MODELING VEGETATION DISTRIBUTION

AND CARBON SEQUESTRATION

IN THE PACIFIC NORTHWEST

by

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STATEMENT OF THESIS APPROVAL

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ABSTRACT

Ecosystems provide many beneficial services to society, but their ability to provide these services will be influenced by climate change. Terrestrial vegetation sequesters significant amounts of carbon, but currently, human activity affects this storage. This research examines changes in vegetation and carbon flux patterns in the northwest United States and southwest Canada using the dynamic global vegetation model LPJ-GUESS. Regional and local simulations were conducted for modern and end-of-century 2.6 and 8.5 RCP scenarios. The results include estimates of changes in net ecosystem exchange and variations in different components of the carbon cycle, including fire activity. Regional net ecosystem exchange remained fairly consistent across the three scenarios, though the northern portion exhibited marked spatial heterogeneity of sink and source locations and the southern portion was highly homogeneous. Local simulations showed the effect of changing vegetation on fire activity. One site with consistent woody vegetation experienced little change in fire activity, while the other site experienced a shift from grass- to tree-dominant vegetation with simultaneous changes in fire. The results have implications for land management as they suggest which areas may release or sequester carbon under future climates due to changes in vegetation and other carbon flux components.

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INTRODUCTION

Climate change poses unknowns for the state of ecosystems in the future. As ecosystems develop from and respond to external and internal forces, responses can be varied, especially as feedbacks may amplify or dampen effects (Higuera et al., 2009). Interactions between environmental conditions, vegetation, and disturbance are complex (Higuera et al., 2009). Therefore, it is important to understand a range of possible future outcomes, particularly for proper management, through the use of dynamic global vegetation models.

Climate and disturbance regimes significantly affect ecosystems through changes in seasonal variability of temperature and precipitation, which can advantage or disadvantage particular vegetation types (Walther et al., 2002). Climate changes may disrupt present vegetation composition and structure and cause shifts to different vegetation patterns in the future. At the same time, changes in disturbance regimes (fire, drought, grazing, etc.), which may be exacerbated by climate, can affect vegetation dynamics by encouraging certain plant types to prosper while others suffer. Changing interactions between climate, disturbance, and vegetation affect ecosystem function.

Through photosynthesis and productivity, vegetation sequesters carbon, which is an important ecosystem service (Millennium, 2005). As climates change, carbon stored in terrestrial vegetation may change. Increases in atmospheric CO_2 levels may allow for more carbon storage by ecosystems, but changes in temperature and the amount and

seasonal timing of precipitation may stress vegetation leading to carbon emission. Currently, terrestrial ecosystems worldwide are a slight carbon sink (IPCC, 2007). The IPCC (2007) predicts a shift overall from sink to source for terrestrial ecosystems this century. These changes will vary spatially (Morales et al., 2007), so recognizing potential changes will aid in management strategies, because potential sinks should be preserved, while potential sources may need adjustments in vegetation composition.

It is the goal of this study to determine how climate affects both vegetation and disturbance and, therefore, carbon flux in the Pacific Northwest. The hypothesis tested here is that climate change and resulting increases in fire will not affect overall carbon flux in the study area. These changes will be examined using a dynamic global vegetation model (DGVM), LPJ-GUESS 3.1 (Smith et al., 2001). Determining the nuances of the climate-vegetation-disturbance relationship and their influence on carbon flux is important.

BACKGROUND

Ecosystem Goods and Services

Ecosystem services provide many benefits to human life. Some benefits of ecosystems are provisioning services, such as food, fiber, and medicinal and cosmetic products, and cultural services, like the spiritual appreciation for nature (Millennium, 2005). Regulating services, which include carbon sequestration, climate and water regulation, water and air purification, disease and pest regulation, and protection from natural hazards, are also important for human well-being. Ecosystem processes and characteristics, like biodiversity, must be sustained over several temporal and spatial scales to provide a range of ecosystem services (Schröter et al., 2014). Biodiversity is strongly correlated to the ability of ecosystems to provide services and their resiliency when experiencing change.

Human use of ecosystem services has increased rapidly, and the majority of services are currently being degraded or used in unsustainable ways (Millennium, 2005). Since humans extract significant amounts from the environment and rely on them for other benefits, the preservation of ecosystem function is crucial for human existence. For example, the loss of an ecosystem's ability to sequester carbon may lead to higher atmospheric CO_2 concentration. Studying how ecosystems might change allows humans to determine what may be gained or lost in terms of these benefits and develop management plans needed to address this vulnerability.

There is indication of widespread ecosystem vulnerability to climate change (Gonzalez et al., 2010). Williams et al. (2007) suggests there is difficulty identifying thresholds for disappearing and novel climates. Significant portions of land may experience vegetation changes from just a slight change in climate. Deserts and tropical evergreen broadleaf forests have the lowest predicted vulnerability while temperate mixed forest, boreal conifer, tundra, and alpine biomes are most vulnerable, likely due to wildfire regime changes (Gonzalez et al., 2010).

Disturbance

Data suggest that many parts of the west face increased fire activity (Westerling et al., 2006). A trend in larger and possibly more severe wildfires is expected to continue, as evident by both long (3000 year) and short (25 year) timescales, and is likely the result of climate change (Dennison et al., 2014; Marlon et al., 2012). Recently, overall burned biomass for the western United States is much lower than expected given increased temperatures and increased drought over the last several centuries (Marlon et al., 2012). Fire exclusion and suppression has resulted in limiting biomass burning, and thus, it is out of equilibrium with current climate (Marlon et al., 2012). Therefore, current practices of fire exclusion and suppression may not be appropriate if the goal is to allow ecosystems to respond to past controls. The deficit will affect future ecosystem vulnerability. The character of fire may change in many western ecosystems, which could impact recovery and, thus, ecosystem services (Romme & Turner, 2015). Modeling vegetation, trends of fire, and their effects on ecosystem function is essential for understanding these future relations and creating appropriate management strategies.

Carbon Sequestration

The global carbon cycle is a complex system of reservoirs and exchanges or fluxes of varying sizes between system components (Figure 1). The atmosphere and oceans are fairly large pools where carbon can be stored, and the amounts of carbon stored are increasing due to anthropogenic behavior, primarily fossil fuel emissions and land use change. Vegetation and soils also store significant amounts of carbon. For the most part, the cycle is generally balanced, except for the release from fossil fuels, which
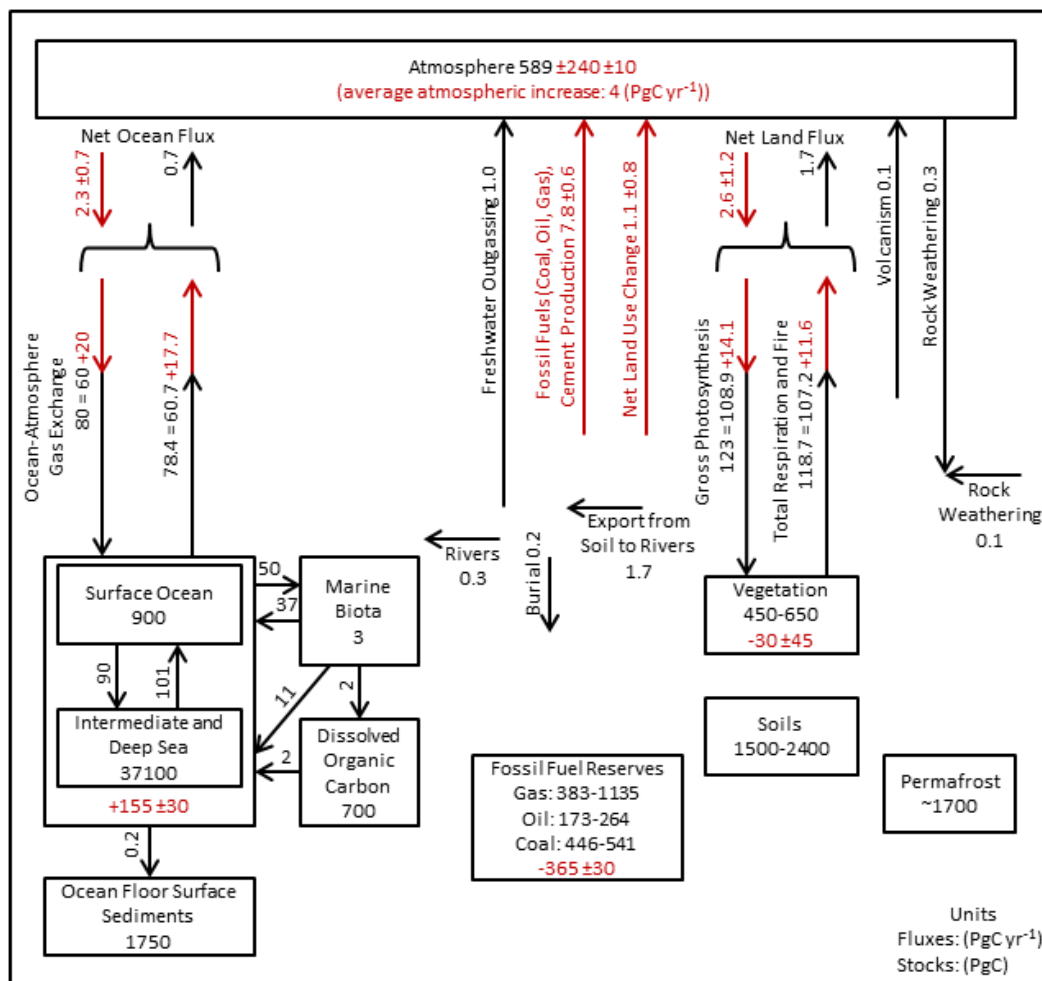

Figure 1. Representation of the carbon cycle. Stocks are represented as boxes in PgC. Fluxes are represented as arrows in PgC yr^{-1}. Black numbers represent pre-Industrial values while red numbers are associated with changes in the cycle due to anthropogenic activity. Modified from IPCC (2013b).

cannot be sustained at the rate of current emissions (IPCC, 2013b).

The terrestrial store (vegetation and soil) is important because large amounts of carbon can be sequestered and help mitigate carbon emissions from fossil fuel burning. This sequestration is measured by net ecosystem exchange (NEE), the balance between carbon stored in terrestrial vegetation less carbon lost (from respiration, decomposition, and fire) to the atmosphere. This fluctuates seasonally with growing and nongrowing periods. Terrestrial vegetation can store significant amounts of carbon, but this ability has been modified as a result of human activities, including land use change and changes in atmospheric CO_2 levels, and may continue to shift under climate change (IPCC, 2013b; Morales et al., 2007). Soil is also a large reservoir of carbon worldwide but has the potential to emit large amounts of carbon with changes in microbial respiration. Reduced occurrence of fire due to fire suppression in places, like the western United States, contributes to the land carbon sink (IPCC, 2007) by reducing the amount of carbon that would potentially be released by fires and storing it instead. Ecosystems have the potential to store more carbon if climate changes, and increased CO_2 supports vegetative success and makes ecosystems more productive. Alternatively, ecosystems could be more stressed, for example, if temperatures increase and water availability is limited, making them respire and release more carbon than they uptake. Also, changes toward greater occurrence of fire could increase the amount of carbon lost and cause ecosystems to become sources. For example, Kurz and Apps (1999) determined that large increases in disturbance in Canadian forests reduced ecosystem carbon storage because fire has the potential to release large amounts of carbon. These changes will depend on specific site characteristics of climate, vegetation composition, and disturbance regime.

Importance of Modeling

Model development is driven by interest in the carbon cycle, and as vegetation is a significant store of carbon, it is important to understand how this reservoir may change. Vegetation modeling seeks to represent natural systems, which allows for investigations that would otherwise not be possible. Past vegetation and controlling processes, such as temperature, moisture, and CO_2 levels, can be tested, and future systems can be predicted by inputting future climate estimations. Modeling future vegetation change is a significant research area, especially as it relates to ecosystem function and effects on society. Recognizing possible outcomes and resulting adaptation strategies for future conditions provides some guidance to policy makers and society in general regarding the uncertainty of climate change. Though it is challenging to predict future climate-disturbance-vegetation linkages, testing different scenarios can give some indication of the changes expected.

The goal is to simulate productivity in response to environmental inputs; changing inputs leads to changing productivity. Models output net ecosystem productivity levels in response to climate and atmospheric CO_2 concentration inputs. Analyzing different scenarios (different climate and CO_2 inputs) provides a framework of how the carbon cycle, specifically the ability of ecosystems to sequester carbon, may change under different climate scenarios. Despite the uncertainties about how net primary productivity (NPP) and NEE will respond to changes in the climate system (Cramer et al., 2001), much can be learned through interrogating a range of possible conditions for the future.

As climate changes, vegetation regimes will likely shift, ecosystems will be disrupted, and society may be impacted, due to changes in ecosystem functions and their

ability to provide services (Pecl et al., 2017). Field observations and remote sensing data have already detected land cover and fire changes in recent times across biomes (Gonzalez et al., 2010). Information on the expected spatial pattern is lacking, however, which makes planning adaptation practices for ecosystems and their resources difficult. Identifying areas vulnerable to changes in vegetation is essential for future management and preservation of ecosystems (Gonzalez et al., 2010). There is also high likelihood that many areas in the future will experience climates unlike those today. Extramural, or no-analog, climates present more uncertainty (Rehfeldt et al., 2006; Williams et al., 2007). Small changes in climate (e.g., a slight temperature increase) have the potential to severely disrupt current ecosystems, making both novel and disappearing climates by the end of the century likely (Williams et al., 2007). Models address these uncertainties by modeling different future scenarios. Uncertainty that is well understood (e.g., year-to-year climate variation) can be accounted for, but uncertainty that is unknown (e.g., future CO_2 levels resulting from high or low emissions) must be determined by inputting a range of representative future climate data and examining outputs. Humans can begin to address future vegetation uncertainties related to climate, carbon flux, and disturbance with the help of models.

Overview of Vegetation Models

Models are useful tools for understanding and demonstrating the effect climate has on vegetation. Statistical models (e.g., Rehfeldt et al., 2006; Williams et al., 2007) are based on the similarity of predictions from known values. Future climate projections that have similar modern analogs, assuming vegetation and climate change in tandem, suggest

vegetation should also be similar. This assumption is based primarily from climate similarities and rarely takes into account other processes, like competition, which highlights a significant limitation for this type of modeling. First, there is no specification of the effects of different factors, like CO_2, since it is only based on similarity and not on natural processes. Predictions outside the range of known climates are limited, again because it is based solely on similarity. Statistical models cannot work with no-analog predicted climates because there is no modern match, which is problematic. At the site-specific scale, comparing future climate simulations to modern climate is problematic because of significant differences in modern versus future CO_2 levels. Therefore, predicting what type of biome may be present in the future is challenging. Also, statistical models are unable to replicate interactions between species (e.g., competition), phenology patterns, and other processes, like disturbance. Because statistical models are simpler than process-based models for the reasons discussed above, they demand less computational power, which may be advantageous in some instances.

Process-based models are more advanced than the statistical models discussed above. They simulate vegetation growth and processes as a function of environmental conditions, which allows them to be used with different climates. Process-based models incorporate relevant vegetation dynamic processes, like photosynthesis, recruitment, mortality, growth, and competition, which are important for simulating the temporal dimension of an ecosystem to its environment. Incorporating the major processes influencing an ecosystem helps depict them as naturally and accurately as possible, avoiding the need for the similarity-based approaches.

BIOME4 (Kaplan et al., 2003) is an example of an equilibrium process-based

model. Equilibrium models incorporate climate to determine a range of factors, like moisture and light availability, which then influence the photosynthesis process to drive growth. These models represent time well, generally running at hourly or subhourly scales, but they do not allow for a changing set of drivers. The model is based off of average conditions of climate, rather than trends. Age structure of vegetation is omitted, and NPP is allocated to specific plant functional types (PFTs). Also, disturbances or changes in disturbance regimes are unable to be introduced. These inherent features generalize inputs and outputs of these models, but they are faster than more complex, dynamic global vegetation models.

Dynamic global vegetation models (DGVMs; Figure 2), like LPJ-GUESS (Smith et al., 2001), have several advantages over the models already discussed. They operate within the boundaries of climate trends and use fluctuations of atmospheric and terrestrial characteristics to represent changes in vegetation patterns through time. Climate trends (temperature, precipitation, CO_2, and insolation) are incorporated. The models are able to
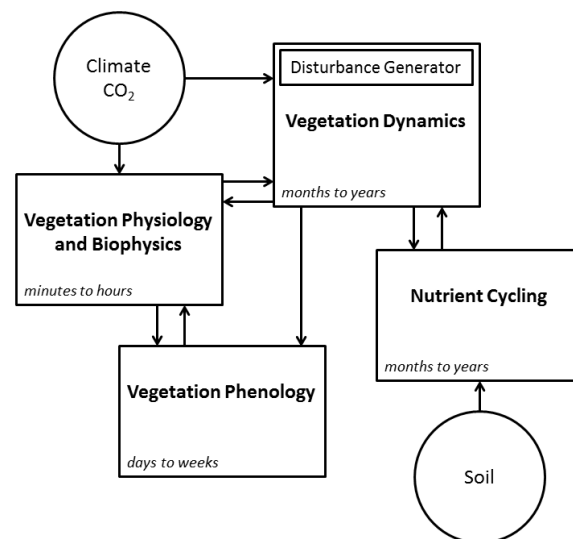

Figure 2. General schematic of DGVM modules with time steps. Modified from Cramer et al. (2001).

simulate changes in response to trends and to changing interannual variability. Day-to-day temperature variations around monthly means as well as changes in the timing of precipitation are included within the dynamic aspect of the models.

Climate, CO_2, and soil data are input into the models. Climate and CO_2 affect vegetation physiology and biophysics, which operate on a fast timescale of minutes to hours. In turn, this influences phenology, which operates on timescales of days to weeks. The models also simulate disturbance events within model runs, including the frequency of fire and the occurrence of extreme droughts or floods, and attempt to capture both the impact and recovery time. Climate determines whether or not a disturbance may occur, which affects vegetation dynamics at months to years timescales, and influences physiology and phenology. The importance of including disturbances is critical as they affect vegetation composition, structure, and dynamics (Thonicke et al., 2001). The model recognizes when a fire could occur under a given frequency but also includes some stochasticity. Vegetation dynamics as well as soils also influence nutrient cycling processes, which are simulated at relatively slow timescales of months to years as that is how the process responds in reality. Through the use of these interactions and feedbacks as well as the timescales, the model attempts to capture linkages between vegetation and the environment.

LPJ-GUESS

LPJ-GUESS is a combination of the LPJ (global scale) and GUESS (landscape scale) models. LPJ DGVM operates like an equilibrium process-based model, while LPJ-GUESS incorporates dynamic processes. Throughout the rest of the paper, LPJ-GUESS will be used to refer to both types of simulations, though it is important to realize there is

a distinction between the different simulations run. Three regional simulations were conducted using the equilibrium process-based version, and three local simulations used the dynamic version.

LPJ-GUESS (Smith et al., 2001) is a complex model, designed to explicitly scale individual processes to defined grid locations, using biophysical and physiological process variables (Cramer et al., 2001). Specific ecosystem processes and their interactions are complex, which the model addresses and replicates (Figure 3). The model essentially "grows" vegetation based on given environmental conditions and processes. LPJ-GUESS incorporates temperature, precipitation, insolation, CO_2, and soil data into processes that affect natural vegetation. The climate data are represented monthly but are downscaled to daily measurements around monthly means during model runs. The model uses several processes to grow vegetation that are calculated using mathematical functions and include photosynthesis (Farquhar equation), carbon allocation, disturbance, cohort structure, recruitment, and mortality. All feed back into each other and are affected by the input data mentioned above. The model simulates biomass production under a given climate for a group of PFTs. Accumulated biomass can be allocated to growth. Growth allows for competitive shading, which initially benefits fast growing, shade intolerant species. Late, shade tolerant plants are likely to outcompete these over time. In addition, the dynamic aspect allows for responses to events or stresses and the development of age cohorts for given PFTs.

Suitable vegetation develops because PFT bioclimatic parameters relate to climate. Only vegetation that can grow under certain given conditions will appear in the model outputs. Climate data are the controls that plants respond to. For the most part, the
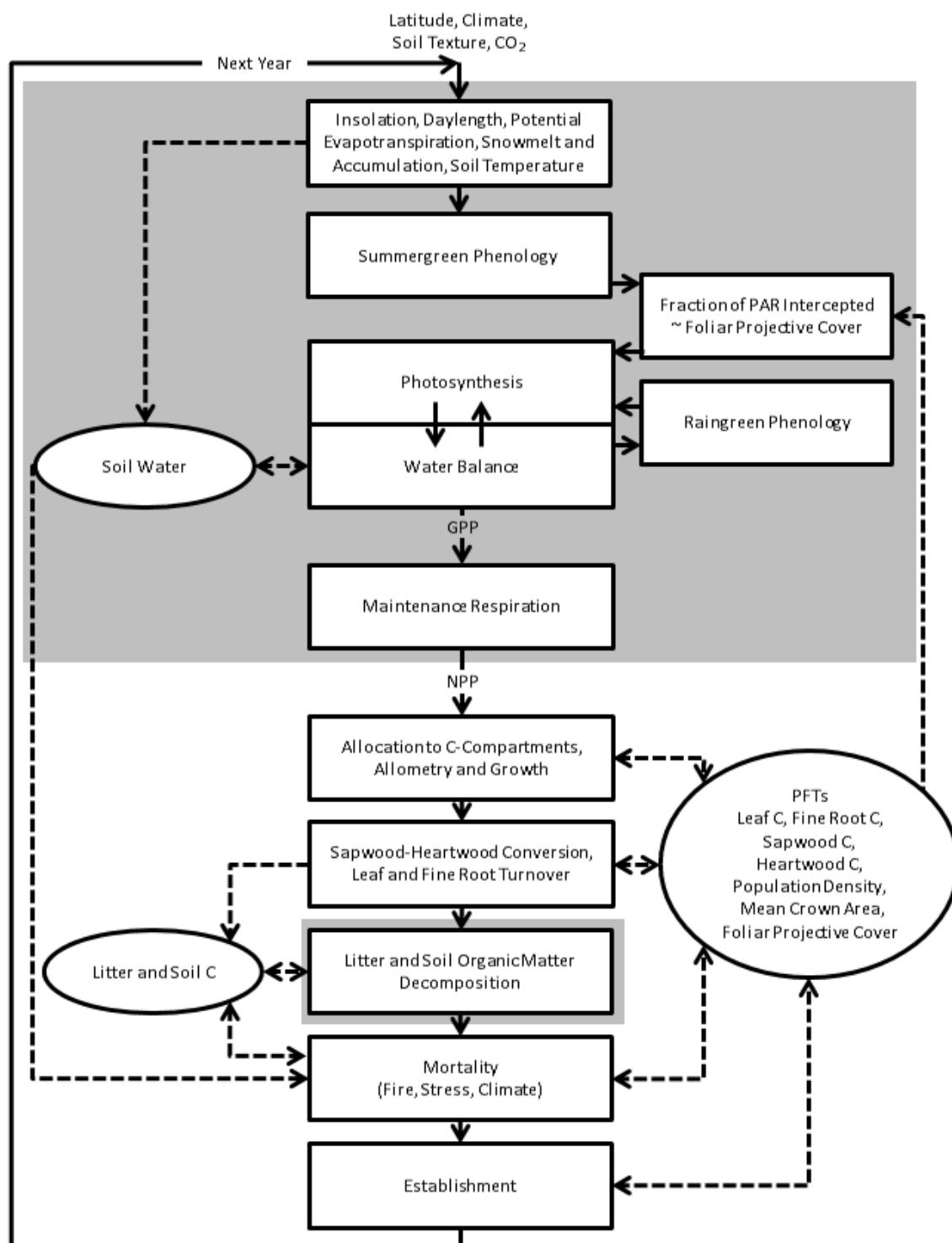
Figure 3. A flowchart of the LPJ-GUESS framework over 1 simulation year. Boxes represent individual processes (modules). Solid lines indicate the order of processes while dashed lines represent information exchange. Shaded backgrounds indicate daily or monthly time steps; the rest are called annually. Modified from Sitch et al. (2003).

processes (physiological, biophysical, and biogeochemical) modeled are based on representations of several plant functions and traits. PFTs are defined by physiological, morphological, phenological, bioclimatic, and fire-response characteristics (Sitch et al., 2003). These include photosynthesis and respiration properties, plant carbon and nitrogen proportions, and others (Cramer et al., 2001; Sitch et al., 2003). NPP and biomass growth are also used to represent PFTs in the model and are based on competition with other vegetation, susceptibility and likelihood of natural disturbance, such as fire, and succession (PFT replacement with time) after disturbance (Cramer et al., 2001). LPJ-GUESS can simulate proportions (population mode) or individual plants (cohort mode), providing information on the demographic structure of the ecosystem. In this paper, biomes will refer to these different compositions of PFTs.

NPP is the difference between gross assimilation and autotrophic respiration while NEE is the difference between NPP and heterotrophic respiration as well. The model recognizes a few reservoirs for terrestrial carbon storage and release. Vegetation is the largest sink and represents carbon gained by biomass. Soil is the largest source, which represents carbon released from decomposition and other microbial activity. Other minor components are reproduction, establishment, and fire. Reproduction represents the associated carbon cost of producing seeds, and establishment represents the cost of initial growth. Fire is the most variable of all components; if a fire occurs, a considerable amount of carbon may be released to the atmosphere, but if not, this is relatively zero. The balance of these different components represents the overall NEE of the ecosystem in the model.

METHODS

Study Area

The northwest United States and southwest Canada is the region of interest. The study area is bounded by 38.0° and 58.0°N and 136.5° and 103.0°W (Figure 4), similar to defined areas in other modeling studies. This region is topographically complex and spans a wide range of ecosystems, which allow for model outputs to capture changes across these varied ecosystem types. Two specific points, one coastal (45.0°N, 122.5°W) and one interior (41.0°N, 104.0°W), were used for time series simulations (Figure 4). The area's current primary ecosystem designations vary from grasslands and deserts to several forest types, under the Level I Ecoregion classifications (Figure 4).

Experiments

A few approaches were used to examine future changes: first, a regional change using population mode and average climates (equilibrium mode) and second, changes at specific point locations using cohort mode and climate time series (dynamic mode). The following sections detail how the data were obtained and adjusted and how the model functions. The experiment list below provides an overview of data, model modes, and objectives. All experiments use the same soil data.

Experiment 1.1: Equilibrium, Modern, Regional

 Data: 1961-1990 cloud cover averages (New et al., 1999), 1961-1990
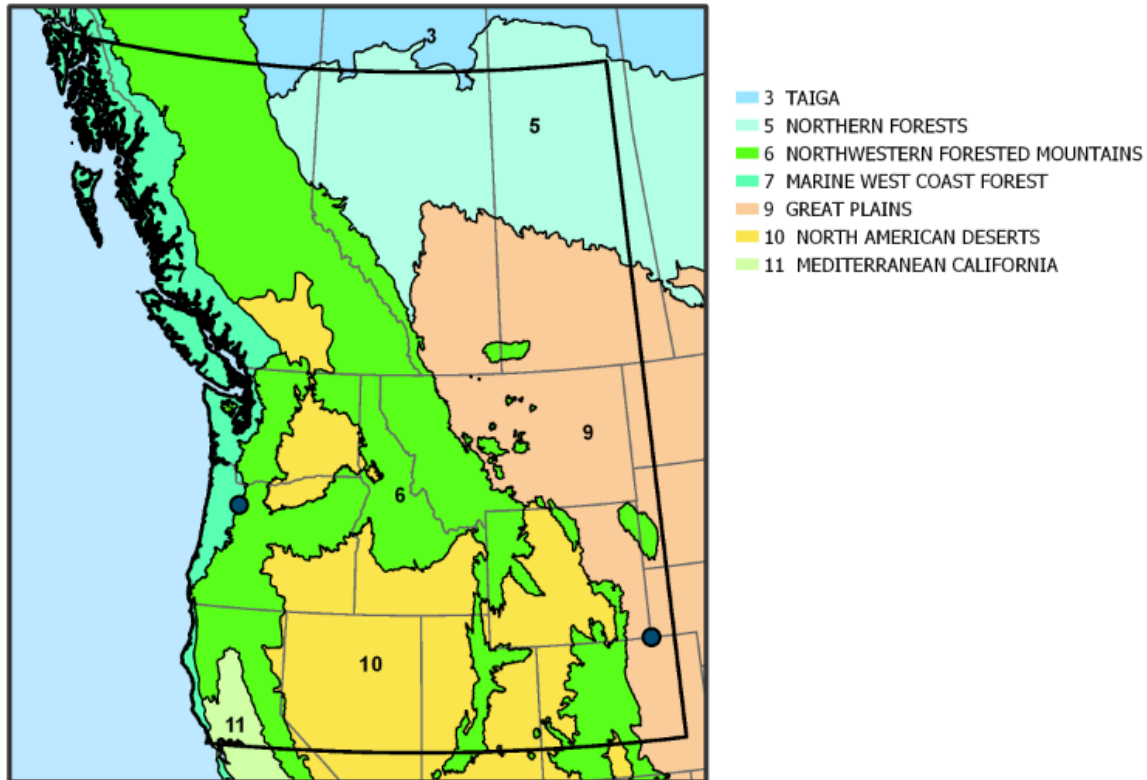
Figure 4. Study area and site locations used for experiments with Level I Ecoregions.

climate averages for temperature and precipitation (New et al., 1999), CO_2 value: 360 ppm

Objective: To examine regional vegetation patterns for modern climate. This will establish a baseline of vegetation and carbon balance from which future simulations can be compared.

Experiment 1.2: Equilibrium, Future, Regional

1.2.1: 2.6 RCP scenario

Data: 1961-1990 cloud cover averages (New et al., 1999), 2071-2100 climate averages for temperature and precipitation (New et al., 1999; Oldenborgh et al., 2009), CO_2 value: 429 ppm (IPCC, 2013a)

1.2.2: 8.5 RCP scenario

Data: 1961-1990 cloud cover averages (New et al., 1999), 2071-2100 climate averages for temperature and precipitation (New et al., 1999; Oldenborgh et al., 2009), CO_2 value: 804 ppm (IPCC, 2013a)

Objective: To analyze vegetation changes due to predicted future climates. Using both the 2.6 and 8.5 RCP data will indicate low and high end emission scenarios and provide a range of potential outcomes.

Experiment 2.1: Dynamic, Modern, Local

Data: 1961-1990 site-specific cloud cover averages (Harris et al., 2014), 1961-1990 climate time series for temperature and precipitation (Harris et al., 2014; Oldenborgh et al., 2009), CO_2 value: 360 ppm

Objective: To understand how specific locations represent vegetation under modern climate, which will again provide a baseline of ecosystem vegetation and carbon flux to compare with future simulations.

Experiment 2.2: Dynamic, Future, Local

2.2.1: 2.6 RCP scenario

Data: 1961-1990 site-specific cloud cover averages (Harris et al., 2014), 2071-2100 climate time series for temperature and precipitation (Harris et al., 2014; Oldenborgh et al., 2009), CO_2 value: 429 ppm (IPCC, 2013a)

2.2.2: 8.5 RCP scenario

Data: 1961-1990 site-specific cloud cover averages (Harris et al., 2014), 2071-2100 climate time series for temperature and precipitation (Harris et al., 2014; Oldenborgh et al., 2009), CO_2 value: 804 ppm (IPCC, 2013a)

Objective: To examine site locations' responses to future climate,

especially in terms of disturbance and carbon flux, with a range of outcomes provided.

With the different model simulations, ecosystem vulnerabilities related to changes in climate should be evident. The effects of changes in climate, CO_2, and disturbance on future vegetation and, therefore, ecosystem services, especially carbon sequestration, in the Pacific Northwest across all experiments are of particular interest.

Data

Soil data available with half degree resolution determined the resolution of model outputs. Soil data from the Food and Agricultural Organization dataset are represented as different soil categories based on their composition and associated characteristics (Zobler, 1986; FAO, 1991) and were used for all experiments.

Standard climate data for 1961-1990, representative of a modern time period, is available from CRU (Climatic Research Unit; New et al., 1999). Insolation data used in the model are a representation of the amount of sunlight or percent of cloud cover. For the mean regional simulations (Experiments 1.1 & 1.2), average monthly cloud cover for the modern period (New et al., 1999) was used for both modern and future runs since future simulated insolation data are lacking. For the locational time series runs (Experiments 2.1 & 2.2), site-specific average monthly cloud cover for the modern period was calculated and used to create a 1000-year repetitive time series. The average was used to maintain consistency, optimizing potential agreements between cloud and precipitation data.

For simulations conducted using climate means, standard climates were used.

Modern simulations (Experiment 1.1) use 1961-1990 climate averages from the CRU dataset (New et al., 1999). Temperature data are represented as monthly averages, and precipitation data are represented as monthly totals. For future scenarios (Experiment 1.2), general temperature and precipitation trends for the defined research area were obtained from the KNMI climate explorer (Oldenborgh et al., 2009). Regional mean monthly temperature anomalies for the future (Figure 5) were calculated based on the CMIP5 simulated climate ensemble mean between 2071-2100 and 1961-1990, using the 2.6 and 8.5 RCP climate scenarios. The calculated monthly anomalies were added to the original observed CRU data for each location. Similar patterns were apparent for both scenarios with the largest increases in temperature during late summer and winter months, though the magnitude of increase differed. Monthly precipitation differences between the time periods (Figure 5) were also added to the original CRU precipitation data. If for any location the calculated monthly precipitation data fell below zero, it was assumed no precipitation occurred (values were reset to zero). Again, anomaly patterns were similar, differing in magnitude. For the region, summer months experienced little change or a decrease while the rest of the year saw increases in precipitation.

For the modern scenarios (Experiments 1.1 & 2.1), CO_2 was set at 360 ppm based on observed modern levels. CO_2 levels were calculated from predicted CO_2 for the end of the century (averaged for the 30-year time period) for the 2.6 and 8.5 RCP scenarios (Experiments 1.2 & 2.2), 429 and 804 ppm, respectively (IPCC, 2013a).

Using regional climate signals for the simulations created some generalizations. Temperatures across the region are expected to increase significantly, and the regional monthly anomalies represent the overall trend well (Figure 5). Coastal areas in the region
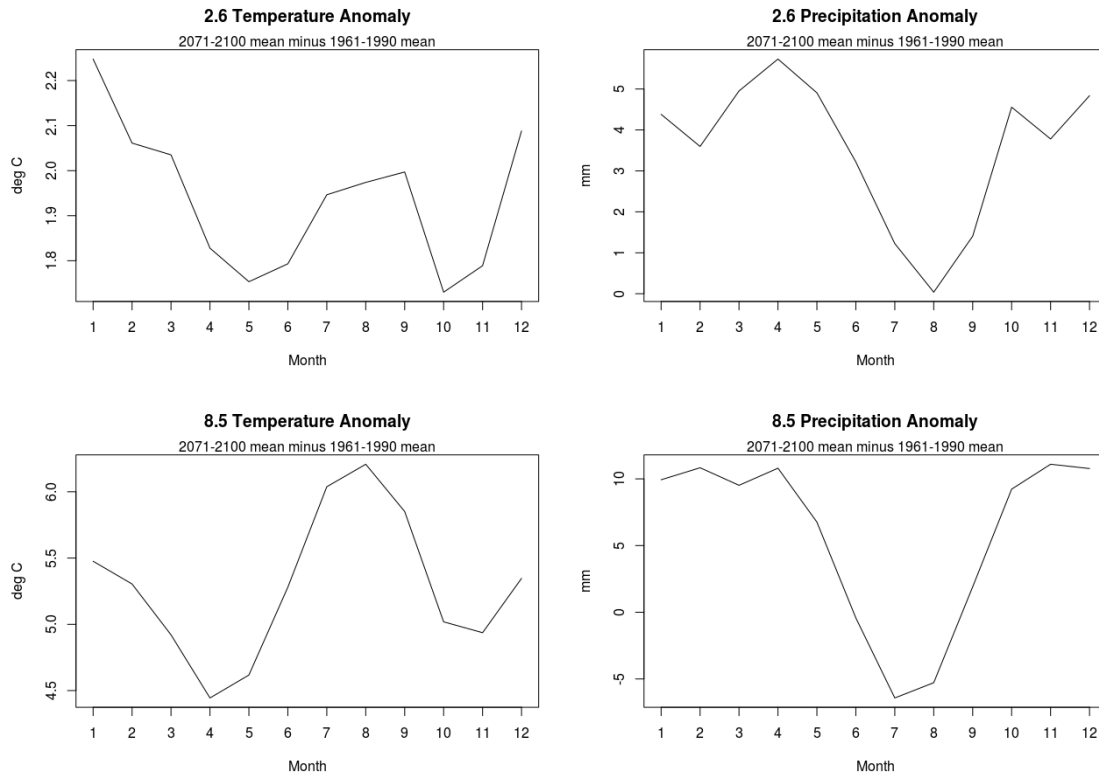
Figure 5. Mean temperature and precipitation anomalies for the region for end-of-century different RCP scenarios. The general yearly pattern is similar with differences in magnitude.

are expected to increase slightly less than interior regions. Therefore, under the regional trend used, coastal areas utilized slightly higher anomalies than expected, and interior regions slightly lower (Figure 6). In terms of precipitation, the regional trend indicated an increase in precipitation in almost all months and a decrease in a few summer months, causing a net yearly increase (Figure 5). Most months showed an increase with minimal geographic variability. Some demonstrated slightly higher amounts among the northern coasts. The summer months show a noticeable difference between northern regions and southern regions. In general, southern regions experience a decrease in summer precipitation while northern regions do not (Figure 7). As a result, for the climate data used, the northern region experiences less summer precipitation in the model experiments
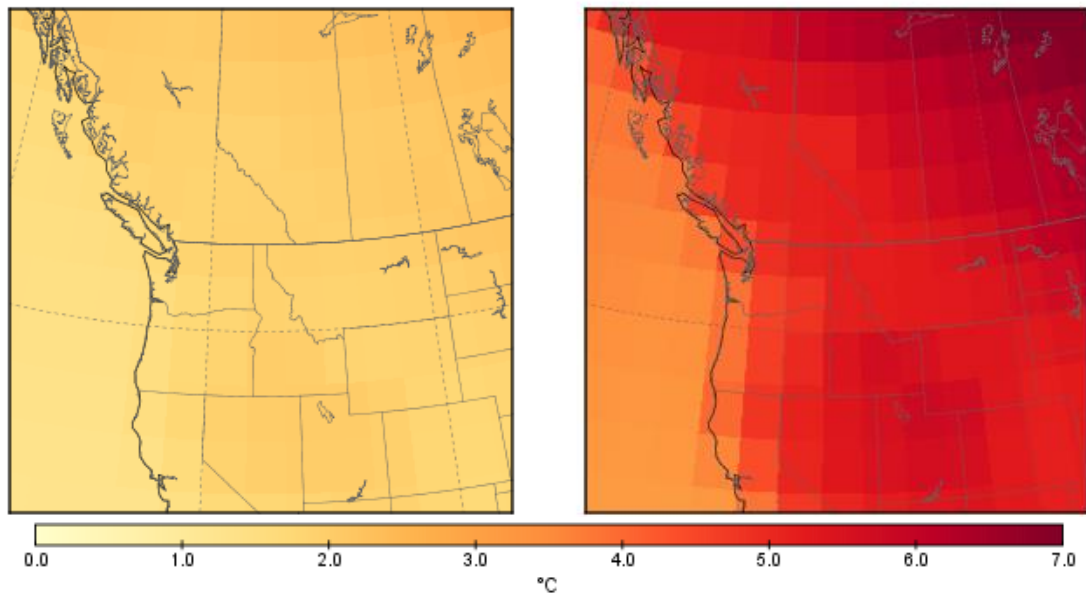
Figure 6. Mean temperature increase (°C) for the 2.6 and 8.5 RCP scenarios. Patterns are similar with differences in magnitude (Oldenborgh et al., 2009).
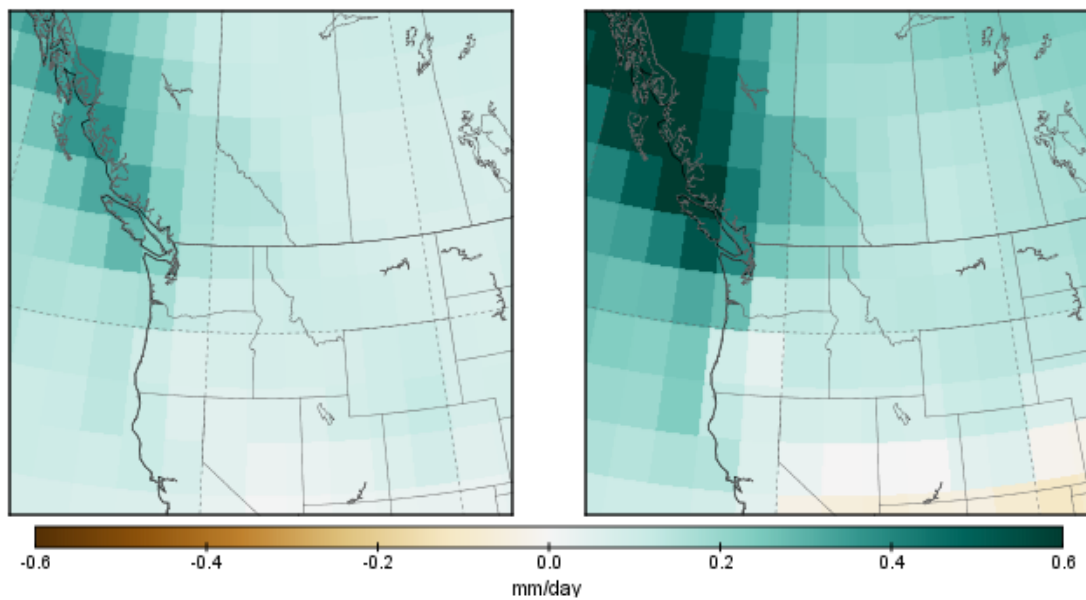

Figure 7. Mean annual change in precipitation (mm/day) for the 2.6 and 8.5 RCP scenarios. Overall, most precipitation increases along the northern coast with less change in southern and interior areas (Oldenborgh et al., 2009).

than may be expected in the future.

Standard deviations and anomalies were calculated using only land points for the region from the CMIP5 mean ensemble. The time series for the modern simulations (Experiment 2.1) were made after calculating monthly regional standard deviations from the 1961-1990 data (Tables 1 and 2), creating a 1000-year time series of values, and applying it to the average CRU temperature and precipitation data of the site. As before, if precipitation was negative, values were reset to zero.

For the future dynamic simulations (Experiment 2.2), a temperature trend was created using the calculated monthly mean anomalies and standard deviations applied to the original CRU data (Table 1), and precipitation trends were created using the estimated precipitation changes (Table 2). Standard deviations from the climate model output were normalized with modern standard deviations. Negative precipitation calculations were again set to zero. Overall, summer months have much narrower standard deviations for temperature than winter months. As these are regional signals, it makes sense that winter would have a larger range given the latitudinal stretch of the region and the implicit latitudinal temperature gradient across it. In the summer, these temperature differences are much smaller. There was not as recognizable a pattern for precipitation. CO_2 values remained the same as in the mean regional experiments.

Model

As discussed above, the DGVM used for this study was LPJ-GUESS. Twelve PFTs, herbaceous and woody (tropical, temperate, and boreal) types, are defined in the model based on several bioclimatic variables, though only seven appeared in model

Table 1. Mean temperature change and standard deviations for the different experiments.

Temperature Change						
	Modern		RCP 2.6		RCP 8.5	
Month	Mean	SD	Mean	SD	Mean	SD
1	0.00	2.88	2.25	3.00	5.48	5.24
2	0.00	2.41	2.06	2.15	5.30	3.62
3	0.00	1.89	2.04	2.29	4.92	2.87
4	0.00	1.44	1.83	1.41	4.44	2.70
5	0.00	0.76	1.75	0.71	4.62	1.98
6	0.00	0.88	1.79	0.71	5.28	3.29
7	0.00	0.60	1.95	0.54	6.04	3.22
8	0.00	1.06	1.97	1.14	6.21	5.81
9	0.00	1.51	2.00	1.39	5.85	6.01
10	0.00	1.22	1.73	1.19	5.02	2.79
11	0.00	2.02	1.79	1.96	4.94	4.64
12	0.00	2.44	2.09	2.71	5.35	3.56

Table 2. Mean precipitation change and standard deviations for the different experiments.

Precipitation Change						
	Modern		RCP 2.6		RCP 8.5	
Month	Mean	SD	Mean	SD	Mean	SD
1	0.00	16.28	4.38	14.00	9.94	19.63
2	0.00	13.38	3.60	14.04	10.84	11.78
3	0.00	10.85	4.95	12.76	9.52	11.72
4	0.00	6.53	5.73	6.13	10.80	6.18
5	0.00	9.86	4.91	10.04	6.76	12.82
6	0.00	10.73	3.22	11.08	-0.43	11.21
7	0.00	10.00	1.22	11.86	-6.43	12.63
8	0.00	11.54	0.04	14.93	-5.28	9.31
9	0.00	12.79	1.41	10.07	1.91	11.64
10	0.00	13.16	4.56	15.25	9.23	13.66
11	0.00	14.32	3.78	15.97	11.10	16.80
12	0.00	13.65	4.84	15.72	10.78	14.81

outputs for the determined study area (Table 3). Adjustments to PFT bioclimatic limits were made following Sitch et al. (2003) and Shafer et al. (2015).

Because the model begins as a blank landscape with no vegetation, the model must be "spun up" so that typical vegetation is established. The spin up allows a range of PFTs to populate grid cells in order to fully capture the vegetation occurring naturally in most dynamic systems. The output then is representative of a more natural ecosystem, including disturbance and a range of cohort ages. A 500-year spin-up was used for this study.

LPJ-GUESS is able to function in multiple different modes: population, cohort, and individual. Population mode is simple and fast but less mechanistic than cohort and individual modes. Vegetation is modeled as "stands," which does not mean a single stand of vegetation, but a landscape consisting of many individual stands. An average individual represents the properties of an entire PFT population. As a result, there is no direct information on demography or size structure of PFTs, stages of stand development, or vertical stand structure. Static climate averages for 1961-1990 and 2071-2100 periods were used for 100-year simulations conducted in population mode (Experiments 1.1 & 1.2).

Table 3. Model PFTs and associated example taxa.

Model PFTs	Example Taxa
BNE: Boreal Needleleaf Evergreen	*Picea*
BINE: Boreal Shade Intolerant Needleleaf Evergreen	*Abies*
TeNE: Temperate Needeleaf Evergreen	*Pinus, Thuja, Tsuga*
TeBS: Temperate Broadleaf Summergreen	*Alnus, Quercus*
IBS: Shade Intolerant Broadleaf Summergreen	*Betula, Larix*
TeBE: Temperate Broadleaf Evergreen	*Arbutus, Quercus*
C3G: Cool (C3) Grass	*Bouteloua*

In cohort mode, one average individual represents all individuals of a PFT cohort (age) in a patch. This provides more detail as there is an age structure and patches, rather than stands. Competition for light, shade-tolerant and shade-intolerant PFT interactions, and succession following disturbance can be simulated. For the dynamic part of the study (Experiments 2.1 & 2.2), climate time series of 1000 years were input into the model for modern and future average climates, and the plants were treated as cohorts under its respective mode. (Individual mode has the possibility of representing individuals in the same cohort differently, such as by size.)

RESULTS

Equilibrium, Regional Outputs

For the mean regional simulations (Experiments 1.1 & 1.2), some distinct patterns were evident in the outputs. First, woody vegetation appears to expand, overtaking some formerly grass-dominant areas (Figure 8). The modern simulation is dominated by a distinct band of grasses and various tree PFTs. In the subsequent simulations, expansion of the tree PFTs can be seen, suggesting that woody PFTs will not be limited under these climate changes. This expansion spreads northerly as well as up slope, as can be seen in the area of the Canadian Rockies, indicating that alpine biomes are contracting. Most

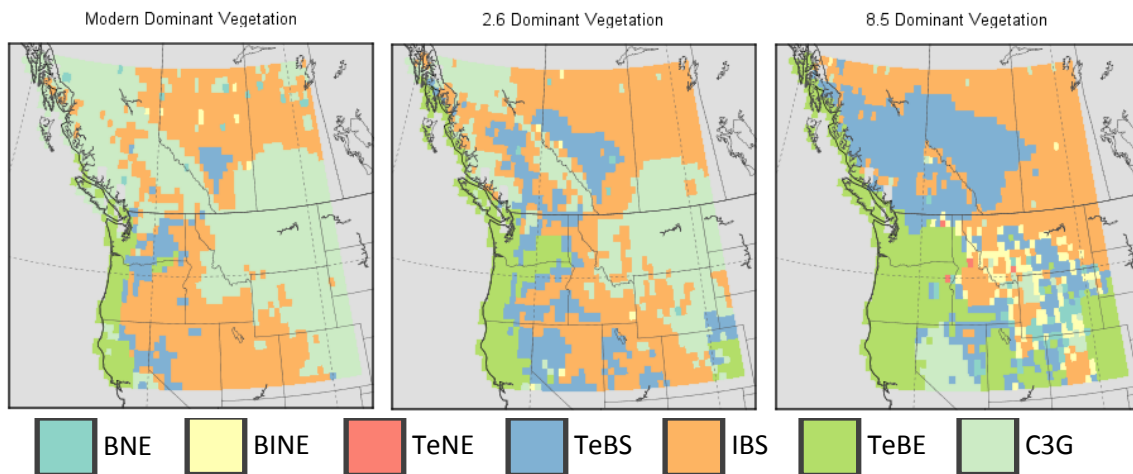Figure 8. Dominant vegetation types for each simulation. The progression across scenarios suggests that woody vegetation will not be limited in the future. BNE: Boreal Needleleaf Evergreen, BINE: Boreal Shade Intolerant Needleleaf Evergreen, TeNE: Temperate Needeleaf Evergreen, TeBS: Temperate Broadleaf Summergreen, IBS: Shade Intolerant Broadleaf Summergreen, TeBE: Temperate Broadleaf Evergreen, C3G: C3 Grass.

noticeably, IBS (Shade Intolerant Broadleaf Summergreen), TeBE (Temperate Broadleaf Evergreen), and TeBS (Temperate Broadleaf Summergreen) were successful. Though IBS became dominant in northern and western portions, this PFT experienced some reduction in southern portions at the expense of others. BNE (Boreal Needleleaf Evergreen), BINE (Boreal Shade Intolerant Needleleaf Evergreen), and TeNE (Temperate Needleleaf Evergreen) also demonstrate increased success across scenarios. C3G (C3 Grasses) displays the most noticeable reduction. Presenting the data as dominant vegetation masks the proportions of other PFTs (Figure 9). While PFT types, like IBS, TeBS, and TeBE, are prevalent, especially under increasing climate scenarios, grasses (C3G) and other less dominant PFTs (BNE, BINE, and TeNE) are still present and serve important roles across the region.

As would be expected given that woody vegetation seems to be unconstrained, overall annual net primary productivity (ANPP) also increased across the scenarios (Figure 10). The general pattern of ANPP shows the most activity along the coast of the
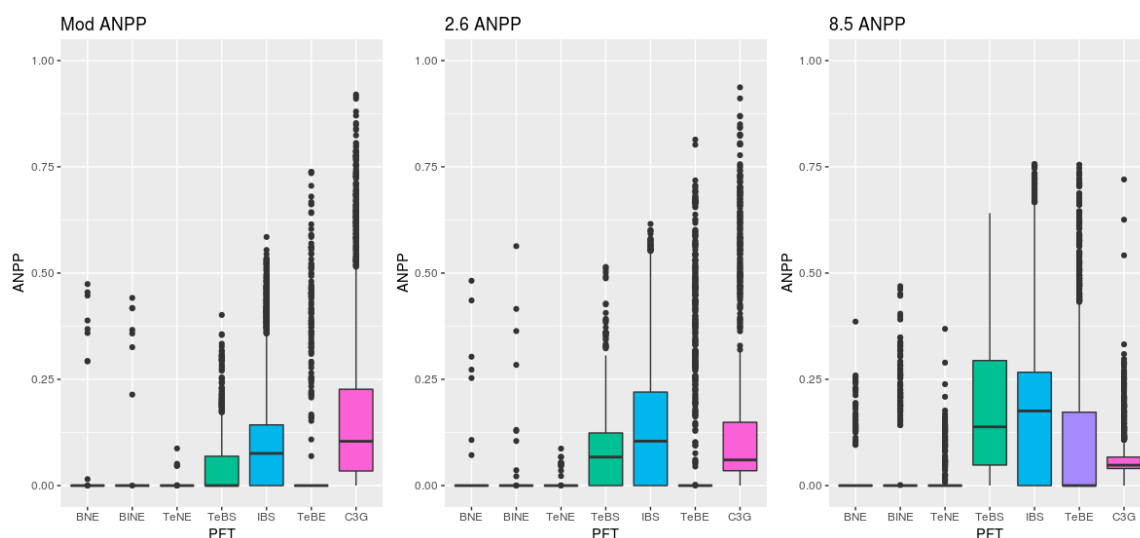
Figure 9. Boxplots of mean ANPP for PFTs present in the region across scenarios.
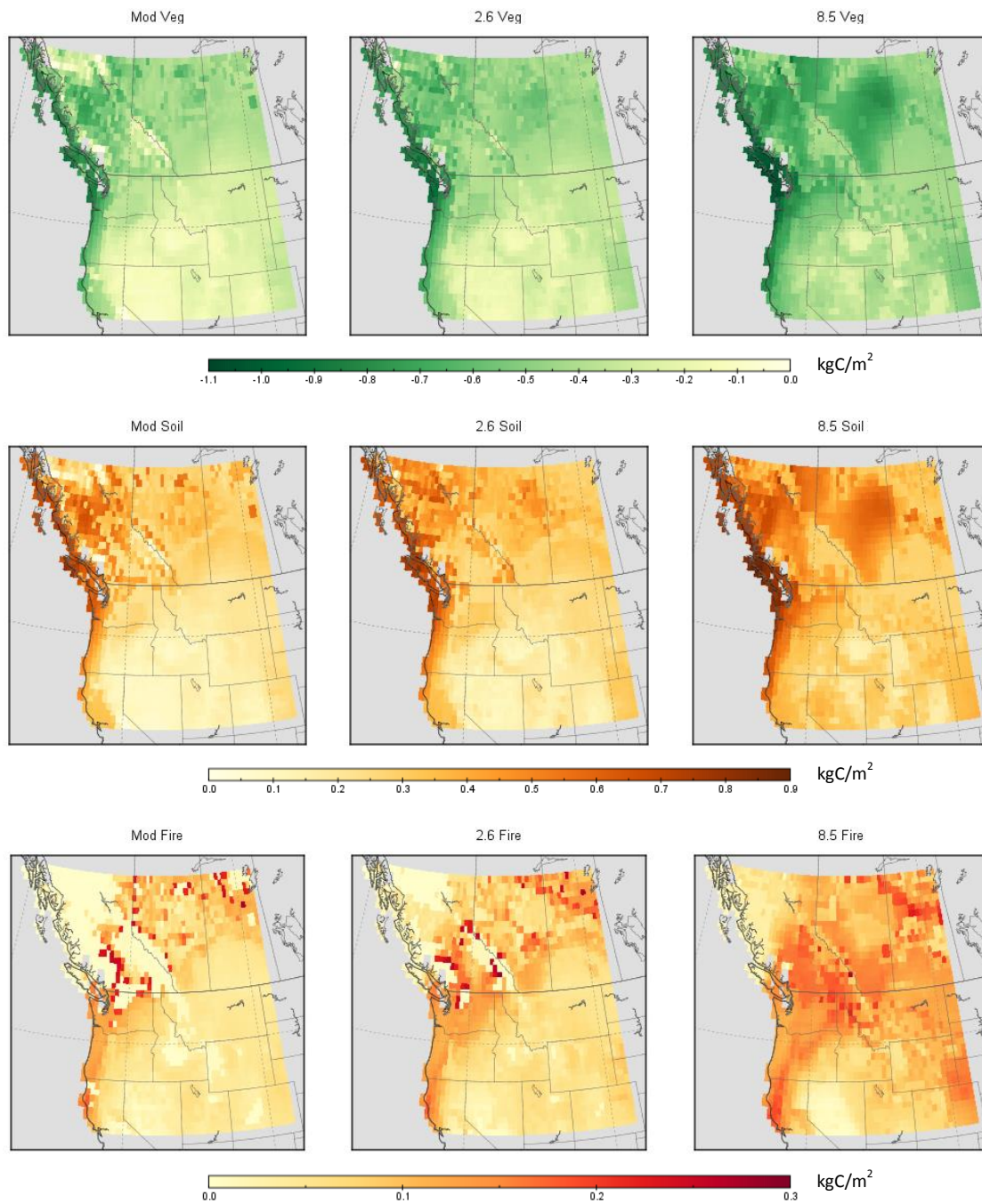
Figure 10. Mean carbon flux from vegetation, soil, and fire across scenarios. Negative values represent sinks while positive values represent sources. All generally increase in their storage (vegetation) or loss (soil and fire) across scenarios with most variability in the northern portion of the region. Note that the scales are different. Carbon flux due to reproduction shows a trend similar to soil, though a much smaller loss.

Pacific Northwest, and while ANPP generally increased across all scenarios, that did not always indicate decreases in NEE. Increases in the amount of vegetation also affect carbon flux from soil, reproduction, and fire. Therefore, an increase in NPP does not always indicate an overall benefit to the ecosystem (becoming a greater sink). Carbon lost through soil, reproduction, and fire also increased across scenarios. Flux contribution influences on NEE vary, with vegetation, soil, and sometimes fire components having significant influence compared to reproduction (Figure 10). The sum of these gains and losses display whether a location will sequester carbon, and looking at these fluxes across future scenarios indicates whether the region will improve or weaken as a carbon sink or source (Figure 11). NEE is fairly stable in the southern portion of the region. Of more interest, the northern portion indicates a varied pattern. Different locations indicate sinks and sources. What is important to note is that while in the 8.5 scenario, there are few locations of sources, the presence of sinks is also significantly reduced. Overall, NEE is not projected to change significantly, and the study region may transition to a source
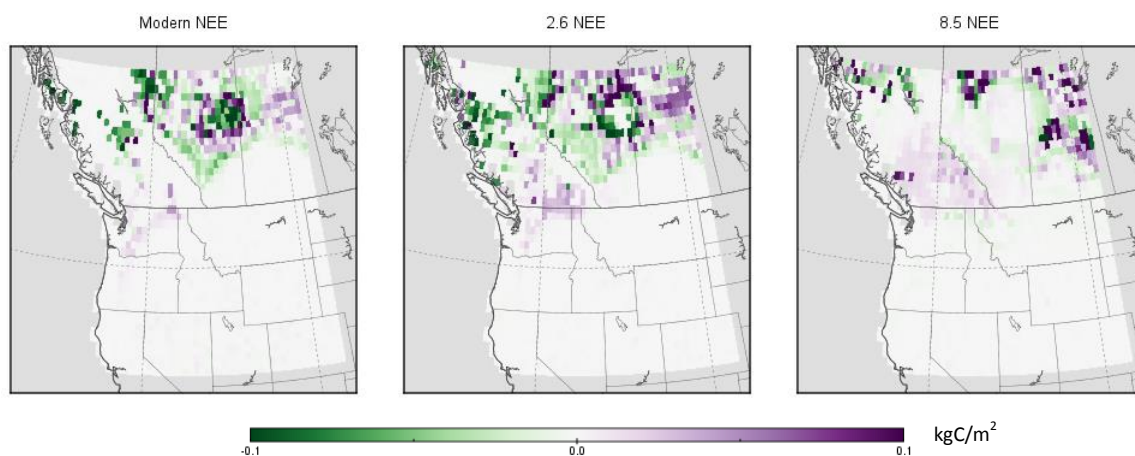
Figure 11. Mean NEE for all scenarios. The southern region demonstrates consistent NEE while the northern portion has more variability.

(Table 4). Vegetation is projected to be a greater sink while reproduction, soil, and fire are projected to be greater sources (Figure 12; Table 4). For these simulations, fire carbon flux is a reflection of increasing biomass, as different PFTs lose a certain proportion depending on their fire sensitivity and a given amount of biomass lost to fire occurs yearly in equilibrium mode. With increased ANPP, vegetation can also allocate resources to aspects other than growth, seen with reproduction, and if the growing period is warmer

Table 4. Mean regional carbon flux values across scenarios.

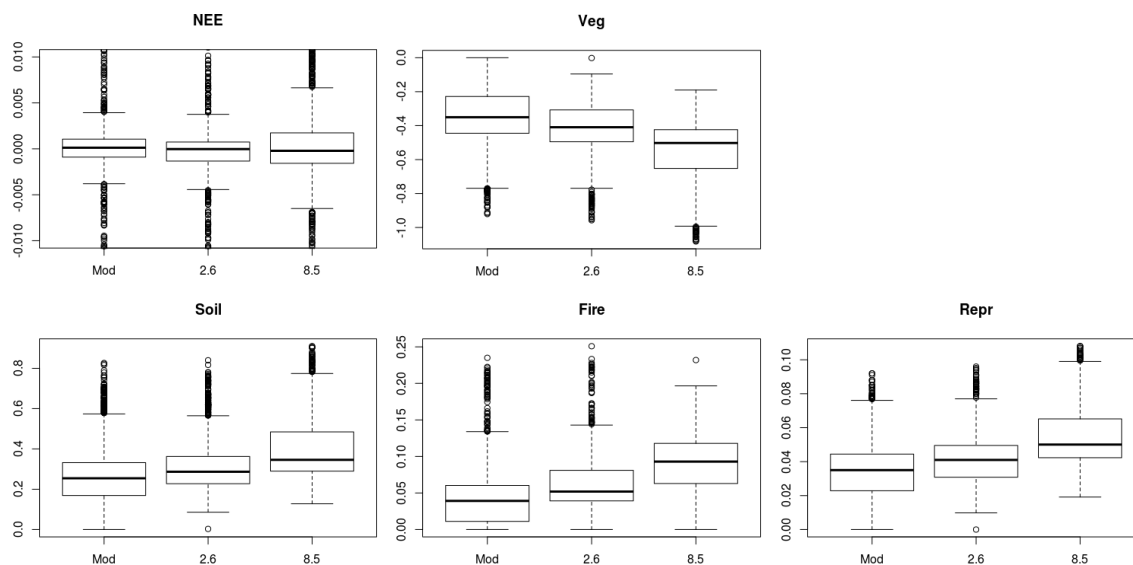| Mean Flux Values (kgC/m^2)			
Flux	Modern	RCP 2.6	RCP 8.5
NEE	-0.0016	-0.0002	0.0028
Veg	-0.3590	-0.4128	-0.5360
Soil	0.2760	0.3106	0.3593
Fire	0.0457	0.0607	0.0900
Repr	0.0359	0.0413	0.0536

Figure 12. Carbon fluxes across scenarios. Negative values represent sinks while positive values represent sources. Note the scale differences. NEE changes little across scenarios. Carbon held in vegetation increases (becomes more negative); all other fluxes also increase.

and longer, soils are also likely to become more active through decomposition and respiration.

Dynamic, Local Outputs

Following the mean modeling runs, a few specific points were selected to see their individual responses to changes in interannual variability, especially in terms of vegetation composition, disturbance, and carbon flux. Details about two locations (Figure 4) follow. The locations were selected from different ecoregions to see how they might respond to climate change scenarios.

Outputs from the 1000-year time series show progressions of vegetation composition and carbon flux over time. The coastal site (Figure 13) shows a gradual transition from temperate deciduous and temperate evergreen during the modern scenario to almost solely temperate evergreen by the 8.5 scenario, and total NPP increases. For the interior site (Figure 14), the modern simulation shows an ecosystem dominated by grasses. In the 2.6 scenario, vegetation fluctuates between grasses and temperate deciduous PFTs, and by the 8.5 scenario, temperate deciduous PFTs are dominant. As at the coastal site, NPP also increases across scenarios.

The carbon flux graphs depict carbon in the different components previously mentioned: vegetation, soil, reproduction, fire, and establishment. Reproduction and establishment are extremely small compared to the other components. Vegetation (represented with negative values as a sink) is equal to the total NPP in the plots of PFTs directly above. Soil and fire are also large components. NEE correlates most strongly with fire events with effects immediately apparent, before returning to a more stable
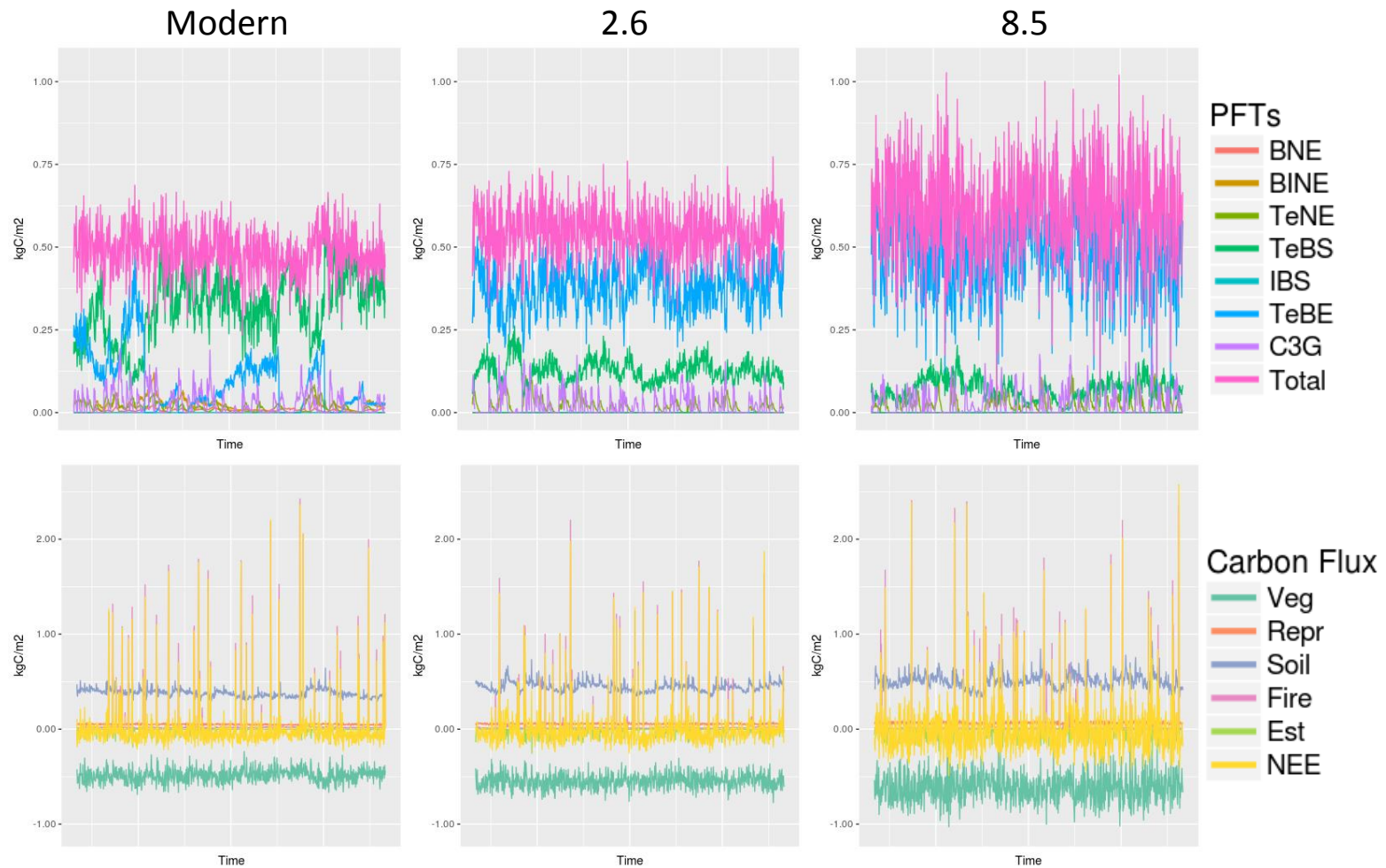
Figure 13. Time series of locational PFTs and carbon flux for 45.0°N, 122.5°W. Fire patterns remain consistent across scenarios. Y-axes represent kgC/m². Years are arbitrary. BNE: Boreal Needleleaf Evergreen, BINE: Boreal Shade Intolerant Needleleaf Evergreen, TeNE: Temperate Needeleaf Evergreen, TeBS: Temperate Broadleaf Summergreen, IBS: Shade Intolerant Broadleaf Summergreen, TeBE: Temperate Broadleaf Evergreen, C3G: Cool (C3) Grass.
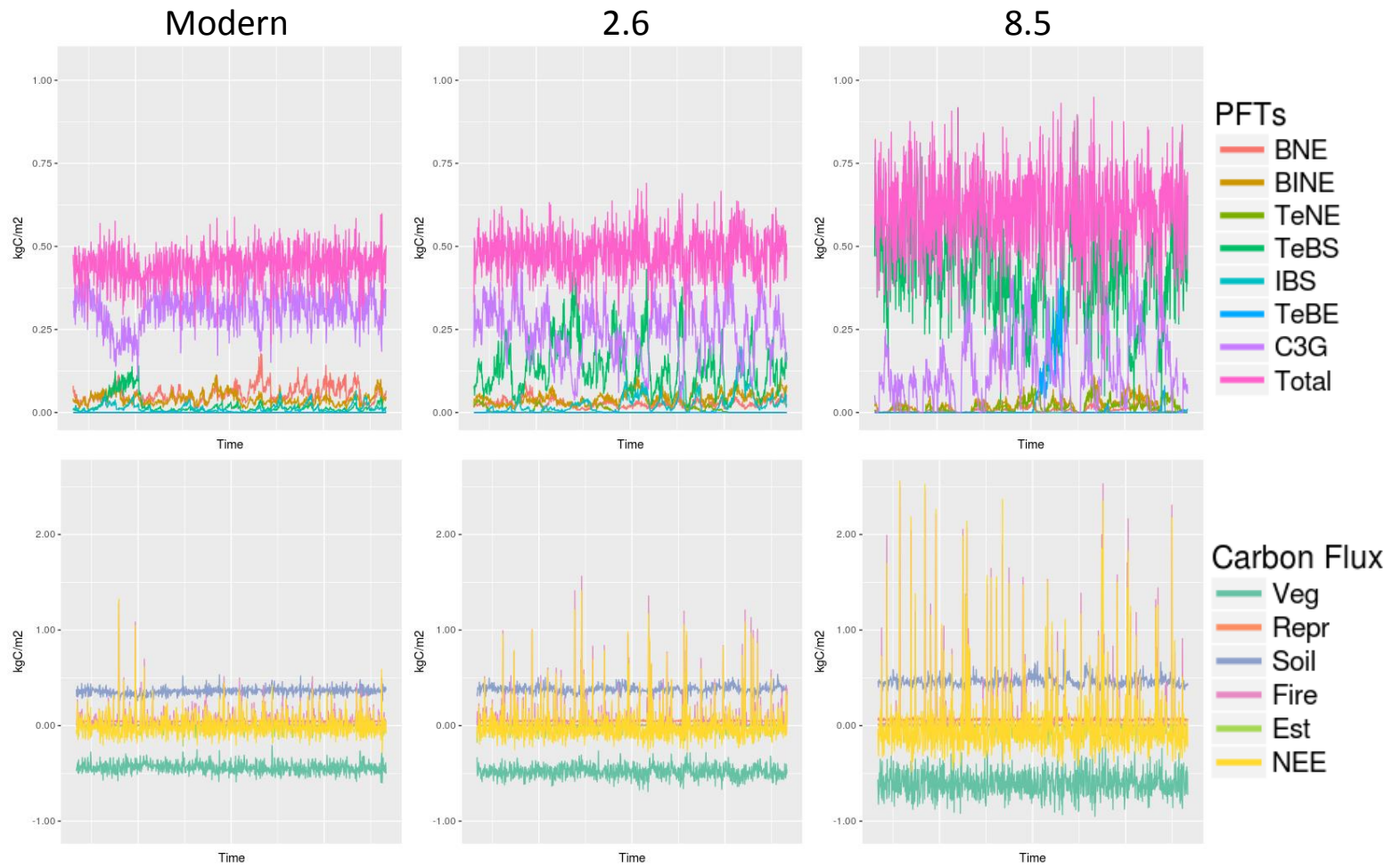
Figure 14. Time series of locational PFTs and carbon flux for 41.0°N, 104.0°W. Fire patterns increase across scenarios. Y-axes represent kgC/m². Years are arbitrary. BNE: Boreal Needleleaf Evergreen, BINE: Boreal Shade Intolerant Needleleaf Evergreen, TeNE: Temperate Needeleaf Evergreen, TeBS: Temperate Broadleaf Summergreen, IBS: Shade Intolerant Broadleaf Summergreen, TeBE: Temperate Broadleaf Evergreen, C3G: Cool (C3) Grass.

level.

The coastal site (Figure 13) presents a fairly consistent pattern with the size and frequency of fires keeping similar. The interior site (Figure 14) shows a different pattern of increasing fire intensity across scenarios. The modern simulation shows very small fires, but by the 8.5 scenario, the amount and size of large fires is noticeable. Examining fire thresholds for the two sites shows distinctive patterns that warrant further discussion (Figure 15). For the coastal site, where the vegetation remained fairly consistent, the fire trends across scenarios are also similar. There are slight increases in the number of larger fires for the final scenario, but overall, the total number of fires and pattern remains constant. The interior site experienced a different pattern, as it transitioned from grasses
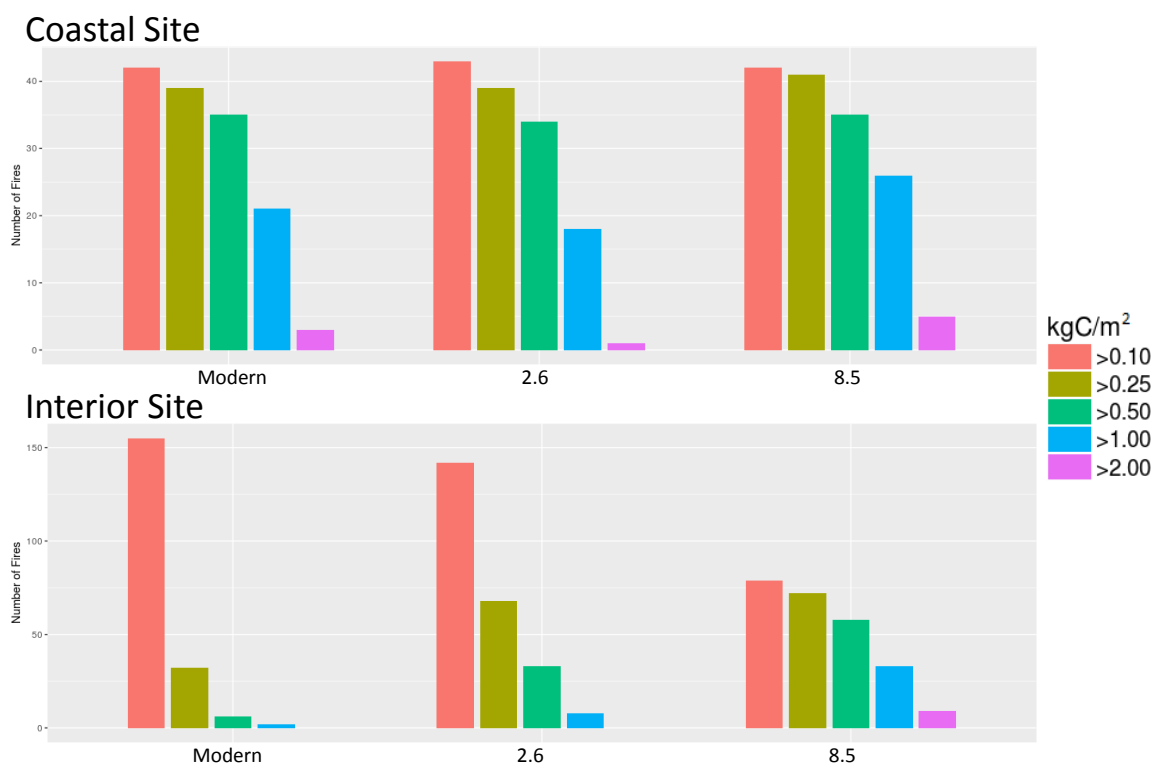
Figure 15. Number of fires greater than specific thresholds at the two sites. Note the different scales.

to a more tree-dominant ecosystem. Therefore, in the first two scenarios, there is a large amount of relatively small fires, and larger fires are infrequent, if they occur at all. The landscape in the first scenario provides little biomass for the especially large fires. The second scenario does show an increase under the larger fire thresholds, which is representative of tree PFTs becoming more present. By the final scenario, the shift in vegetation composition causes more, larger fires to occur, as there is available biomass, and reflects an ecosystem more similar to that occurring at the previous site.

DISCUSSION

The results have implications for the study region's ecosystem distribution, carbon sequestration, and fire patterns under different climates. The contraction of grass-dominant ecosystems in the study region at the end of the century is supported by Shafer et al. (2015). In their study, migration of trees upslope caused grasses to become less dominant in alpine areas. Also, future simulated vegetation showed contraction of alpine, shrub-steppe, and xeric shrub vegetation while woodlands and forests expand; maritime cool forests and cold forests persisted. As dominant vegetation transitions (Figure 8), certain biomes may still persist but likely experience changes in PFT percentages. Changes in PFT composition can affect carbon flux and fire regimes of an ecosystem.

A positive feedback between temperature and fire may occur (Flannigan et al., 2009). If climates, and seasonal weather in particular, become warmer and drier, more fires can occur. Increasing occurrence of fires is linked to increases in greenhouse gas release, helping to further elevate temperatures, and therefore, promote more fires as a positive feedback. Increases in the length and intensity of summer droughts will also encourage more wildfires in the west (Westerling et al., 2006). This pattern of frequent fires, though, may only be short-term if ecosystems are not sustained and fires do not have fuels available. Changes in forest compositions and tree densities will affect carbon pools (Westerling et al., 2006). Ecosystems will become sources of carbon if they cannot recover, do not recover before the time of the next fire, or if forest structure changes,

resulting in lower carbon stocks (Rocca et al., 2014).

Warmer temperatures, extended growing seasons, and physiological effects from increased CO_2 increases vegetation productivity (Morales et al., 2007). Carbon flux predictions for Europe indicate that both NPP and heterotrophic respiration (Rh) may increase in some regions (Morales et al., 2007). For example, shifts from sinks to sources are expected for many Mediterranean region ecosystems, due to water balance changes; temperate forests in northern European regions are affected by growing season length and carbon assimilation and generally function as carbon sinks. Though vegetation compositions and spatial distributions of NEE change, the net effect on the carbon balance is predicted to be relatively small (Morales et al., 2007), similar to the results of this study. Compared to the Pacific Northwest, the pattern in Europe showed distinct regional differences between northern and southern regions. For this study, there were shifts in NEE in some northern locations but stability in the southern portion. Again, these changes are important to consider because they will affect ecosystem function, carbon sequestration, and climate change mitigation. The different patterns between Europe and the Pacific Northwest are interesting and may be accounted for by regional climate differences and choice of climate models used.

Antecedent precipitation often increases fuel loads in xeric biomes and encourages fire, through increased fuel loading, especially if followed by dry conditions (Swetnam & Betancourt, 1998). No change or decreases in precipitation in summer months when ecosystems are particularly susceptible to fire in the western United States may have led to increases in fire across the scenarios. Warmer temperatures also mean that more precipitation would fall as rain and snowmelt would occur earlier, extending

the length of fire season, and also potentially supporting increases in fire (Westerling et al., 2006). At the same time, given that climate caused increases in ANPP, it is also possible that increases in vegetation caused fires to remove a greater proportion of biomass.

The coastal site experiences a less pronounced shift in vegetation with slight increases in fire, which may be due to extended fire season length or more intense summer warming. The interior site's transition from grass to woody PFTs with a simultaneous increase in fire makes it likely that this increase is due to vegetation change.

The effect of climate change on fire regimes can be amplified or dampened by vegetation (Higuera et al., 2009). Vegetation controls the size, abundance, and spatial patterns of fuels in an area. Higuera et al. (2009) suggest that future fire regimes will be determined directly by climate-fire relationships as well as by indirect impacts of climate on vegetation. Therefore, the patterns presented in the time series outputs may be a reflection of vegetation-mediated fire regime changes following climate change. Disturbance, such as fire, as well as climate and soil, influences vegetation composition (Thonicke et al., 2001). However, in these model outputs, shifts in vegetation type and abundance appear to also have a significant influence on fire, as seen with the interior site.

Disturbance may be represented too simplistically within the model. While fire is based on a probability of occurrence under certain moisture conditions, biomass removed is represented as a proportion of certain PFTs. Fire events respond to climate, but when vegetation changed, there was also more to burn. This more simplistic representation may be the reason for the differences seen in size of fires across scenarios, a response to

vegetation composition rather than a direct response to climate. The representation of carbon flux, however, appears to be more complex, with the inclusion of the different fluxes and their interactions.

Because regional climate data were used, the results should be interpreted with some care. The use of one signal generalized regional differences. Minimums and maximums in both temperature and precipitation were eliminated due to the choice to use a regional signal. Therefore, using an average signal can cause some potential changes at sites with climate differences to be missed. Especially in dry areas, increases in precipitation may have caused misleading results. In future studies, spatial climatic differences in future projections should be accounted for as the region experiences a range of temperature and moisture conditions. Overall, however, this study introduces some of the outcomes that may result from climate change.

CONCLUSION

Through the use of LPJ-GUESS, changes in vegetation and associated carbon sequestration were analyzed. Regional simulations demonstrated shifts in vegetation types, increases in fire, and resulting changes in NEE patterns. Future simulations indicate increases in woody PFTs. This suggests that these PFTs will not be limited under proposed climate changes; grasses may be limited from new competition. Despite this, carbon flux patterns remain similar. Across all scenarios, the northern portion of the study region consistently showed the most variability, largely due to fire; carbon flux levels for vegetation, soil, and reproduction presented more predictable patterns. The southern portion was much more stable, maintaining fairly consistent NEE levels.

Specific sites showed changes in PFT compositions and increases in ANPP across scenarios. There is a clear relationship with NEE and fire events, and across scenarios, there was evidence of changes in number and size of fires, which affects the amount of carbon lost.

Climate-fire-vegetation interactions are complex. They all directly and indirectly influence each other. Distinguishing the magnitude and direction of influence can be difficult. In this study, it appears that fire was affected by climate, either through or amplified by vegetation changes.

Human communities will be threatened by potential increases in fire across the region. Fire will also affect the carbon balance by changing the ability of ecosystems to

sequester carbon and mitigate its release into the atmosphere. Modeling potential outcomes allows for a discussion of management policies into the future. By understanding the spatial patterns and the causes behind them, resource and land managers can begin planning for these changes and work to alleviate some of the risks.

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