Carbon Sequestration in Managed Temperate Coniferous Forests Under Climate Change

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Abstract. Management of temperate forests has the potential to increase carbon sinks and mitigate climate change. However, those opportunities may be confounded by negative climate change impacts. We therefore need a better understanding of climate change alterations to temperate forest carbon dynamics before developing mitigation strategies. The purpose of this project was to investigate the interactions of species composition, fire, management, and climate change in the Copper–Pine Creek valley, a temperate coniferous forest with a wide range of growing conditions. To do so, we used the LANDIS-II modelling framework including the new Forest Carbon Succession extension to simulate forest ecosystems under four different productivity scenarios, with and without climate change effects, until 2050. Significantly, the new extension allowed us to calculate the net sector productivity, a carbon accounting metric that integrates aboveground and belowground carbon dynamics, disturbances, and the eventual fate of forest products. The model output was validated against literature values. The results implied that the species optimum growing conditions relative to current and future conditions strongly influenced future carbon dynamics. Warmer growing conditions led to increased carbon sinks and storage in the colder and wetter ecoregions but not necessarily in the others. Climate change impacts varied among species and site conditions, and this indicates that both of these components need to be taken into account when considering climate change mitigation activities and adaptive management. The introduction of a new carbon indicator, net sector productivity, promises to be useful in assessing management effectiveness and mitigation activities.

1 Introduction

As a global society, we depend on forests and land to take up about $2.5 + 1.3 \, \mathrm{PgC \, yr^{-1}}$, about one-third of our fossil emissions (Ciais et al., 2013). A reduction in the size of these sinks could accelerate global change by further increasing the accumulation rate of greenhouse gases in the atmosphere. However, even a minor improvement to these biological sinks could help mitigate climate change because of their large scale.

Temperate forests offer many opportunities for increasing carbon sinks; however, the risk of negative climate change effects and poor management decisions may limit these opportunities. For example, starting from 2000 a bark beetle outbreak (*Dendroctonus ponderosae*) caused in part by climate change (warmer winters), combined with the management response (increased logging), created a large carbon emission in the central interior of the province of British Columbia (BC), Canada (Kurz et al., 2008). In contrast, increased tree species productivity due to climate change effects could help create a net carbon sink, even with an increase in wildfire (Metsaranta et al., 2011). Without an integrated, landscape-scale understanding of climate change impacts on forests, we are limited in our management capacity to maintain the existing carbon storage or enhance sink strength.

Forest carbon dynamics depend on the management regime, expected growth and mortality rates, regeneration ingress, decomposition rates, and natural disturbances (Canadell and Raupach, 2008). The existing literature documents the complexity of forest carbon dynamics to potential

rising temperatures, changing precipitation patterns, increasing atmospheric CO_2, and nitrogen availability. For example, stand-level modelling of future conditions in Colorado found that projected carbon stocks varied with future climate scenarios, and in some cases stocks decreased as the area became non-forested due to a loss of tree species viability (Buma and Wessman, 2013). In their study, adaptive management maintained forest carbon stocks in most climate scenarios, but with different species and lower tree densities than currently occur in the ecosystem. In contrast, results from Oregon using an earth system model projected increased net primary productivity and net biome productivity in the future forest ecosystem, although more intensive management increased net emissions (Hudiburg et al., 2013). Other studies have found minor climate change effects on net primary productivity and forest carbon stocks and that greater differences were caused by local variation in growing conditions (e.g. Scheller et al., 2012). Because of these divergent results, climate change effects on temperate forests are not yet generalisable.

An additional aspect of forest carbon dynamics typically excluded from ecosystem studies is the storage of carbon in harvested wood products. The storage and emissions from wood products have been shown to be important for considering emissions due to forest management, climate change mitigation activities, and life cycle assessments (e.g. Hennigar et al., 2008; Smyth et al., 2014; Lamers et al., 2014). While the combination of ecosystem and wood product carbon dynamics is recognised as important, there is a mixture of indicators (typically stocks) and terms in the literature. Here we propose a new metric, net sector productivity, to facilitate calculation and comparison among studies. This metric is based on the net ecosystem productivity minus emissions from disturbances and wood products.

Our purpose was to improve our understanding of the interactions of species composition, climate change, fire, and management in temperate forest ecosystem carbon dynamics. The Copper–Pine Creek valley in north-western BC provides an exemplary landscape because it includes a variety of forest ecosystems with naturally varying climate envelopes, tree species composition, management activities, and natural disturbance rates within a relatively small area of under 750 km^2. Furthermore, a recent study in a neighbouring area by Nitschke et al. (2012) demonstrated stand-level responses to climate change as an interaction of species response, existing stand conditions, disturbance type, competition, and resource availability. To achieve our purpose, we had the following objectives: (1) project species productivity in different site types using downscaled circulation model projections and a mechanistic tree species productivity model; (2) parameterise a new extension of the LANDIS-II landscape model that estimates ecosystem carbon dynamics; (3) assess model behaviour by comparing it with the available literature on carbon stocks and fluxes; (4) project ecosystem dynamics until 2050 under different productivity scenarios; and

(5) assess the landscape-scale responses of carbon fluxes and stocks under climate change.

2 Methods

2.1 Study area

The study area is 734 km^2 of forest and woodland in north-western BC (Fig. 1). Bounded on the east by the town of Smithers and agricultural land, the predominantly conifer forests cover the narrow valley bottom, rolling hills, and steep mountain sides. The climate is in transition between the coast and the continent with cold, snowy winters and mild, dry summers (mean annual temperature ranges from 0.5 to 3.1 °C). The treed area has been mapped into seven biogeoclimatic zones (BC Environment, 1995) which also form the LANDIS-II ecoregions for the modelling (Table 1). The forest is predominately unharvested and mostly over 100 years in age (Fig. 2).

2.2 Model structure, parameters, and carbon indicators

We simulated the forest dynamics using LANDIS-II, a spatially explicit forest landscape modelling framework used to integrate ecosystem processes, management, and disturbances (Scheller et al., 2007). LANDIS-II is a framework within which users can choose amongst different extensions to simulate stand dynamics and disturbances. The 39-year simulation period (2012–2050) was run at a 100 × 100 m grid cell resolution and a 1-year time step.

The Forest Carbon Succession v2.0 (ForCSv2) extension for LANDIS-II calculates how cohorts of trees reproduce, age, and die (Dymond et al., 2012). Furthermore, changes in cohort biomass carbon, dead organic matter (DOM), and soil carbon are tracked over time (Fig. 3). In addition to the carbon stocks for each of 14 pools, ForCSv2 reports the fluxes: turnover, net growth, net primary production (NPP), heterotrophic respiration (R_h), net ecosystem productivity (NEP, NPP minus R_h), net biome productivity (NBP, NEP minus losses due to disturbances), transfers between pools, losses from the ecosystem due to logging, and carbon emissions due to decay or combustion. The accumulation of biomass carbon through growth and reproduction generally follow the Biomass Succession (v2) extension and the methods outlined in Scheller and Mladenoff (2004). The primary exceptions are that we added root pools and their growth, turnover, and mortality dynamics, and added greater user control over disturbance impacts. For the Copper–Pine Creek study area, root parameters were based on literature values (Li et al., 2003; Mokany et al., 2006; Yuan and Chen, 2010). The modelling of decay in dead organic matter and soil pools generally follows the methods described in Kurz et al. (2009). That paper also provided the decay parameters for the Copper–Pine Creek study. More detail is available in

Table 1. Ecoregions for LANDIS-II, biogeoclimatic variant names as used in BC, and fire regime zones as used in this study.

Ecoregion number[a]	Biogeoclimatic variants[b]	Climate[c] MAT[c] (°C)	1961-90 MAP[d] (mm)	Climate MAT (°C)	2040-69 MAP (mm)	Fire regime zone	Fire return interval
1	Engelmann spruce – subalpine fir, moist cold parkland	0.3	1307	2.8	1404	Upper slopes	700
2	Engelmann spruce – subalpine fir, wet very cold parkland	0.5	1602	2.9	1732	Upper slopes	700
3	Engelmann spruce – subalpine fir, moist cold	1.4	1081	3.8	1161	Upper slopes	700
4	Engelmann spruce – subalpine fir, wet very cold	1.6	1291	4.0	1395	Upper slopes	700
5	Sub-boreal spruce, moist cold, Babine	2.2	851	4.6	910	Lower slopes	400
6	Interior cedar – hemlock, moist cold, Nass	2.3	899	4.7	964	Lower slopes	400
7	Sub-boreal spruce, dry cool	3.1	521	5.5	548	SBSdk	200

[a] Ecoregion number based on rank order of mean annual temperature. [b] BC Environment (1995). [c] Source: PCIC (2012). [d] Mean annual temperature. [e] Mean annual precipitation.

the user's guide (Dymond et al., 2015). Terminology follows Chapin et al. (2006) and positive values of NEP and NBP indicate forest sinks.

The ForCSv2 extension is integrated with harvesting, fire, and wind extensions of LANDIS-II. When a disturbance occurs, species-age cohorts may be killed by the disturbance extension. The transfers of carbon from biomass pools to dead organic matter, air, or the forest products sector are controlled by user input. In addition, disturbances can trigger emissions and transfers from the dead organic matter or soil pools. For the Copper–Pine Creek study area, wildfire impacts on carbon pools were based on Campbell et al. (2007). For harvest impacts, the model transferred 80 % of the merchantable-sized wood biomass out of the ecosystem during an event; any other killed biomass was transferred to the DOM pools.

LANDIS-II has stochastic processes including wildfires and natural regeneration. Therefore, we calculated landscape averages and standard deviations from 20 Monte Carlo replicates to conduct t tests comparing the results without climate change effects against the results from the average productivity with the climate change scenario in 2050.

The harvested carbon output from ForCSv2 was run through the British Columbia Harvested Wood Product (v1) model (Dymond, 2012) to estimate storage and emissions on an annual basis. Those wood product emission estimates and wildfire emissions were subtracted from NEP to calculate the net sector productivity (NSP).

2.3 Model input data

2.3.1 Growth and reproduction

For the Copper–Pine Creek study area we gathered species life history parameters required by ForCSv2 from the literature (Table 2). The main sources of information were Klinka et al. (2000) and Burns and Honkala (1990). Additional information for *Populus tremuloides* (At, trembling aspen) and *P. balsamifera* (Ac, poplar) was available from Peterson et al. (1996). However, these reviews provided insufficient information for parameterising the seed dispersal algorithm in ForCSv2. We found additional information on seed dispersal for *Picea Engelmannii X glauca* (Sx, interior spruce; Squillace, 1954; Roe, 1967), *Pinus contorta* var. *latifolia* (Pl, lodgepole pine; Boe, 1956; Dahms, 1963), trembling aspen (McDonough, 1986), *Tsuga heterophylla* (Hw, western hemlock; Pickford, 1929; Beach and Halpern, 2001), poplar (Zasada et al., 1981), *Abies amabilis* (Ba, amabilis fir; Heatherington, 1965), and *Betula papyrifera* (Ep, paper birch; Bjorkbom, 1971; Greene and Johnson, 1995). Longevities were capped at the maximum ages documented in the local forest inventory to reflect local conditions.

The spatial forest inventory data set maintained by the Government of BC provided the plant species and age information for the initial communities map (BC MFLNR, 2011). The leading species in the inventory was most frequently *Abies lasiocarpa* (Bl, subalpine fir; 62 %) and the second most frequent was lodgepole pine (14 %). Most stands did not have a second species listed (76 % of area). When it was listed, the second species was most frequently interior spruce.

For each ecoregion, historical daily weather data were collected from corresponding meteorological stations and anal-
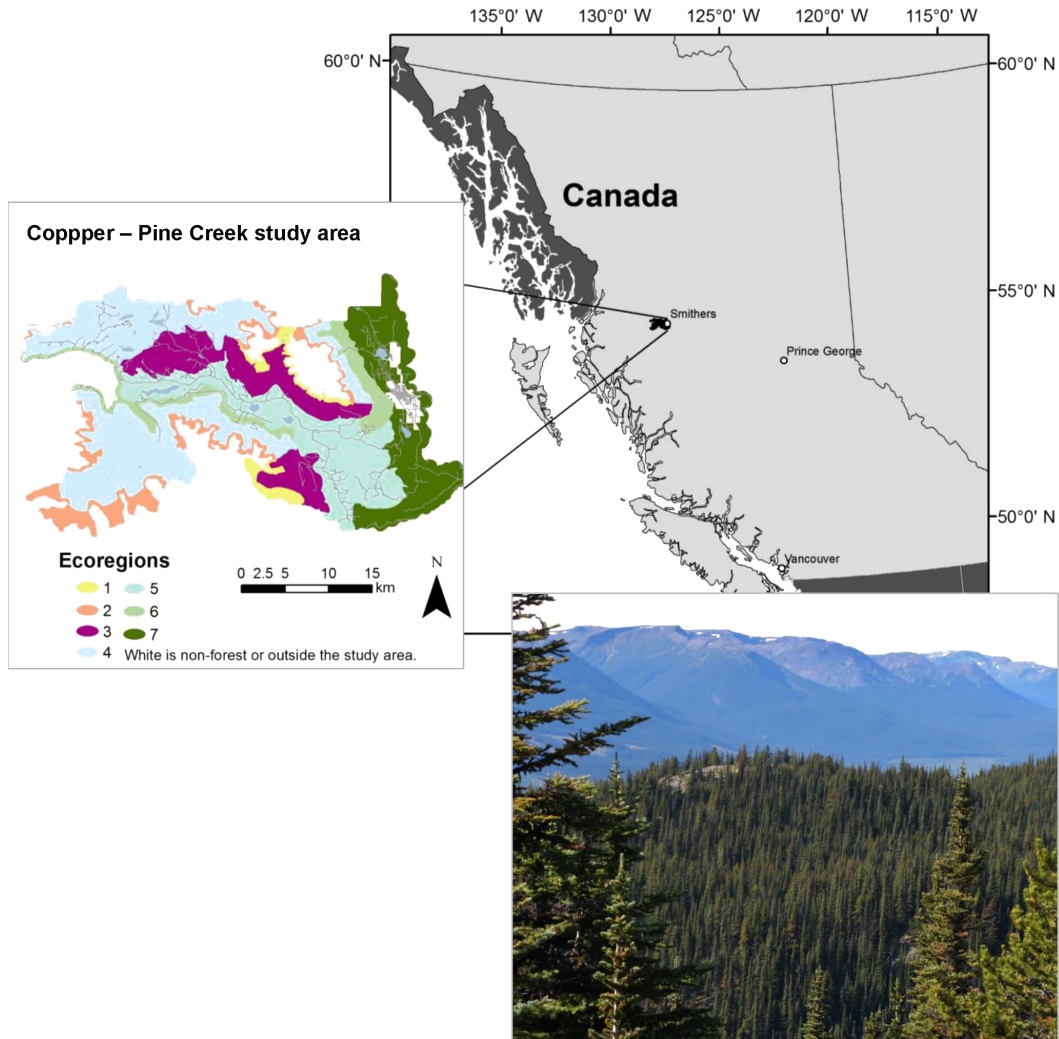
Figure 1. The Copper–Pine Creek study area (black polygon) near Smithers, Canada; ecoregions for LANDIS-II modelling and photograph looking south-west across part of the study area. See Table 1 for ecoregion descriptions.

ysed using a rank and percentile test. Based on the rank and percentile test, 10 historical years of climate data were selected for each ecoregion and used as the historical climate scenarios in the analysis. The 10 years of data represent the 90th, 75th, 50th, 25th, and 10th percentiles for both observed annual precipitation and mean annual temperature (Nitschke et al., 2012). A direct adjustment approach was used to create climate change scenarios from the selected historical climate data and global climate model (GCM) predictions for the study region (Nitschke et al., 2012). Monthly outputs from five GCMs were obtained from the Pacific Climate Impacts Consortium (PCIC, 2012). The GCMs and emission scenarios selected were Hadley GEM-A1B, Hadley CM3-A1B, MIROC HIRES-A1B, GISS AOM-A1B, and Canadian GCM3-A2. Climate change is projected to increase the study area's mean annual temperature by 1 to 3.5 °C by the 2041–2070 period, depending on the global climate models (PCIC,

2012). Mean annual precipitation projections are more variable, with models showing increasing, decreasing, or unchanging precipitation. The monthly minimum and maximum temperatures and precipitation were used to model the probability of establishment (P_{est}), maximum aboveground net primary productivity (ANPP), and maximum biomass inputs for ForCSv2.

We used the Tree and Climate Assessment Tool Establishment Model (TACA-EM) to estimate the P_{est} through natural regeneration based on parameters in Table 3 using the aforementioned historical and climate change scenarios for each ecoregion (Nitschke and Innes, 2008; Nitschke et al., 2012). TACA-EM estimates the probability of a tree species regenerating naturally given soil and climate site conditions (Nitschke and Innes, 2008). The TACA-EM probabilities are for a 3-year period, so we divided them by 3. The output from TACA-EM was linearly interpolated between climate

Table 2. Life history attributes for LANDIS-II.

Species code	Species	Longevity (years)	Sexual maturity (years)	Shade tolerance class	Fire tolerance class	Effective seed dispersal (m)	Maximum seed dispersal (m)	Probability of resprouts	Minimum age for re-sprouting	Maximum age for re-sprouting	Post-fire regeneration
Ac	*Populus trichocarpa*	200	10	1	3	50	199	0.75	10	199	Resprout
At	*Populous tremuloides*	200	10	1	3	50	499	0.5	10	149	Resprout
Ba	*Abies amabilis*	340	25	5	3	38	120	0	0	0	None
Bl	*Abies lasiocarpa*	400	20	3	3	38	99	0	0	0	None
Ep	*Betula papyrifera*	200	30	2	2	50	470	0	15	199	Resprout
Hw	*Tsuga heterophylla*	325	20	5	3	50	1399	0	0	0	None
Pa	*Pinus albicaulis*	325	10	1	3	50	101	0	0	0	None
Pl	*Pinus contorta*	300	7	1	3	20	199	0	0	0	Serotiny
Sb	*Picea mariana*	250	10	4	3	20	101	0	0	0	None
Sx	*Picea Engelmannii X glauca*	325	30	2	3	30	299	0	0	0	None

Table 3. Life history attributes for TACA-EM and TACA-GAP. See Table 1 for species codes.

Species code	Base temp (°C)	Bud burst (GDD[a])	Chilling req.[b] (Days)	Lethal temp. (°C)	Drought[c] tol.	GDD min	GDD max	Frost tol.	Frost days	Wet soils tol.	AHMI[d]	D max[e] (cm)	H max[f] (m)	A max[g] (yr)	Shade tol.
Ac	4.6	175	70	−60	0.13	258	5263	0.5	295	0.55	62.3	200	4500	250	1
At	3.5	189	70	−80	0.4	227	4414	0.9	284	0.3	40	95	3900	200	1
Ba	4.3	307	91	−35	0.4	206	3877	0.3	305	0.55	41.4	182	6200	440	2
Bl	2.6	119	60	−67	0.25	198	5444	0.9	320	0.75	28.7	150	4100	320	2
Ep	3.7	231	77	−80	0.3	237	4122	0.9	285	0.3	40	76	3000	140	1
Hw	4.1	277	56	−39	0.25	328	5861	0.1	265	0.55	36.8	225	8000	500	2
Pa	3	120	70	−55	0.4	216	3352	0.9	320	0.05	34.2	200	3500	600	1
Pl	2.9	116	63	−85	0.42	186	3374	0.9	320	0.5	37.9	130	4500	335	1
Sb	3	123	56	−69	0.3	144	3060	0.9	305	1	42.7	46	2700	250	2
Sx	2.9	146	45	−58	0.3	139	3331	0.9	305	0.5	43.2	171	5100	430	2

[a] GDD is growing degree days. [b] Req. is requirement. [c] Tol. is tolerance. [d] AHMI is annual heat moisture index. [e] D max is maximum diameter. [f] H max is maximum height. [g] A max is maximum age.
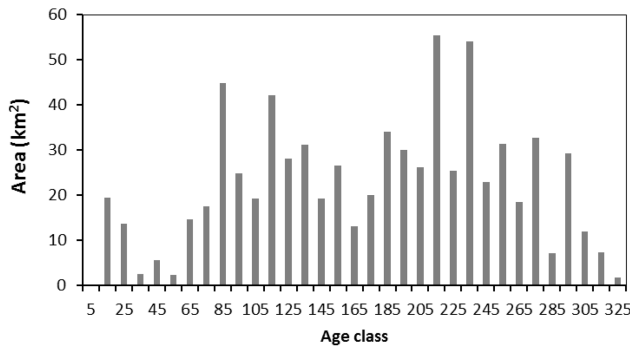

Figure 2. Age class distribution in 2011 for the Copper–Pine Creek study area.

periods and used as annual input to LANDIS-II. The simulation of natural regeneration for each site (grid cell) depends on neighbouring species composition, seed dispersal distances, available light, species shade tolerance, a random number between 0 and 1, and the P_{est} input value (Scheller and Domingo, 2012).

We used the Tree and Climate Assessment Tool Growth and Productivity (TACA-GAP) model to estimate maximum ANPP and maximum biomass variables for each species in each ecoregion. TACA-GAP uses the growth and response functions in the BRIND (Shugart and Noble, 1981) and ZELIG++ (Burton and Cumming, 1995) models, but is run

at a daily time step to incorporate the snow, soil moisture, and phenology components of TACA-EM (Nitschke et al., 2012). The TACA-GAP simulated individual species growth potential (biomass) over a range of soil and climate conditions (Table 3). TACA-GAP is a mechanistic gap model to estimate individual species growth potential (biomass) over a range of soil and climate conditions. The model does not simulate stand dynamics and interspecific competition, but rather the impacts of climate variability on growth over time. Species growth is a function of the maximum height, age, and diameter that a species can empirically achieve modified annually by temperature (sum of growing degree days), drought/soil moisture (proportion of the year underwater deficit), and frost damage (number of growing season frosts). Species parameterisation followed Nitschke et al. (2012). The estimates of maximum potential biomass and maximum potential aboveground net primary production (ANPP) from TACA-GAP were linearly interpolated between climate periods and used as annual input to LANDIS-II. ForCSv2 calculated the actual ANPP for each species-age cohort on a grid cell as a function of the maximum ANPP for a species, the amount of living biomass existing at a site for that species, and competition (the biomass of all existing species and the potential growing space available as provided by the maximum biomass; Scheller and Mladenoff, 2004). Cohort mortality is a function of age, competition, or disturbance impacts. As weather stations are not located in the parkland ecoregions (i.e. 1 and 2), regeneration and biomass variables

were set to 50 % of the non-parkland ecoregion values (i.e. 3 and 4 respectively). From the ensemble of future climate projections, we generated an average and standard deviation for productivity annually for the 2012–2050 simulation period for each species in each ecoregion. To represent the uncertainty in future productivity, we defined the average productivity, low productivity (average minus 1 standard deviation), and high productivity (average plus 1 standard deviation) as scenarios. The growth parameters were "high" for all species in all ecoregions for the high scenarios, or all average, or all low. While it is unlikely that productivity of all species in all ecoregions will go in a single direction, this does give us the bounding box of productivity rates and plausible futures. Further research work will refine these scenarios.

2.3.2 Disturbances

To parameterise the fire regimes we used a combination of available information and scenarios representing possible disturbance regimes. Natural resource managers in the study area typically assume rates of natural disturbance based on the biogeoclimatic zones (BC Environment, 1995). We analysed the fire maps maintained by the Government of BC from the study area and the surrounding region indicated a much lower fire cycle than is assumed by managers (data not shown). Furthermore, studies by Haughain et al. (2012) and Boulanger et al. (2012) also indicate a low fire hazard in the region. Based on the climate parameters and spatial arrangement in the study area, the ecoregions were grouped into the fire regime zones listed in Table 1. The disturbance return intervals for the fire regime zones were assumed to be double those used for forest management. Climate change alterations to the fire regimes are expected to be small, and therefore none were simulated (Haughain et al., 2012).

Given the large impact fires can have on carbon dynamics, we ran 20 Monte Carlo simulations. T tests between the no climate change and the average productivity scenario were used to evaluate whether the impact of climate change on carbon indicators is greater than the interannual variability in fire impacts. Natural resource management in the study area is primarily focused on harvesting, recreation, and cultural values. In BC constraints on harvesting include wildlife trees, old-growth retention requirements, adjacency requirements, visual quality concerns, water quality, and recreation activities. Therefore, we used different management zones in simulating a range of harvesting and reforestation activities. Harvesting and planting prescriptions were based on the forest stewardship plans for the Wetzink'wa Community Forest Corporation (2009) and BC Timber Sales–Babine (2007; Table 4). Local forest managers reviewed the harvest parameters and results for accuracy.
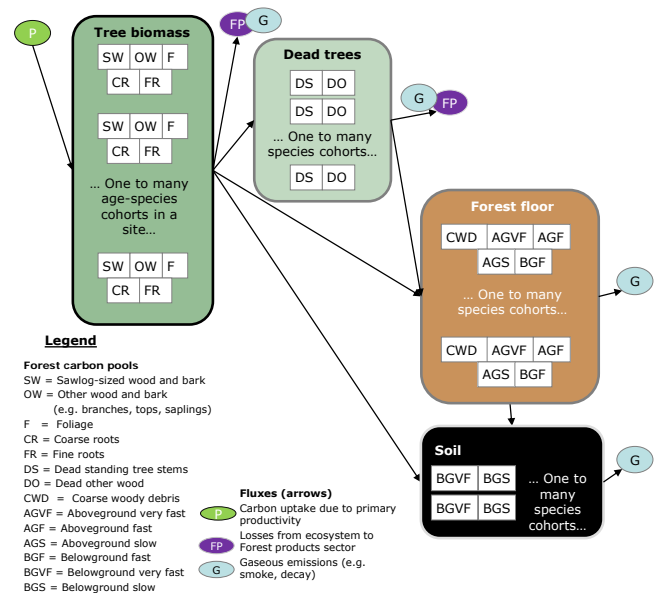

Figure 3. Simplified pools and fluxes represented in the Forest Carbon Succession module (v2) for LANDIS-II. In the left panel, carbon accumulates in the tree biomass pools based on the primary productivity input data. When mortality of a whole or part of a tree occurs, the carbon is transferred to the dead organic matter and soil pools in the three right-hand panels, or may be removed from the ecosystem through harvesting or combustion. As decay occurs, carbon is transferred among the dead organic matter and soil pools, eventually entering the belowground slow pool (BGS) or being emitted from the ecosystem. Fire and harvesting can also cause transfers or emissions from the dead organic matter pools.

3 Results

To determine the credibility of our model results, we conducted a model comparison based on literature values (Table 5). However, the literature review demonstrated that carbon stocks in forests are highly variable with site type and age. The ForCSv2 carbon stock estimates for Copper–Pine Creek were within the range of other published values for temperate coniferous forests, except for the coldest ecoregions (1 and 2), which were relatively low. Likewise, carbon fluxes can vary depending on site type, age, interannual weather patterns, disturbances, and different models. The ForCSv2 results seem reasonable compared to the literature values, except again for ecoregion 1, which had a relatively low NPP and R_h. The NPP and R_h for ecoregion 7 were on the high end relative to the literature values for temperate coniferous forests.

Overall, the probability of establishment decreased by 2050 for most species in most ecoregions (data not shown). The one exception was amabilis fir, which is currently at the northern edge of its range.

Climate change alterations of site-level productivity were projected by the TACA-GAP model. The difference between

Table 4. Summary of management prescriptions for different natural resource managers in the study area – the Wetzin'kwa Community Forest (WCF) and the British Columbia Timber Sales (BCTS).

Name	Time period	Harvest rate (% yr^{-1})	Planting
Pine-targeted clear cut	2012–2017	1 to 1.8	Interior spruce, subalpine fir, lodgepole pine
WCF-Clearcut early	2012–2017	1	Interior spruce, subalpine fir, lodgepole pine
WCF-Clearcut	2018–2060	0.33	Interior spruce, subalpine fir, lodgepole pine
BCTS-Clearcut north-west	2015–2035	2 to 4	Interior spruce, subalpine fir, lodgepole pine
BCTS-Clearcut south-west	2012–2060	0.8 to 1.2	Interior spruce, subalpine fir, lodgepole pine
Forest health patch-cut (1 ha)	2012–2060	0.08 to 0.3	Interior spruce, subalpine fir, lodgepole pine

Table 5. Model comparison of various temperate forest carbon indicators between published values and this study. Means $\pm$ SD. Units are g C m^{-2} or g C m^{-2} yr^{-1}.

Forest carbon indicator	Stand models[a]	Eddy covariance studies[b]	Stock change model[c]	2012, this study		
				Ecoregion 1	Ecoregion 4	Ecoregion 7
Aboveground biomass	2500 to 36 000	4952 ± 3417	8472 to 9786	1160 ± 489	4454 ± 2048	9770 ± 2132
Roots	800 to 8000	1209 ± 875	1876 to 2050	339 ± 207	1301 ± 600	2853 ± 623
DOM and soil	6700 to 16 850		16 016 to 27 619	2384 ± 840	15 855 ± 5157	27 300 ± 6655
Total ecosystem	23 900 to 30 900		28 114 to 41 290	3883 ± 1230	21 610 ± 6848	39 922 ± 8607
NPP		281 ± 127	463 to 541	37.8 ± 24	197 ± 126	642 + 161
R_h		396 ± 155	397 to 578	38.4 ± 13	253 ± 94	563 + 117
NEP		93 ± 185	−36 to 75	−0.55 ± 17	−56.7 ± 89	79.4 + 134
NBP			−93 to 71	−0.55 ± 17	−75.6 ± 375	56.9 + 541

[a] Fredeen et al. (2005) and Kranabetter (2009) sites are in or near the Copper–Pine Creek study area. Gower and Grier (1989); Pregitzer and Euskirchen (2004). [b] Luyssaert et al. (2007); needle-leaved, boreal humid sites. [c] Stinson et al. (2011); Bulkley Valley Timber Supply Area results extracted from the results database. Includes the Copper–Pine Creek study area except ecoregions 1 and 2.

maximum ANPP under the 2041–2070 climate and under the 1961–1990 climate depended on tree species, ecoregion, and global circulation model (Fig. 4). Productivity increased in ecoregions 3 and 4 where all the tree species appear to be currently living in conditions with cooler climates and shorter growing seasons or wetter soils than their optimum conditions (Table 3). In ecoregions 5–7 the results were more variable, depending on the change in conditions relative to the species-specific parameters. Given the decline in productivity by many species in ecoregion 7, these species appear to already be at or beyond optimum climate conditions.

Landscape-scale productivity projections differed in trend and magnitude, depending on whether the ecoregion was cooler and moister (4) or warmer and drier (7). Cooler and moister ecoregions were projected to have significantly higher NPP and NEP because increased species-level productivity outweighed the increasing temperature, causing greater R_h (Fig. 5a and b). Even the low productivity scenario was projected to have greater carbon sinks than no climate change in those ecoregions. The increased carbon sinks resulted in significantly higher carbon stocks in ecoregions 1–4 by 2050 (Table 6). (Results for all ecoregions presented as Supplement Figs. S1 and S2). The statistical tests indicate

when the impact of climate change on carbon indicators is greater than the interannual variability in fire impacts.

For the warmest and driest ecoregion (7), the NPP in the average scenario was projected to decrease significantly by 2050 due to climate change impacts (Fig. 5c and d). Resulting from that decreased productivity and the increased R_h as temperatures increased, the NEP was significantly lower in the average productivity scenario at 2050 (Fig. 5). The range between the low and high productivity scenarios indicates the large uncertainty in future projections. The declines in carbon sinks in the average productivity scenario resulted in significant reductions in stocks by 2050 (Table 6).

Projections for ecoregion 6 produced different trends than any other ecoregion. NPP in the average productivity scenario was projected to increase to a small, but significant degree over no climate change, likely due to higher productivity in some species offsetting declines in other species (Fig. 5e). In contrast, NEP was lower in the average productivity scenario compared to no change, indicating that increased productivity was less than the increase in R_h, causing the net carbon balance to decline (Fig. 5f). However, the range of values in NEP and NBP between the high productivity and low productivity scenarios was larger than the difference between the no change and average productivity scenario.

Table 6. Carbon stock estimates in 2012 and 2050 by scenario and ecoregion. Means and standard deviations were calculated between model simulations. P values are between the 2050 no climate change and average productivity scenarios. Units are $\mathrm{g\,C\,m^{-2}}$.

Ecoregion	2012		2050 no CC		2050 average productivity		
	Mean	SD	Mean	SD	Mean	SD	P
	Aboveground biomass						
1	1158	2	994	12	1249	13	<0.01
2	2138	1	2015	12	2400	14	<0.01
3	2928	3	3674	34	4406	31	<0.01
4	4448	2	6310	36	7182	35	<0.01
5	10 413	15	11 619	59	10 984	87	<0.01
6	10 439	29	12 671	187	12 761	173	<0.01
7	9688	87	9141	260	7961	167	<0.01
	Dead organic matter and soil						
1	2381	2	2484	16	2676	13	<0.01
2	6079	0	6045	14	6322	26	<0.01
3	7629	1	7632	17	8231	79	<0.01
4	15 828	1	15 122	29	15 382	199	<0.01
5	28 321	6	29 455	97	28 681	723	<0.05
6	32 731	17	32 289	149	31 816	348	<0.01
7	27 128	4	27 798	370	26 359	1405	<0.01
	Total ecosystem						
1	3875	2	3758	39	4201	96	<0.01
2	8842	1	8650	23	9177	193	<0.01
3	11 412	0	12 375	65	13 004	698	<0.05
4	21 574	2	23 270	47	23 047	1359	
5	41 778	4	44 518	89	41 598	394	<0.01
6	46 207	55	48 620	77	44 974	2581	<0.01
7	39 667	34	39 329	626	35,903	1141	<0.01

Figure 4. Average ANPP differential from the 1961–1990 climate to 2041–2070 climate average estimated by the TACA-GAP model for the five main modelling ecoregions in the study area. Input NPP for ecoregions 1 and 2 was set at 50 % of regions 3 and 4 respectively.

The NBP in different ecoregions not only represents the carbon flux, but also reflects the different disturbance regimes (Figs. 6 and S3). Overall, the map of NBP shows a shift towards a stronger carbon sink. In ecoregions 1 and 2, fires are rare and there is no harvesting, resulting in small standard deviations and less spatial diversity in the NBP mosaic. Throughout the other ecoregions there was a finer mosaic of values throughout most of the landscape in 2050, reflecting the occurrences of harvesting and fires. The largest standard deviations for NBP are in ecoregion 7, which had harvesting and the most frequent fires.

For the landscape as a whole, NPP had a small but significant increase under the average productivity scenario compared to no climate change by 2050 (Fig. 7a). The relatively small change was due to the positive and negative changes in different ecoregions offsetting each other. Similarly, the decline in aboveground biomass in the warmer and drier ecoregions was offset by the increase in biomass in the cooler ecoregions in 2050, resulting in a projected increase in total aboveground biomass for the study area (Fig. 7b). The total landscape NEP followed similar trends to ecoregion 7, with climate change projections resulting in a reduction of NEP, although the landscape was a net carbon sink in most years and most scenarios. Accounting for the loss of carbon due to
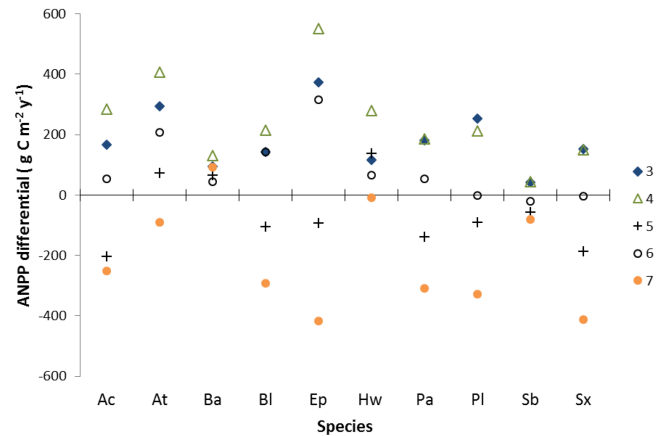
disturbances by using NBP lessened the differences between the simulations with or without climate change. The landscape was projected to have a NBP closer to zero under the average productivity scenario compared with a sink under no change.

Climate change was projected to have no effect on the ability of forest managers to achieve the harvest as currently planned (Fig. 8a). However, the harvest rate markedly affected estimates of net carbon fluxes, with the lowest flux values in the first decade when harvest rates were highest (Fig. 8b). Similarly, the difference between the NSP and NBP is greatest during that first decade when harvest rates are high, and therefore considering the storage of carbon in wood products created a noticeable difference at the landscape scale. However, there were no visible trends in the NSP between the no climate change scenario and the average productivity scenario, although only one replicate is shown (Fig. 8c).

Despite our efforts to model climate change effects for each, there were no apparent changes to the distribution of the leading species (Fig. S4). There was however a marked reduction of subalpine fir and an increase in lodgepole pine and interior spruce as leading species through management activity. In contrast, the climate change scenarios did show a marked change in aboveground biomass stocks and spatial distribution of western hemlock (Fig. 9).

4 Discussion

The purpose of this study was to improve our understanding of the interactions of species composition, climate change, fire, and management in temperate forest ecosystem carbon dynamics. Therefore we simulated the climate change im-
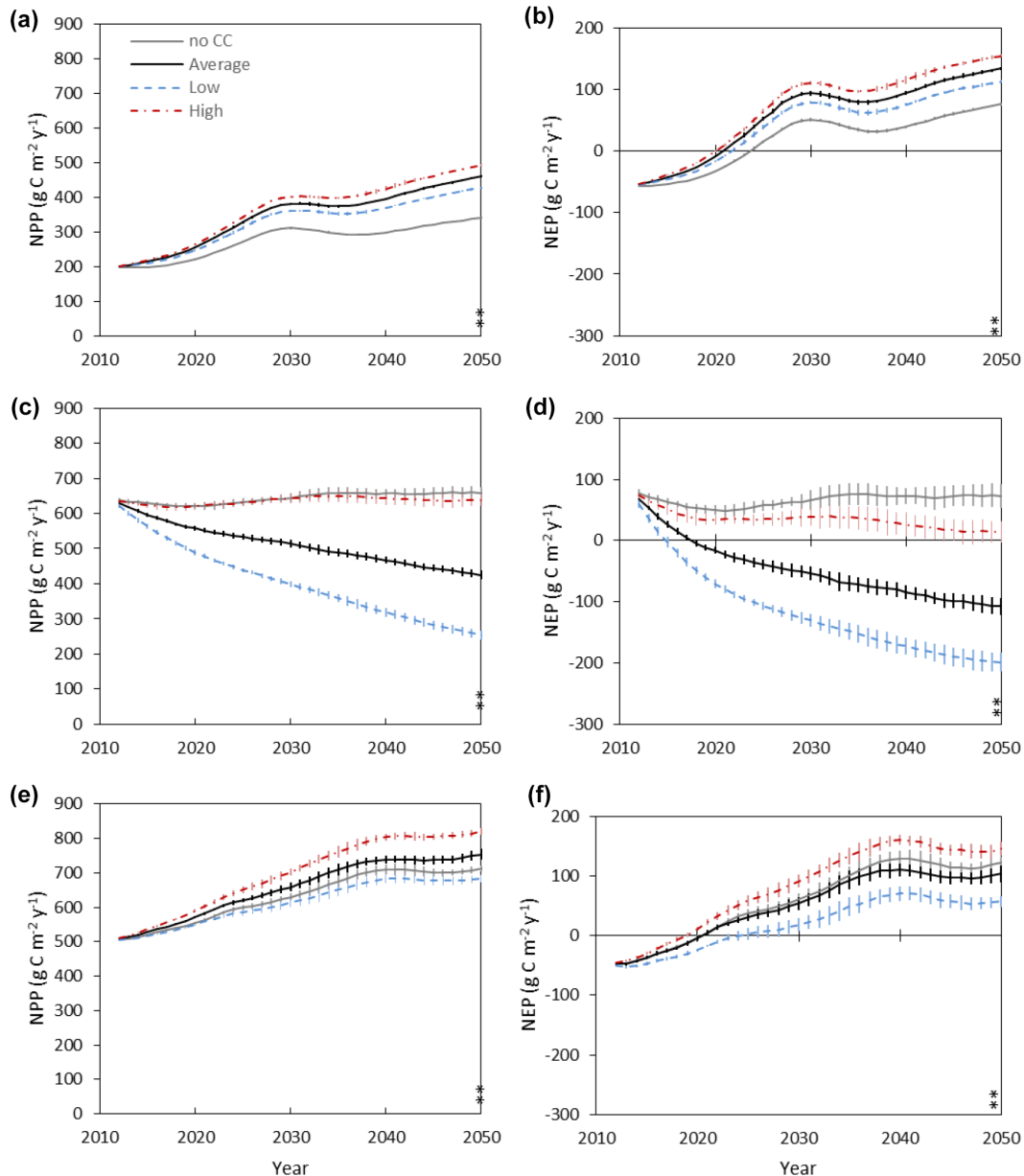
Figure 5. Climate change impact projections on the NPP and NEP (average + SD) for ecoregions 4 **(a, b)**, 7 **(c, d)**, and 6 **(e, f)**. The asterisk notes *t* tests that were significantly different between the no change scenario (no CC) and climate change average productivity (** $P < 0.01$) in 2050. Note: *y* axes vary.

pacts on productivity and natural regeneration interacting with management and wildfires within a region with steep elevational gradients using a new extension for LANDIS-II. Our results indicate that the effects of climate change on forest productivity and ecosystem carbon dynamics may be significant and substantial, but not uniform. The direction and magnitude of responses depended on the combination of species and site conditions, implying a dependence on how close the current and future climate was to the species optimum. The uncertainty of the changes depended on the assumed productivity and the natural disturbance rate.

These results also demonstrate that the ForCSv2 extension to LANDIS-II can provide credible and useful information on future carbon dynamics.

4.1 Climate change effects on carbon fluxes and stocks

In this study, tree productivity (as estimated by NPP and aboveground biomass) was projected to have the greatest downside risk in the most productive ecoregions (currently having the highest NPP and biomass), which implied that species were at or beyond their optimum conditions. In con-
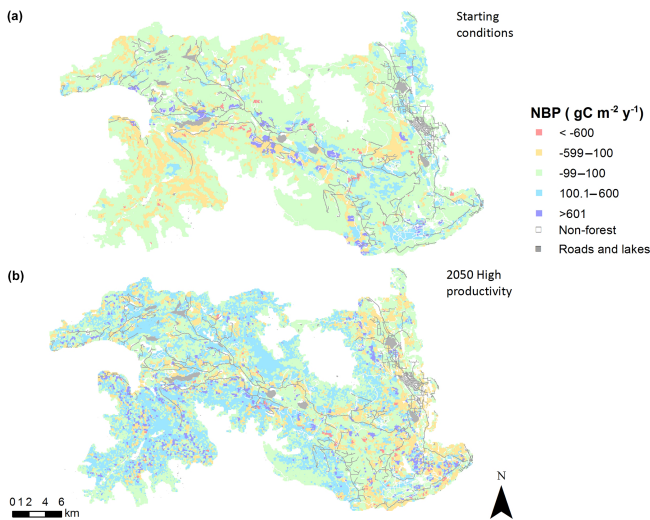
Figure 6. Spatial distribution of NBP under the starting conditions **(a)** and in 2050 under the high productivity scenario **(b)**.

trast, the results indicated that the species in the least productive ecoregions were able to take advantage of warmer conditions so as to have increased productivity under climate change. These results are consistent with the literature indicating that more productive areas within a region are likely to experience negative climate change impacts compared to less productive areas (e.g. Boisvenue and Running, 2010), but are in contrast to other studies that do not show this pattern (e.g. Scheller et al., 2012; Creutzburg et al., 2016). Carbon stocks tended to follow changes in productivity, increasing in ecoregions with greater productivity and decreasing where productivity was projected to fall, indicating a lower influence of changing decay rates on the stocks over this simulation period.

Over the landscape as a whole, there was a wide range of projected changes in NPP. Other landscape-scale studies of temperate conifer forests have projected increases (e.g. Crookston et al., 2010; Steenberg et al., 2011; Ma et al., 2014), decreases (e.g. Scheller et al., 2012; Galvez et al., 2014; Ma et al., 2014), or little change (e.g. Scheller et al., 2012; Creutzburg et al., 2015; Ma et al., 2014) in biomass or carbon stocks due to climate change.

As with NPP and carbon stocks, net carbon fluxes were highly sensitive to the ecoregion in both absolute terms and in the impact of climate change. The NEP and NBP results indicated likely greater carbon sinks due to the productivity projections in the cooler and moister ecoregions, whereas for the more productive ecoregions the projections ranged from little difference to greatly increased carbon emissions due to lower growth and higher decay rates. Those results differed from those presented by Hudiburg et al. (2013) for temperate coniferous forests in Oregon, where cumulative NBP was projected to increase in all regions by the end of the century. However, those increases were smallest on the coast, the

highest productivity region. Note that their study included a much larger range of climate conditions and CO_2 fertilisation effects on productivity. The divergent range of responses over the Copper–Pine Creek elevational gradient are consistent with a review of expected climate change impacts on the mountainous regions of Europe (Lindner et al., 2010).

Ecoregion 6 provides the most interesting and counterintuitive results because NPP was projected to increase, but NEP decreased, indicating that increases in productivity were insufficient to counter increased R_h. Furthermore, the climate change impacts on NBP were negligible, but the decline of total ecosystem stocks was significant. This case exemplifies the complexity of forest carbon dynamics and the importance of using integrated ecosystem-scale models such as LANDIS-II to assess climate change impacts.

Our uncertainty estimates for the different indicators were the range in values between the high productivity and low productivity scenarios. This is likely an overestimate of uncertainty because it is unlikely that all species in all ecoregions would follow the same trend of improving or declining productivity.

4.2 Management implications

The projected leading species of the study area was, to a great extent, driven by management activities, planting in particular. This result reinforces the opportunities identified by others to adapt to climate change through management (e.g. Steenberg et al., 2011; Buma and Wessman, 2013). Adaptation may take the form of planting species currently viable, but with provenances more suitable to future climatic conditions than the ones in the local geographic area (Rehfeldt et al., 1999). That action could also provide climate change mitigation if it prevents declines in productivity. In addition, increasing tree species diversity may increase resilience to forest health damage or as a strategy for dealing with the uncertainty in future projections (Dymond et al., 2014).

The harvest rate in our study was highly variable over time due to the mortality caused by mountain pine beetle triggering salvage logging in the near term in the Wetzink'wa Community Forest (Fig. 8a). Similarly, BC Timber Sales anticipates logging rates decreasing within the study area by about 2020 in part because they operate across a much larger area. The planned harvest was achieved in the simulations despite declining productivity in some areas. This was likely due to the age class distribution of the forest being over 100 years old (Fig. 2). The near-term harvest relies on trees that have already reached maturity, and therefore the growing stock already exists on the landscape. A longer simulation period that incorporates harvesting of second growth stands may have different results. The changing productivity could lead to changes in harvest rates. If monitoring substantiates the projected productivity increases in ecoregions 3 and 4, there may be capacity to increase harvest. This would be consistent with the results found by Steenberg et al. (2011) that
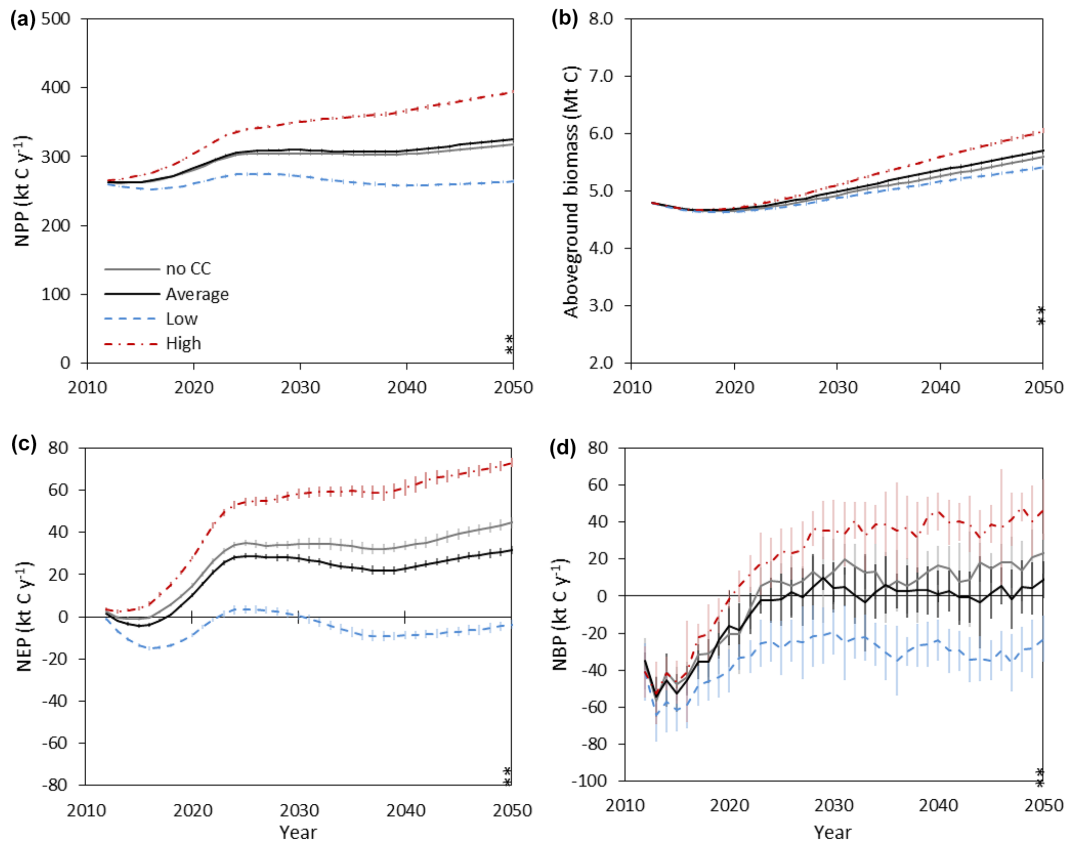
Figure 7. (a–d) Landscape total carbon fluxes and aboveground biomass stocks (average + SD) for no climate change, average, and high or low productivity scenarios. The asterisk notes t tests that were significantly different between the no change scenario (no CC) and average productivity scenario (** $P < 0.01$) in 2050.

sustainable harvest could increase assuming higher productivity under climate change.

The NSP provides a metric that is sensitive to management changes in the forest, as indicated by the larger difference between the NSP and NBP when harvest rates were higher (Fig. 8b). Based on the wood product model documented behaviour (Dymond, 2012), the NSP will likely also be sensitive to the lifespan of products and their disposal. Therefore, we suggest this metric would be particularly useful when assessing climate change mitigation options available to the forest industry.

4.3 Modelling confidence and caveats

This study not only assessed climate change impacts on the productivity of the Copper–Pine Creek valley, but also provided a test case for the ForCSv2 extension to LANDIS-II. Unfortunately, whether the model is based on allometric equations (field plots), flux tower data, or more complex simulation models, it is nearly impossible to directly measure carbon stocks or fluxes, and so we must rely on model intercomparisons. The comparison of carbon stocks and fluxes with literature values in Table 5 provides some confidence

that the ForCSv2 output is reasonable, although the variability is large. Therefore, this model is likely most useful for assessing differences between climate, management, or disturbance scenarios, rather than for predicting absolute values.

The LANDIS-II modelling of aboveground biomass, tree species growth, competition, and natural regeneration has been extensively investigated and the strengths and weaknesses are understood (e.g. Simons-Legaard et al., 2015). The landscape NPP and aboveground biomass are highly sensitive to the input variables: maximum NPP and maximum biomass for each species in each ecoregion and the growth parameter r. Also, they found the aboveground biomass tended to increase as the duration of the simulation increased over 30 years. Since the ForCSv2 extension biomass dynamics are based on the Biomass Succession extension analysed in their study, we can assume a similar sensitivity for NPP, aboveground biomass, NEP, NBP, and NSP.

The ForCSv2 DOM and soil dynamics are built from the CBM-CFS3 (Kurz et al., 2009). The CBM-CFS3 has also been investigated for parameter sensitivity (e.g. White et al., 2008), compared with field estimates of carbon stocks (Shaw et al., 2014) and with other estimates of NEP (e.g. Wang et al., 2011). White et al. (2008) found that the DOM and soil
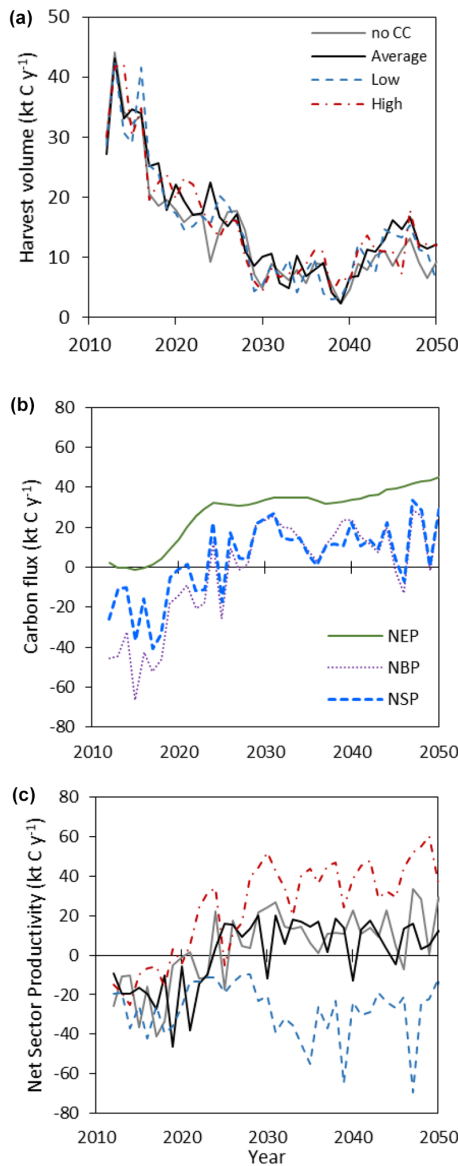
Figure 8. Relationship between harvest rate and carbon fluxes for a single replicate. Removal of carbon from the ecosystem through logging **(a)**. NEP, NBP, and NSP for a single replicate without climate change **(b)**. Net sector productivity for a single replicate of each scenario **(c)**.
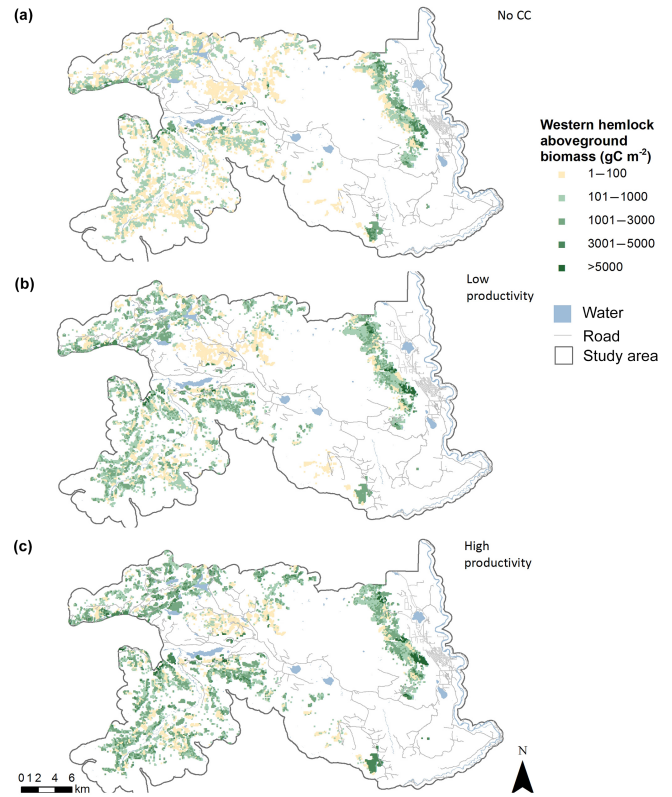
Figure 9. Western hemlock biomass distribution in 2050 with no climate change (no CC) and high and low productivity scenarios.

carbon stocks and stock changes were most sensitive to the base decay rates for the aboveground and belowground slow pools and the transfer to air for the aboveground and belowground very fast pools. Shaw et al. (2014) found that the CBM-CFS3 model output was reliable for estimating total ecosystems stocks for the forests of Canada. However, they did find it overestimated deadwood and underestimated forest floor and mineral soil carbon stocks, primarily in stands of balsam fir and white and black spruce due to the model not representing moss. Those stand types are not found in the

Copper–Pine Creek study area. Wang et al. (2011) demonstrated the large uncertainty between different estimates of NEP among six models over 8 years for a relatively small area around a flux tower (-200 to $+850 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$). The CBM-CFS3 results were within the range of other estimates.

The productivity estimates used as input to ForCSv2 did not include the positive impact of CO_2 or N fertilisation (Wu et al., 2014) or negative impact of provenance (local adaptation; e.g. O'Neill and Nigh, 2011). These would increase the uncertainty of model outputs.

Forest pests and diseases can have major impacts on forest carbon dynamics (e.g. Kurz et al., 2008) and damage may increase in the future (Woods et al., 2010). They were not included in this simulation modelling study due to a number of factors including the insect damage from the recent mountain pine beetle outbreak being taken into account in the starting inventory and the difficulty in estimating future outbreak events within the relatively short (38 years) simulation period. Future research will incorporate simulations of forest pests and diseases.

5 Conclusions

The results indicated that the relative position of species optimum to current and future site conditions strongly influenced

projections of landscape carbon dynamics. Those productivity rates interacted with respiration and disturbance rates to shape the dynamics of net carbon fluxes of the ecosystem, biome, and sector. Climate change effects on forests vary with species, site conditions, management, and fire regime; therefore, all of these components need to be considered when planning climate change mitigation and adaptive management. This type of future research may consider ForCSv2 as a viable model within the LANDIS-II framework.

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