-fir dominated 8.7% of the landscape after 100 yr, mostly in the valley floor, central to the study area. It also leads to 6.2% lower dominance

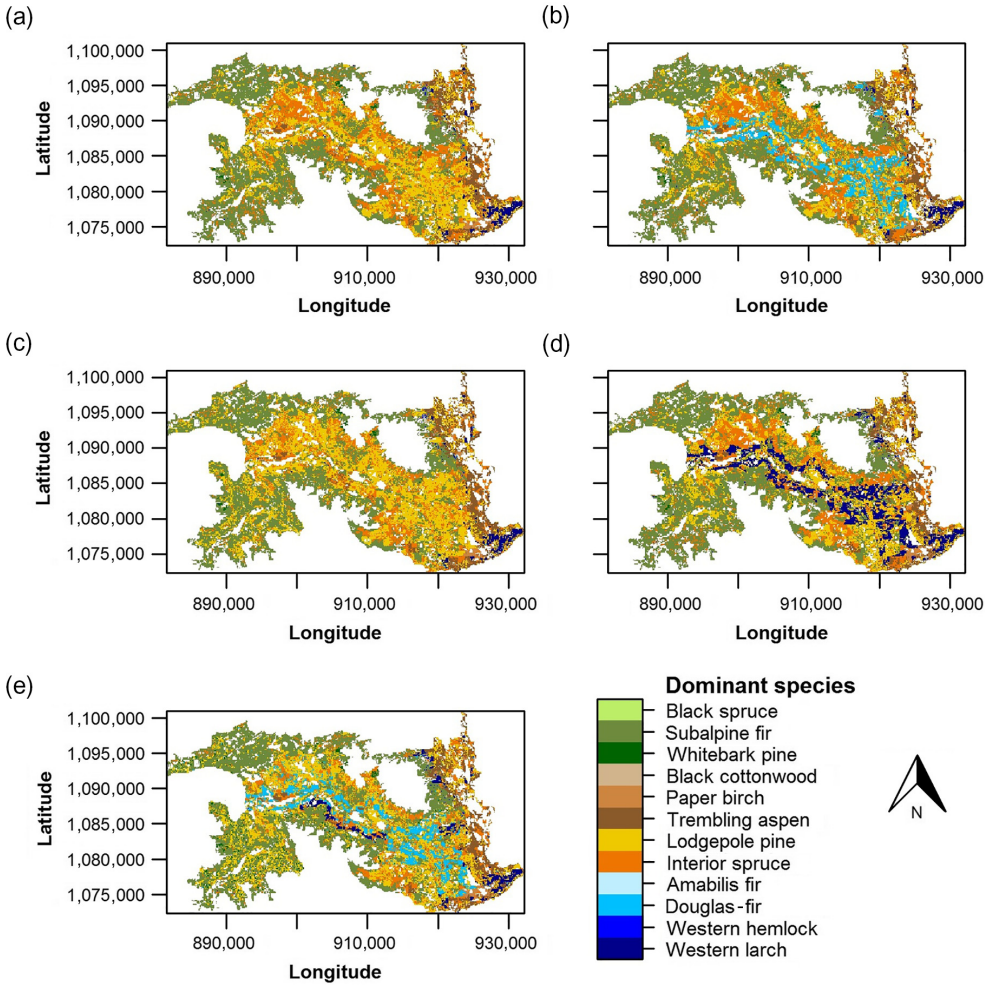


Fig. 11. The dominant tree species in the landscape under the baseline climate scenario per planting regime in 2115. The results of one of the simulations, thus not the average of all replications, is shown: (a) stocking standards, (b) adding Douglas-fir, (c) adding lodgepole pine, (d) adding western larch, and (e) diversification.

of lodgepole pine (Fig. 11b). The simulations with adding lodgepole pine to the planting in the coldest and cold fir–spruce and moderate fir–hemlock ecoregions increased its dominance by 6% of the landscape, largely replacing interior spruce in the coldest fir–spruce ecoregion (Fig. 11c). Western larch is successful in the new ecoregions of moderate pine and moderate fir–hemlock, dominating the central valley floor (10% of the landscape) and replacing both lodgepole pine and interior spruce as leading species (Fig. 11d). The map of dominant species under the diversification regime looks like a blend of the single novel species maps (Fig. 11e). The coldest fir–spruce ecoregion has area shifted from interior spruce to lodgepole pine. The moderate pine shifting to more Douglas-fir, and the moderate fir–hemlock, is dominated by more western larch. The cold fir–spruce ecoregion is largely consistent with the stocking standards except for the sprinkling of cells dominated by whitebark pine. In the diversification regime, black spruce, western redcedar, and whitebark pine were planted in addition to several traditionally planted species (Table 2). Western redcedar did not initially occur in the landscape. After 100 yr of planting, there was a small amount present but it was not the dominant species in any of the grid cells (Fig. 11e; Appendix S1: Table S7). Black spruce was not dominant in any of the grid cells either but the dominance

of whitebark pine increased from 0% to 2%. Adding ponderosa pine was largely ineffective and changing the leading species with only 0.6% of the area after 100 yr (map not shown). Similarly, when no management occurred, the projected future dominance of species is similar to the projected future under the stocking standards (map not shown).

Even with no climate change effects, the diversification regime did not lead to the desired proportions as stipulated by the benchmark (Fig. 12). Whereas the desired species were present, the proportions per tree species were not always met. Lodgepole pine became more dominant at the expense of hybrid spruce in all but the warmest spruce–pine–aspen ecoregion. Douglas-fir was somewhat too dominant in all but the warmest spruce–pine–aspen ecoregion where it was underrepresented. In the warmest spruce–pine–aspen ecoregion, the proportion of black cottonwood (*Populus trichocarpa*)/trembling aspen/paper birch (*Betula papyrifera*) was much too large. Running several other diversification strategies where the species planted differed did not significantly improve the proportions (data not shown).

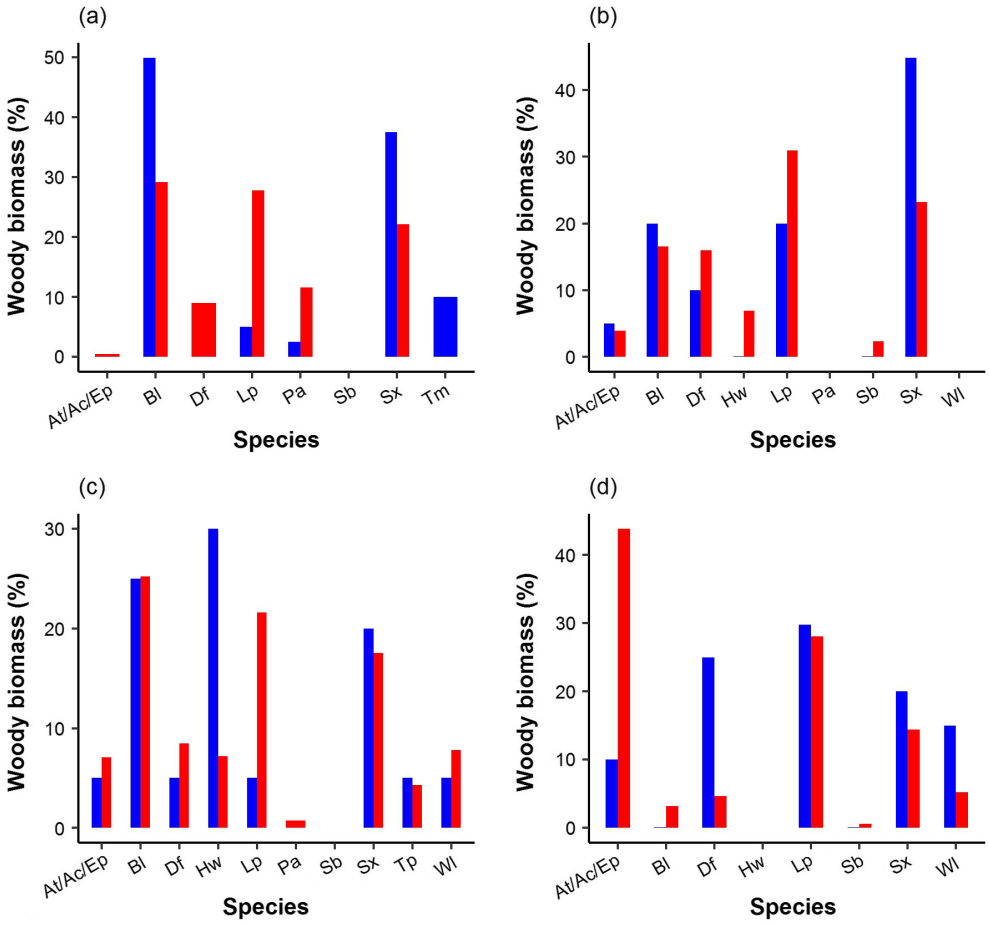


Fig. 12. The percentage woody biomass per species according to the benchmark for each ecoregion (blue bars) and under the diversification planting regime and the baseline climate conditions (red bars); (a) the coldest and cold fir–spruce ecoregions, (b) the moderate pine ecoregion, (c) the moderate fir–hemlock ecoregion, and (d) the warmest spruce–pine–aspen ecoregion. Ac/At/Ep: mix of black cottonwood, trembling aspen, and paper birch; Bl: subalpine fir; Df: Douglas-fir; Hw: western hemlock; Lp: lodgepole pine; Pa: whitebark pine; Pp: ponderosa pine; Sb: black spruce; Sx: hybrid spruce; Tm: mountain hemlock (*Tsuga mertensiana*); Tp: western redcedar; Wl: western larch.

Discussion

The climate is changing (IPCC 2013). However, there are many possible futures, and climatologic effects on the forest ecosystem in our study region differed per scenario. For the study region as a whole, if no adaptive forest management occurs, and if the changing climate will follow the HADGEM climate scenario that predicts the highest increase in mean annual temperature and the largest decrease in average precipitation in comparison with the other scenarios, the aboveground carbon stocks in the forest will increase a little but the NPP, NEP, and NBP all will decrease. These trends will result in a net source of emissions to the atmosphere creating a positive feedback to climate change. If, on the other hand, the CGCM3 climate scenario (an intermediate increase in mean annual temperature and an increase in the average precipitation) proves to be the more accurate scenario, then NPP, NEP, and aboveground carbon stocks will likely increase and the NBP will initially increase and will then remain stable. It is important to note that increased productivity does not necessarily equate to increased carbon sequestration (Körner 2017); that is, CGCM3 scenario result in a higher NPP, NEP, and aboveground biomass than the baseline conditions but the NBP is the same because of increased decay and loss of dead organic matter and soil carbon stocks. Increased decay rates occurred because of warmer temperatures and therefore shorter residence time in the soil and dead organic matter. If the HADCM3 is the more accurate scenario (the lowest increase in mean annual temperature and a small decrease in average precipitation), then we will not observe many changes but for an initial increase in the NBP after which it is projected to decrease, netting a source of emissions. These results indicate that the biological system is most sensitive to forecasted changes in precipitation, which is in agreement with findings by Dymond et al. (2016) who only tested an ensemble of climate futures. The differences in the projected future temperature and precipitation regimes lay at the foundation of these variable results, and unless the climate scenarios will become more in agreement with each other, it is impossible to predict the changes in the NPP, NBP, and carbon stocks in our study region accurately. Forest managers will therefore have to deal with a high level of uncertainty, thus increasing the importance of resilience.

The simulations themselves generate some more uncertainty. We chose not to alter fire regimes following the climate scenarios because it has been predicted that future changes to the fire regimes will be small (Haughian et al. 2012), but this may not hold true. An increase in fire frequency could be beneficial or detrimental to certain species. Also, since no large outbreaks of mountain pine beetle infestations, one of the prime pests to cause future damage to Canadian forests (Johnston et al. 2010), have occurred in our study region in the recent past, we only accounted for the occurrence of one to two short outbreaks, causing a relatively small amount of lodgepole pine to die. It is, however, possible that a larger outbreak of mountain pine beetles will occur in the future. In addition, other pests or pathogens may cause damage we did not account for.

Our results do indicate that, irrespective of the climate scenario, the stocking standards generally led to lower indicators of resilience for species diversity, biomass stocks, and lower or similar NPP, NEP, and NBP compared to targeted adaptation regimes across all climate scenarios, including the baseline. These results suggest that the stocking standards, which already include some adaptation provisions, need to be adjusted further if we want to mitigate negative effects of climate change.

Furthermore, our results showed that, surprisingly, the no management regime leads to the smallest increase in aboveground biomass stocks. This is likely because most of the forest consists of old growth and neither harvesting nor planting occurred in this regime, but trees did continue to grow and die due to, for example, fire and mountain pine beetle infestation. Indeed, aboveground biomass stocks under the no management regime were relatively stable over time in comparison to those under planting regimes, except for under the HADGEM climate scenario they declined; likely due to decreased growth rates and increased mortality rates related with adverse climate conditions.

Targeted adaptation by adding individual novel species to planting regimes led to variable results that depended on the ecoregion and climate scenario. For instance, planting ponderosa pine or western larch had beneficial effects on the species

diversity and, depending on the climate conditions experienced, potential beneficial effects on the harvest rates. The planting ponderosa pine regime, however, only leads to high amounts of aboveground biomass in the warmest ecoregion, the warmest spruce–pine–aspen ecoregion, and especially so under the HADGEM climate scenario. Planting Douglas-fir had beneficial effects on the species diversity and resulted in higher harvest rates than the stocking standards irrespective of the climate conditions experienced. The effects were, however, relatively minor and not always consistent across ecoregions. The fact that the NEP is projected to increase in the future under nearly all planting regimes under baseline and CGCM3 climate conditions but to decrease under all but the diversification regime under HADGEM climate conditions may indicate a stronger influence of among others climate and past disturbance and management than differences in planting regimes on NEP (Böttcher et al. 2008).

The adding lodgepole pine regime differed from the stocking standards in three of the five ecoregions and generally had larger effects on the resilience indicators than the addition of the other single species. Comparing with the stocking standards, adding lodgepole pine generally increased diversity, aboveground biomass, growth rates, and harvest rates. The higher harvest rates was likely due to lodgepole being available to harvest at age 50 while the other species could not be harvested until age 80. Lodgepole pine is a valuable tree species for the timber industry, and even though our results suggest that it can be exploited over a larger part of the study region than is currently used, there are certain aspects regarding lodgepole pine stands that we were unable to account for in our model. Lodgepole pine is sensitive to many pathogens, diseases, and other abiotic factors such as seedling breakage by heavy snowfall (Van der Kamp and Spence 1987, Woods et al. 2000, Teste and Lieffers 2011). Dothistroma needle blight has, for instance, caused large mortality in pine stands in British Columbia, which was linked to changing weather patterns and climate change (Woods et al. 2005, Welsh et al. 2014). Another potential negative effect of increasing the proportion of pine, be it lodgepole, ponderosa, or whitebark, is the increased risk of infestations by the mountain pine beetle in British Columbia (Dymond et al. 2006). Even though we did account for some level of damage caused by mountain pine beetle outbreaks, the levels we accounted for may be over- or underestimations. The sensitivity analysis showed that a reduced growth rate of lodgepole pine may significantly affect the results. We therefore stress the importance of assessing the current and predicting the future levels of damage caused by these biotic and abiotic factors before drawing conclusions from our simulations regarding potential benefits of planting more lodgepole pine than at present.

In contrast to adaptation by adding individual species, the performance of the diversification regime was more consistent. Compared to the stocking standards, the diversification regime increased the following indicators of resilience: tree species diversity, aboveground biomass, NPP, NEP, and NBP. It, however, generally decreased the harvest rates. Given that the biomass stocks increased under the diversification regime but the achieved harvest decreased, it may be that the harvest model parameters could be adjusted so that the results were similar to the single-species addition rates. Effects were smaller or non-existent in the warmest spruce–pine–aspen ecoregion likely because it had the most diverse planting program under the stocking standard regime (four species) and the diversification regime only added subalpine fir and black spruce, neither of which were projected to increase their productivity with climate change in that ecoregion (Appendix S1: Table S2). Our results for the diversification regime are somewhat comparable to the findings reported by Duveneck and Scheller (2015) who simulated planting of three climate suitable deciduous species from warmer regions into the boreal–temperate transition zone. Their results showed that under a low emission scenario, aboveground biomass stocks and harvest rates were unaffected by climate change, but adding climate suitable species increased both metrics. Under a high emission scenario, climate change decreased aboveground biomass stocks and harvest rates, but less so with the climate suitable planting. Our study represents a middle ground between current practices and more aggressive out planting like in the study by Duveneck and Scheller (2015). While in their study the effect of planting a mix of three tree species that were absent or present in low abundance in their study regions was simulated, we simulated the effect of single novel trees added and the effect of a

diversification regime in which we planted a suit of species based on existing plans for diversification benchmarks within the region developed through a stakeholder-consultation process (Mah and Astridge 2004), which is likely to increase the acceptance by foresters. While our diversification regime approached some targets of the benchmarks, especially for the species present, it did not reach expected proportions within 100 yr. Generally, the proportion of lodgepole pine was too large, suppressing species like hybrid spruce. The fact that the benchmarks were developed for much larger areas than our study region may be one reason for this discrepancy. A second factor contributing to the discrepancy is that the model only planted species as equal proportions, but the benchmarks often target very different proportions. It is further likely that not only the planting regimes but also the harvest regimes would have to be altered extensively to reach the proportions as stipulated by the benchmark by 2115.

Our findings that the diversification regime increased several indicators of forest resilience concur with those of others, indicating that higher tree species diversity may lead to higher stocks of organic carbon in forest soils and to higher productivity levels (Zhang et al. 2012, Gamfeldt et al. 2013, Vesterdal et al. 2013, Liang et al. 2016). A study of forest management adaptation options in Austria, while more comprehensive than ours, found options like promoting mixed stands of species adapted to changing climatic conditions, forestry techniques encouraging complexity, and increased intensity of forest management were available to move away from current management and reduce vulnerability in timber supply, carbon stocks, and productivity although not necessarily to zero vulnerability (Seidl et al. 2011). It has also been found that diversifying the forest in combination with harvesting the most dominant or high-risk tree species may lead to greater ecological resilience, higher harvest rates, and higher net revenue over time than business-as-usual strategies (Dymond et al. 2014, 2015*b*). However, those studies also demonstrated that it may not be possible to increase the diversity of some forests through planting alone. Jactel et al. (2005) found that tree species diversity increased the resilience of trees to insect pest damage. In a comprehensive synthesis, Thompson et al. (2009) also concluded that most scientific studies strongly support that forest resilience is dependent on biodiversity at multiple scales. Several studies provide evidence that species diversity, and especially functional diversity, is positively linked with the stability and recovery potential of forest ecosystems and with their tolerance to extreme environmental conditions (Walker 1995, Tilman 1996, Peterson et al. 1998, Noss 2001). Diversification to manage uncertainty is, however, not straightforward in the timber sector since it is vulnerable to changes in the international market (Ince et al. 2011, Keenan 2015).

Conclusions

This study identified both potential positive and negative impacts of climate change, depending on the existing forest ecosystem, potential future climate, and management choices. In the face of this uncertainty, increasing species diversity where possible appears to be a potential way to increase ecosystem resilience including increasing carbon sequestration. The question arises whether there is an optimal species diversity and whether there is a threshold after which ecosystem resilience does not further increase or even decreases. In our diversification regime, we planted a limited number of novel species in the study region. The observed variety of the climate scenarios in which it is, for instance, projected to become drier under the HADGEM climate scenario but wetter under the CGCM3 climate scenario can be largely explained by the relatively large variability of future climate change predictions in our study area which is caused by its position in the transition zone where coastal and continental climates meet. The changes in elevation that drive local climates in our study area can help us understand how variability might occur across latitudes. In temperate and boreal forest ecosystems in regions where the variability of future climate change predictions is narrower, more targeted planting recommendations could be drawn up based on our methods. Seeing the rate of ongoing climate change, more species planting trials need to be set up to confirm our findings and that of others and to identify possible problems with, for example, pests and pathogens that we were unable to include in our simulations. Clearly, forest adaptation planning will therefore have to be decided on the local level, rather than broad-brush approaches to ensure the continued provision of ecosystem

services provided by the ecosystem. This will give us the greatest chance at leveraging those adaptation practices to also mitigate climate change.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1981/full