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Evaluating carbon storage, timber harvest, and habitat possibilities for a Western Cascades (USA) forest landscape

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Abstract. Forest policymakers and managers have long sought ways to evaluate the capability of forest landscapes to jointly produce timber, habitat, and other ecosystem services in response to forest management. Currently, carbon is of particular interest as policies for increasing carbon storage on federal lands are being proposed. However, a challenge in joint production analysis of forest management is adequately representing ecological conditions and processes that influence joint production relationships. We used simulation models of vegetation structure, forest sector carbon, and potential wildlife habitat to characterize landscape-level joint production possibilities for carbon storage, timber harvest, and habitat for seven wildlife species across a range of forest management regimes. We sought to (1) characterize the general relationships of production possibilities for combinations of carbon storage, timber, and habitat, and (2) identify management variables that most influence joint production relationships. Our 160 000-ha study landscape featured environmental conditions typical of forests in the Western Cascade Mountains of Oregon (USA). Our results indicate that managing forests for carbon storage involves trade-offs among timber harvest and habitat for focal wildlife species, depending on the disturbance interval and utilization intensity followed. Joint production possibilities for wildlife species varied in shape, ranging from competitive to complementary to compound, reflecting niche breadth and habitat component needs of species examined. Managing Pacific Northwest forests to store forest sector carbon can be roughly complementary with habitat for Northern Spotted Owl, Olive-sided Flycatcher, and red tree vole. However, managing forests to increase carbon storage potentially can be competitive with timber production and habitat for Pacific marten, Pileated Woodpecker, and Western Bluebird, depending on the disturbance interval and harvest intensity chosen. Our analysis suggests that joint production possibilities under forest management regimes currently typical on industrial forest lands (e.g., 40- to 80-yr rotations with some tree retention for wildlife) represent but a small fraction of joint production outcomes possible in the region. Although the theoretical boundaries of the production possibilities sets we developed are probably unachievable in the current management environment, they arguably define the long-term potential of managing forests to produce multiple ecosystem services within and across multiple forest ownerships.

Key words: ecosystem services; forest management; landscape analysis; trade-offs.

Introduction

Since the multiple-use era of public lands management in the USA, forest policymakers and managers have sought ways to consider socioeconomic and ecological trade-offs associated with timber harvesting and other forestry activities (Kline et al. 2013). Initial work by Gregory (1955) and later by Bowes and Krutilla (1989), among others, developed analytical methods for evaluating the capability of forest landscapes to produce different combinations of multiple outputs (e.g., timber, forage, water) based on neoclassical economics theory of joint production (e.g., Bowes and Krutilla 1989:xvi). However, until recently, attempts to apply such methods have been mostly limited to (1) theoretical efforts examining spatial, temporal, and other issues that complicate the process of solving joint production forest management problems (e.g., Swallow et al. 1990, 1997, Swallow and Wear 1993, Boscolo and Vincent 2003, Alix-Garcia 2007), and (2) optimization models identifying joint production possibilities for timber production and fairly limited sets of wildlife species or ecological indicators (e.g., Arthaud and Rose 1996, Kangas and Pukkala

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1996, Rohweder et al. 2000, Calkin et al. 2002, Lichtenstein and Montgomery 2003, Nalle et al. 2004). Although these efforts demonstrate the potential utility of joint production economic theory for evaluating landscape-level joint production and trade-offs, most have been limited in the diversity of management regimes evaluated and the number of ecosystem services examined. Ideally, analysis would characterize outcome possibilities for ecosystem services across a full range of management options available to managers.

Understanding the effects of forest management on carbon and other ecosystem services is of particular interest, as policies for increasing carbon storage on federal lands are being proposed to address climate change (e.g., Ellenwood et al. 2012). USDA policy (U.S. Department of Agriculture 2014), including a new Forest Service Planning Rule (U.S. Department of Agriculture, Forest Service 2012), for example, calls on the U.S. Forest Service to lead efforts to mitigate and adapt to climate change. Despite significant recent interest in managing forests and their products to both store carbon and slow its release to the atmosphere (e.g., McKinley et al. 2011), studies of how carbon dynamics are influenced by a wide range of different forest management regimes within specific ecosystems are limited. Potential co-production of other ecosystem services on federal forest lands would tend to make policy and management efforts to increase carbon storage more attractive by reducing their social costs (Englin and Callaway 1995). However, the degree to which polices and management regimes intended to store more carbon would either complement or compete with production of other services is uncertain.

A challenge in joint production analysis of multiple ecosystem services in forest management contexts is representing the temporal and spatial interactions among ecological conditions and processes that influence joint production relationships (Swallow et al. 1990, Swallow and Wear 1993). For optimization models to remain tractable, they often must be specified in ways that either oversimplify joint production relationships or restrict evaluation to a limited set of management variables (e.g., rotation length) and their influence on just a few ecosystem services (Swallow and Wear 1993:117). Englin and Callaway (1995), for example, used a modified Faustmann model (Faustmann 1849) to examine joint production of carbon storage, timber, and several non-timber ecosystem services, including habitat, but limited their evaluation to the effects of rotation age. McCarney et al. (2008) used an optimization model to examine carbon storage, timber, and wildlife habitat in Canada but were similarly restricted in the range forest management scenarios evaluated. Moreover, they addressed carbon and habitat as constraints on timber harvest that limited the breadth of production possibilities that could be evaluated. The necessity for simplification in how management and ecosystems are portrayed in optimization models can inhibit evaluating the combined influence of a broader array of management variables, including tree size limits, harvest patch sizes, and their spatial arrangement, and site preparation practices, among others, that can influence carbon storage, timber harvest, and habitat outcomes either intentionally or via disturbance effects to soil, stand structure, and other ecosystem characteristics.

Simulation models, an alternative to optimization, may offer greater opportunities for addressing both the temporal and spatial complexity of forest landscapes in joint production analysis (e.g., Swallow et al. 1990:265). To date, however, their use to evaluate carbon, timber, and habitat have been similarly limited in the range of management variables considered. Seidl et al. (2007), for example, examined carbon storage, timber production, and biodiversity in Austria, but focused on just four forest management and three biomass utilization scenarios, limiting the study's ability to characterize a broad range of production possibilities (Seidl et al. 2007:72). Moreover, at 249 ha, the study-area landscape arguably was too small to adequately consider outcome responses for wildlife species ranging over larger areas (Seidl et al. 2007:72). In other studies, Schwenk et al. (2012) simulated carbon, timber, and habitat outcomes in Vermont (USA) for four management prescriptions, while McLaughlin (2013) simulated carbon, timber, and Northern Goshawk (*Accipiter gentilis*) habitat outcomes in coastal British Columbia (Canada) for five management scenarios. We sought to build on this work by simulating a more extensive set of forest management scenarios than addressed by previous landscape simulation models. Our simulated scenarios were characterized by a broad range of disturbance intervals and harvest intensities and provide a comprehensive view of carbon storage, timber, and habitat possibilities available on a 160 000-ha Western Cascade forest landscape.

A body of previous work provides a foundation for joint production analysis of carbon storage, timber, and wildlife habitat in western Oregon. Empirical models for simulating carbon storage responses to forest management and timber harvest in Pacific Northwest (USA) forest ecosystems have existed for decades (e.g., Harmon et al. 1990, 2009, Mitchell et al. 2009). These include efforts to augment stand- and landscape-level analysis of forest ecosystem carbon stores with estimates of carbon stored in wood products (Harmon et al. 1996, Harmon and Marks 2002, Nunery and Keeton 2010, Mitchell et al. 2012). However, none of these carbon modeling efforts simultaneously examined forest management effects on habitat for various wildlife species. The influence of forest structure and management on habitat for various species largely is known from decades of empirical studies (e.g., McGarigal and McComb 1995, Lance and Phinney 2001), research syntheses, including expert opinion (e.g., Johnson and O'Neil 2001), and landscape-scale modeling (e.g., Hansen et al. 1995, Shifley et al. 2006, Spies et al. 2007*b*). The long-term and landscape-scale effects of forest management in the Pacific Northwest typically have been examined using species-specific habitat suitability models based on vegetation structure and landscape characteristics (e.g., Spies et al. 2007a, Morzillo et al. 2014). Drawing on these works, we compiled and used landscape simulation models of vegetation structure, forest sector carbon, and habitat to characterize the range of steady-state joint production possibilities for carbon storage, timber harvest, and habitat for seven wildlife species.

Our objectives were to (1) characterize the general relationships (shapes and degree of complementarity or competition) of production possibilities for combinations of carbon storage, timber, and habitat, and (2) identify management variables that most influence joint production relationships. We used model outputs to examine how the choice of forest management practices intended to increase carbon storage might influence joint timber and habitat outcomes over time. Although we expected to find increased carbon storage to be complementary with habitat for species that thrive in late successional forest conditions vs. those favoring early successional conditions, we were less certain about the ranges of carbon storage over which complementarity might exist. Additionally, we were less certain about how increased carbon storage might influence habitat for species favoring other forest structural attributes not necessarily associated solely with stand age, such as the juxtaposition of stand with open vs. closed canopy, edge contrast, snags, and other variables. Lastly, we were uncertain about which forest structural characteristics might be most influential in carbon–habitat relationships for individual species.

Our results demonstrate how forest management, particularly disturbance interval and intensity, establish the bounds of joint production possibilities for carbon, timber, and wildlife habitat. By systematically examining a broad range of management regimes from no harvest to intensive timber utilization and from short to very long rotations, our study goes well beyond previous studies that examined limited numbers of management regimes. We based our evaluation on steady-state or dynamic equilibrium values of timber, stored carbon, and wildlife habitat under different management regimes to define the theoretical limits (or ecological potential) of producing combinations of these ecosystem services on Western Cascade forest landscapes. Such information can be useful in the political contexts in which national forest management occurs by enabling stakeholders to test prevailing assumptions about the degree to which various ecosystem services can be produced in combination with others on a given landscape. Although it is unlikely that steady-state values can be achieved given the long time-frames required and the occurrence of natural disturbances, they provide a common reference for comparing the relative effects of different management regimes on ecosystem services and biodiversity. We plan to examine the time trajectories (or transient) effects of different management regimes applied to the initial conditions of this landscape in a future paper.

Methods

General approach

Our analysis involved combining existing ecosystem and habitat models to simulate landscape changes for an array of forest management regimes, both currently in use and hypothetical, for a forest landscape in the Western Cascades of Oregon. Specifically, we used the model LandCarb (Harmon 2012) to simulate ecosystem processes, forest vegetation and growth, timber harvest, and carbon dynamics and stores resulting from various management scenarios. We used LandCarb outputs characterizing forest conditions to inform a set of habitat capability models for seven wildlife species. We used these coupled models to define long-term steady-state levels of carbon storage, timber harvest, and wildlife habitat that could be produced on the landscape, including which management and landscape variables enhanced production, which variables reduced production, and which variables ultimately limited production. We also identified the general relationships between carbon storage, timber, and habitat, including the ranges of production over which these ecosystem services were complementary or competitive. Ecosystem services are complementary if they respond similarly to management such that they tend to increase or decrease together. Ecosystem services are competitive if they respond differently to management such that an increase in one ecosystem service tends to coincide with a decrease in the other. We did not address the potential effects of climate change, because we sought to identify the current capability of the study area landscape to jointly produce stored carbon, timber, and wildlife habitat, consistent with the joint production possibilities framework.

Study area

Pacific Northwest forests have the potential to store significant amounts of carbon (Smithwick et al. 2002, Keith et al. 2009), making them an important consideration in federal policy concerning efforts to mitigate climate change by increasing carbon storage. We conducted our simulations on a 160 000-ha focal landscape, 89% of which is forested, in the Western Cascades of Oregon. Topography is mountainous with elevations ranging from 267 to 1845 m. Climate is variable, with mean annual temperature ranging from 5° to 11°C and mean annual precipitation ranging from 158 to 328 cm. Forests are primarily coniferous and include long-lived tree species of the western hemlock (*Tsuga heterophylla*) and silver fir (*Abies amabilis*) potential vegetation zones (Franklin and Dyrness 1973); Douglas-fir (*Pseudotsuga menziesii*) is the primary timber species. The landscape currently is under a mix of private and federal ownerships and managed for a range of ecosystem services, values, and conditions, from intensive timber production to standing old-growth forests. However, we applied our simulated management scenarios uniformly across the landscape to identify the long-term consequences of each management scenario applied over time. Although our combined models also can be used to simulate heterogeneous management across different landowners, uniform application of management scenarios across the landscape enables easier interpretation of how the ecosystem responds to each management scenario.

Forest carbon models

Carbon dynamics and stores for the forest ecosystem and in wood products (both in use and disposal) were simulated using the LandCarb model (Harmon 2012, Mitchell et al. 2012). Basic ecological processes regulating carbon flows and stores in the forest were represented at a grid cell resolution of 1 ha. Modeled processes included photosynthesis, the allocation of photosynthate (products of photosynthesis) to different plant parts, respiration of plants and decomposers, mortality caused by plant part shedding or whole plant death, soil formation, combustion and charcoal formation associated with fires, and removal of carbon via harvests. The processes of photosynthesis and respiration were controlled by temperature as well as the amount of light and water available. We assumed that carbon removed via harvest from either live or dead pools was initially processed in manufacturing where it was either directly lost to the atmosphere or converted to various products having varying lifespans (e.g., paper, buildings). These products also had assumed carbon losses associated with decomposition, combustion, and disposal with the potential for recycling and reuse, incineration, or storage in landfills.

Initial vegetation conditions were based on gradient nearest neighbor land-cover data (Ohmann and Gregory 2002) species distributions for the study area applied to bare ground (Harmon 2012). Simulations began with a 600-yr spin-up period to establish initial live, dead, and soil carbon stores for 2008 base year based on growth, mortality, and decomposition processes and disturbance history (Appendix S3). Study area soils were assumed to have a loamy texture, 5% coarse fragment, and 1 m depth. Climate data were monthly mean values for precipitation and temperature (average, minimum, and maximum) reported as 30-yr normal at an 800-m resolution by the PRISM Climate Group (2015). These data were summarized for three climate zones, which were defined by elevation (103–688 m, 688–1273 m, and 1273–1858 m). Monthly solar radiation inputs, both diffuse and direct, were estimated using the program SolarRad (Harmon and Marks 1995) for 45 radiation zones defined by combinations of elevation, slope, and aspect.

We aggregated simulated carbon pools for both the forest ecosystem and wood products systems. We considered forest ecosystem carbon as the sum of all live, dead, soil, and charcoal carbon in the forest. Soil in this case includes the highly decomposed carbon present in the mineral soil and on the forest floor. Less decomposed material is termed dead and includes dead foliage, dead roots (both fine and coarse), dead branches, and dead wood. We considered wood products as the sum of all products in use, such as paper and short- and long-term structures, as well as those that had been disposed of in open dumps and landfills. We did not track potential substitutions among wood and alternative products, such as steel and concrete, because of unresolved questions about how long forest substitution displacements last and the degree to which they are subject to leakage (e.g., Law and Harmon 2011). We considered forest sector carbon to be the sum of forest ecosystem and wood products carbon.

To understand the underlying factors controlling the forest carbon response, we compared the average carbon input into the forest to the turnover time of carbon in the forest. Turnover time reflects the average number of years that carbon stays within the forest system. The average input was computed by averaging the net primary productivity (NPP), the rate at which new biomass is added to an ecosystem, as estimated by LandCarb over the last 100 yr of each 1000-yr simulation, which is the time required to develop steady-state conditions for all of the regimes. We computed turnover time as the average carbon store in the forest divided by the sum of the losses associated with decomposition, harvest, and combustion by prescribed fires. As with NPP, these variables were averaged over the last 100 yr of each simulation. We also computed the carbon turnover time for wood products by dividing the store of wood products by the amount of carbon being harvested from the forest ecosystem during the last 100 yr of each simulation.

Wildlife habitat models

We selected seven focal wildlife species representing different habitat requirements based on management interest (e.g., endangered, threatened, sensitive, indicator), successional stage association (early, late), and landscape configuration association (e.g., interior forest, edge; Table 1). Although our analysis focused on defining steady-state landscape-level conditions for carbon, individual stands need not be in a steady state. Thus, our habitat models and associated wildlife responses were based on stand-level values as individual stands progressed through forest successional stages. We first developed habitat capability index (HCI) models for each focal species composed of key habitat elements for western Oregon using empirical data derived from the scientific literature for our focal species and methods from McComb et al. (2002) and Spies et al. (2007*b*; Appendix S1). We then adapted the HCI models to the scale and structure of the Landcarb model. The source models for Northern Spotted Owl, Western Bluebird, Olive-sided Flycatcher, and Pileated Woodpecker have been empirically tested using data from coastal Oregon (McComb et al. 2007, Spies et al. 2007*b*). Empirical data were not available for testing the other habitat models, but sensitivity analysis was conducted on the red tree

Table 1. Wildlife habitat associations and HCI variables for focal species§.

Species	Key habitat characteristics	Variables†	Range‡
Mule deer (*Odocoileus hemionus*)	mixed forest and edge for hiding and thermal cover and foraging	average dbh	14–26
		canopy closure (%)	5–65
		number canopy layers	≥1
Northern Spotted Owl (*Strix occidentalis caurina*)	old-growth forest	diameter diversity index	≥7.5
		trees/ha ≥ 75 cm dbh	≤65
		trees/ha, 10 cm ≤ dbh < 25 cm	≤25
		trees/ha, 25 cm ≤ dbh < 50 cm	≤80
Olive-sided Flycatcher (*Contopus cooperi*)	edge contrast between mature forest for nesting and open areas for foraging	canopy closure (%)	>65
		snags (>5 m) per ha, dbh ≥10 cm	25–32
		live trees per ha, ≥10 cm dbh	>90
		height (m) of trees in adjacent pixel (edge contrast)	≥65
Pacific marten (*Martes caurina*)	mature forest; snags and downed logs for denning	diameter diversity index	>3.5
		volume down logs (m^3/ha), ≥50 cm diameter	≥160
		snags (>5 m) per ha, 50 cm ≤ dbh <75 cm	≥3
Pileated Woodpecker (*Dryocopus pileatus*)	range of forest types with snags for nesting and foraging	volume down logs (m^3/ha),, ≥50 cm diameter	≥23
		snags (>5 m) per ha, dbh ≥75 cm	≥2
		snags (>5 m) per ha, 50 cm ≤ dbh <75 cm	≥3
		live trees/ha, ≥50 cm dbh	≥180
Red tree vole (*Arborimus longicaudus*)	mature coniferous forest	canopy closure (%)	>96
		diameter diversity index	>8
		quadratic mean diameter for stand	>50
		density/ha of Douglas fir ≥ 50 cm dbh	>100
Western Bluebird (*Sialia mexicana*)	early successional forest with snags for nesting	canopy closure (%)	≤20
		snags (>5 m) per ha, dbh ≥50 cm	≥5
		snags (>5 m) per ha, 25 cm ≤ dbh <50 cm	≥15

§Value of each index ranges from 0 (non-habitable) to 1 (best habitat condition).
†Adapted from McComb et al. (2002) and Spies et al. (2007*b*), with the exception of mule deer.
‡Number provided indicates the range for which value of each index equals 1.

vole model to identify key variables (Spies et al. 2007*b*). All models were examined by several experts and initial model results were mapped to verify that the results were consistent with current understanding of the ecology of each species.

The area (i.e., cells in a grid) used to identify a meaningful landscape scale that could allow occupancy for each species varied based on the approximate home range size for each species, from 1 ha for Western Bluebird to 240 ha for Northern Spotted Owl (McComb et al. 2002, Spies et al. 2007*b*). We did not consider scales beyond the home range, such as indicators of connectivity, because although our landscapes were relatively large, they were discrete and for species with large home ranges, a larger landscape would be needed to realistically address connectivity issues. HCIs were standardized on a 0–1 scale, with 0 indicating unsuitable conditions for a species and 1 representing optimal conditions. HCI values of >0.33 were used to represent habitat conditions that could be used by a species when reporting results, consistent with previous studies (e.g., Spies et al. 2007*b*). Our habitat models did not address species populations. Rather, they focused only on whether structure and composition elements at the home-range scale would likely be present to support a species individual or pair if found at that location. Variables selected for the HCI models were based on empirical data from published literature and the ability to link those variables to LandCarb output variables. We verified that HCI models resembled habitat conditions of corresponding forest characteristics by visually inspecting maps of model variables created for the study area landscape using gradient nearest neighbor land cover data (Ohmann and Gregory 2002).

Vegetation structure models

LandCarb does not directly track all of the forest structure variables used in the HCI models, necessitating a crosswalk between the HCI models and LandCarb output variables. Using data from regional forest inventories (Bechtold and Patterson 2005), we developed predictive models of the structure variables, where the predictors were limited to forest structure variables that LandCarb does track. These variables included biomass of live and dead standing trees, biomass of dead and down coarse woody debris, forest stand age and height, the number of forest layers, and climatic and topographic variables (Appendix S2). Structural attributes that were absent (i.e., zero) on more than 5% of the inventory plots were modeled using a two-step process that involved first using logistic regression to predict attribute presence or absence, followed by multiple regression to predict attribute abundance where present. Structural attributes with fewer than 5% 0 values were modeled solely with multiple regression. Potential predictor variables in these models were transformed to satisfy, to the extent possible, the assumptions of linear regression (e.g., linearity, constant variance, normally distributed errors). We modeled the number of forest layers, an ordered categorical attribute ranging from 0 to 3, using a qualitative limited dependent variable regression model included in the PROC GLIM procedure of SAS, version 9.3 (SAS Institute, Cary, North Carolina, USA; Appendix S2).

We evaluated predictions from the structural attribute models by comparing them with observed values from the gradient nearest neighbor (GNN) model (Ohmann and Gregory 2002) for each 1-ha cell in the study area. The assessment was done visually with histograms, scatterplots, and residual plots from linear regression (Appendix S2: Table S3). However, because the GNN predictions are based in part on the same forest inventory data used in developing the structural attribute models, they do not constitute an independent data set. Still, our assessment suggests that the structural attribute models predictions are fairly representative of GNN values.

Table 2. Management variables and value ranges used in LandCarb simulations.

Management variable	Value range
Live tree harvest interval (yr)	25, 37, 50, 62, 75, 100, 125, 150, 175, 200, 250, 500, infinite
Harvest block size (ha)	10, 100, 500, 1000
Harvest intensity (% cell harvested)	25, 50, 100
Harvested wood utilization (%)	0, 20, 40, 60, 80
Snag felling at harvest	yes, no
Prescribed fire	yes, no
Dead tree (standing and down) salvage (%)	0, 100
Dead tree salvage interval (yr)	10, 20, 40
Snag salvage with live-tree harvest	yes, no
Arrangement of harvest areas to either minimize or maximize height contrasts between adjacent forests.	dispersed, adjacent

Management regimes simulated

We examined a wide range of current and hypothetical management regimes described by varying levels of eight separate management variables, including harvest block size, harvest intensity, felled wood utilization, snag felling (but not salvaged) at harvest, prescribed fire, dead tree (both standing and down) salvage, dead tree salvage interval, snag salvage with live-tree harvest, and the arrangement of harvest areas to either minimize or maximize height contrasts between adjacent forests (Table 2). These management regimes reflected a range of approaches, from maximizing timber harvesting to improving habitat for late seral species (e.g., providing snags and downed logs). For each of these 38 general management regimes, we simulated up to 13 different harvest intervals (rotation ages) spanning from 25 to 500 yr, plus a no-harvest scenario, resulting in simulations of 495 unique management scenarios. Simulations involving partial harvest at intervals >125 yr on large blocks were not always feasible because of physical space limitations of the study area landscape and so were eliminated. We chose to simulate management scenarios spanning this range and diversity to describe as much of the landscape production possibilities space as possible, independent of potential cost and other operational constraints.

To ease interpretation of simulated outcomes, we categorized management scenarios into three general management emphasis groups: (1) retention of live and dead wood for wildlife with limited removal for timber, (2) mixed objectives, including timber removal with some retention for wildlife (roughly similar to current industrial practices under the State Forest Practices Act), and (3) maximum removal (or utilization) of live and dead wood. The retention for wildlife group included scenarios in which live trees were either killed by prescribed fire or felled, but not all harvested, to create snags and downed dead wood that are important habitat features for many wildlife species. The maximum utilization group featured harvesting all live and dead trees. These two groups arguably represent extreme scenarios that are unlikely in the present to be fully implemented due to economic, biodiversity, and policy constraints. We defined the mixed objectives group to include scenarios ranging from clear-cut harvest with a 100% salvage of dead trees at the time of the clear-cut to clear-cut harvest but with 80% of felled trees harvested and no salvage of dead trees. Each management emphasis group was simulated across a full range of disturbance intervals (25–500 yr). Although management regimes often are defined in terms of rotation length, we defined the management emphasis groups only in terms of disturbance (or harvest) intensity and used knowledge of disturbance interval (or rotation length) to help explain variation in carbon, timber harvest, and habitat outcomes within each group.

Simulations and output

Our simulations involved repeating each management scenario over as much of the landscape as possible until the long-term rates of change in output variables were negligible such that a stationary cycle or steady-state was evident. Steady-state conditions, which we use as a common reference condition, generally were achieved in 300 yr from 2008 initial conditions for many ecological variables and in over 900 yr for wood products derived from the longest harvest intervals (Appendix S3).

However, we ran each of our simulations for 1000 yr to ensure that steady-state conditions were met. Stochastic elements of the LandCarb model result in a degree of variation in steady-state solutions and include which species occupy stands, mortality within stands, and most significantly, the selection of grid cells to harvest. We computed the mean and standard error of each output variable to characterize the quasi-steady-state reached during the final 100 yr of each simulation. Additionally, we conducted validation analysis of the LandCarb predictions by comparing key output variables with gradient nearest neighbor (Ohmann and Gregory 2002) and LiDAR-based estimates.

Using the results of our simulations, we plotted carbon, timber harvest, and habitat responses against each other to characterize the joint production possibilities space for each output pair and to examine trade-offs among ecosystem services associated with pursuing one management scenario vs. another. Our habitat response represented the percent of the landscape meeting a habitat quality threshold of HCI >0.33 at steady state. We prepared additional plots of response variables against the key ecological variables influencing those responses to ease interpreting the various shapes of the joint production possibilities sets. Although the precise inner and outer limits (or bounds) of joint production possibilities for each output pair could not be determined, they can be inferred based on visual inspection of each plot. We classified the joint production output pair as either complementary, competitive, compound, or neutral based on visual inspection of the outer bound. Our classification of compound indicated output pairs exhibiting characteristics of both complementary and competitive relationships, dependent on their level of production.

Results

Our results focus on the steady-state values for carbon, timber harvest, and wildlife habitat outcomes and

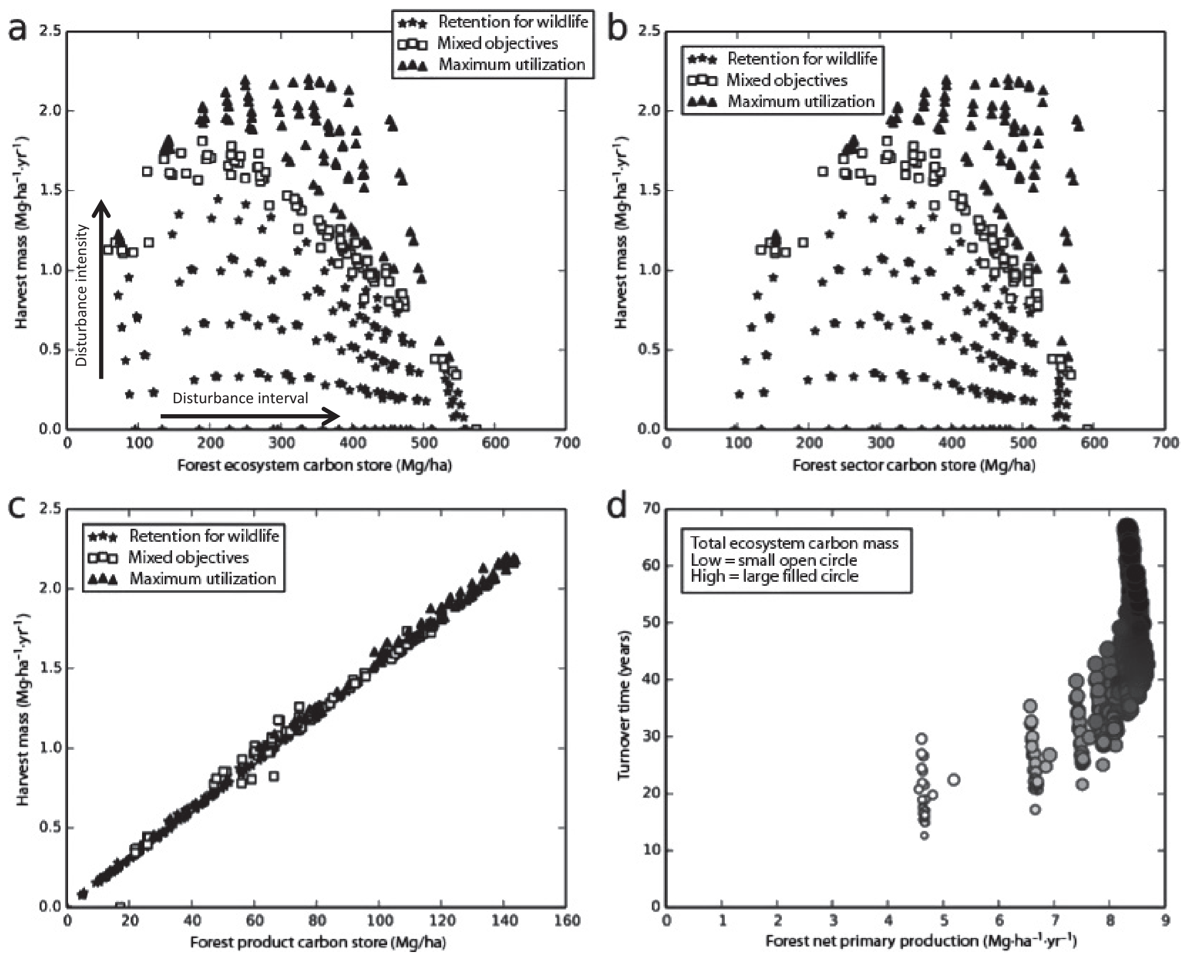

Fig. 1. Joint production possibilities for annual timber harvest mass and (a) forest ecosystem carbon store, (b) forest sector carbon store, and (c) forest product carbon store resulting from individual simulated management scenarios identified by general management emphasis group. Panel (d) shows the relationship between forest net primary production of stored carbon and turnover time.

associated forest conditions. Comparisons of LandCarb predictions with gradient nearest neighbor (Ohmann and Gregory 2002) and LiDAR estimates of aboveground live biomass, standing dead tree mass (>25 cm dbh, where breast height is 1.37 m), and downed large wood mass (>25 cm diameter at the large end) suggest that the LandCarb predictions represent reasonable estimates of these key carbon variables for the study area (Appendix S4).

Carbon storage and timber harvest possibilities

Timber harvest and forest ecosystem carbon.—Landscape-wide, the average forest ecosystem carbon store for simulated scenarios ranged from 57 to 633 Mg C/ha, the lower value resulting from a scenario of repeated clear-cut harvests every 25 yr with site preparation by prescribed fire, and the upper value resulting from a scenario of no harvests, prescribed fires, or other stand-replacing disturbances (Fig. 1a). The amount of timber harvested generally increased with higher levels of disturbance (or harvest) intensity, ranging from 0 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in cases in which trees were cut but not removed to 2.2 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ in cases where all live and dead trees were harvested. Forest ecosystem carbon increased most notably with longer disturbance intervals and to a lesser extent less intensive harvests. For example, among the least intensive harvest scenarios, a scenario with longest harvest interval (500 yr) stored 420 Mg C/ha more carbon than a scenario with the shortest harvest interval (25 yr). Among the most intensive harvest scenarios, the longest harvest interval stored 381 Mg C/ha more than the shortest harvest interval. Conversely, at intermediate harvest intervals (e.g., 100 yr), the least intensive harvest scenarios stored 106 Mg C/ha more than the most intensive harvest scenarios.

The overall shape of the joint production possibilities space for timber harvest and forest ecosystem carbon was compound, with outer regions defined by rotation lengths of maximum utilization scenarios (Fig. 1a). Timber harvest and forest ecosystem carbon stores were complementary at rotations of 75 yr, relatively neutral at rotations from 75 to 250 yr, and competitive at rotations over 250 yr. Considering only mixed objective scenarios, a complementary relationship was present at rotation ages below 50 yr and carbon stores below about 150 Mg C/ha and a competitive relationship present at rotation ages and carbon stores above those.

Timber harvest and forest sector carbon.—Forest sector carbon stores ranged from 94 Mg C/ha for a management scenario of a 25-yr harvest interval to 633 Mg C/ha for a scenario of a 500-yr harvest interval (Fig. 1b). The overall pattern of the timber harvest and forest sector carbon plot was similar to that of the harvest and forest ecosystem carbon plot but shifted to the right by the amount of additional carbon stored in wood products. The influence of harvest interval and intensity also were largely the same. The rightward shift is a result of harvest reducing forest ecosystem carbon at higher levels of harvest intensity and harvest also storing (forest sector) carbon in the form of wood products. Similar to the timber harvest and ecosystem carbon stores plot, production possibilities for harvest and forest sector carbon stores suggest a compound shape, but with an expanded complementary region up to 500 Mg C/ha.

Timber harvest and wood products carbon.—Carbon stored in wood products ranged from 0 Mg C/ha in no-harvest scenarios to 144 Mg/ha in scenarios with the highest harvest intensity and harvest intervals of 125 yr (Fig. 1c). The proportion of total forest sector carbon stored in wood products for scenarios featuring any harvest decreased with longer harvest intervals from a high of 57% for 25-yr harvest intervals to a low of 0.8% for 500-yr harvest intervals. Given that the turnover time varied little (58–67 yr; mean of 65 yr), the amount of carbon stored in wood products was complementary with timber harvesting, regardless of the management regime examined.

Key factors in carbon dynamics.—Two factors appeared to cause forest carbon to increase with disturbance interval: increases in the average landscape NPP and increases in turnover time. From the shortest to the longest harvest interval, NPP and turnover time increased from 4.6 to 8.6 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ and 13 to 78 yr, respectively (Fig. 1d). Increasing NPP was the primary influence up to a harvest interval of 50–62 yr, whereas increasing turnover time was the primary influence for harvest intervals over 100 yr. Both NPP and turnover time increased between harvest intervals of 62–100 yr. When harvest intervals exceeded 200 yr, NPP declined slightly, by up to 3% between harvest intervals of 200 and 500 yr, for example. An additional factor was how much carbon was removed during disturbance. Both site preparation using prescribed fire and increased harvest intensity reduced turnover time and hence the amount of carbon stored in the forest landscape. In contrast, forest carbon responded little to harvest block size despite it ranging from 10 to 1000 ha.

Wildlife habitat

Plots of habitat for seven focal species combined with forest sector carbon stores and timber harvest, as well as species-by-species plots, show a mix of complementary, competitive, neutral, and compound relationships (Appendix S5). These relationships result from the presence or absence and spatial arrangement of key forest characteristics favored by each species. We highlight joint production outcomes for three species representing very different habitat relationships, Northern Spotted Owl (*Strix occidentalis caurina*), Western Bluebird (*Sialia mexicana*), and Olive-sided Flycatcher (*Contopus* *cooperi*), to demonstrate the types of information that joint production analysis of forest management can produce. A complete set of joint production plots for all seven wildlife species examined appears in Appendix S5.

Northern Spotted Owl.—Northern Spotted Owl habitat (HCI >0.33) was complementary with forest sector carbon, with both generally increasing with older forests (Fig. 2a). Northern Spotted Owl habitat mostly was absent at forest sector carbon stores below 300 MgC/ha but increased sharply above that to about 550 MgC/ha, at which point owl habitat was present on 80% of the landscape. The narrowness of the production possibilities space suggests a close association between Northern Spotted Owl habitat and forest sector carbon store, as owls especially thrive in multi-storied old-growth forests that also store significant amounts of carbon. Similar close complementarity with forest sector carbon was found with habitat for red tree vole (*Arborimus longicaudus*; Appendix S5), an important prey species of Northern Spotted Owl. Owl–carbon complementarity existed across all three management groups, with owl habitat primarily a function of stand age and thus disturbance (or harvest) interval.

The production possibilities for Northern Spotted Owl habitat and timber harvest ranged from largely competitive to neutral depending on the management group examined (Fig. 2b). At the outer boundary, owl habitat ranged from 0% to 80% of the landscape at maximum harvest levels of about 2.0 Mg C·ha^{-1}·yr^{-1} and could be prevalent across 80% of the landscape at any harvest level below that. This suggested a neutral relationship between owls and timber harvest, when very long-rotation maximum utilization scenarios, removing all live and dead trees including frequent salvage, were considered. Alternatively, the outer boundary defined by the mixed objectives management group indicated a competitive relationship, with owl habitat declining from a high of 80% of the landscape at about 0.5 Mg C·ha^{-1}·yr^{-1} harvested to 0% of the landscape at roughly 1.7 Mg C·ha·$^{-1}$yr^{-1} harvested as disturbance interval declined from infinite rotation (no harvest) to 25 yr.

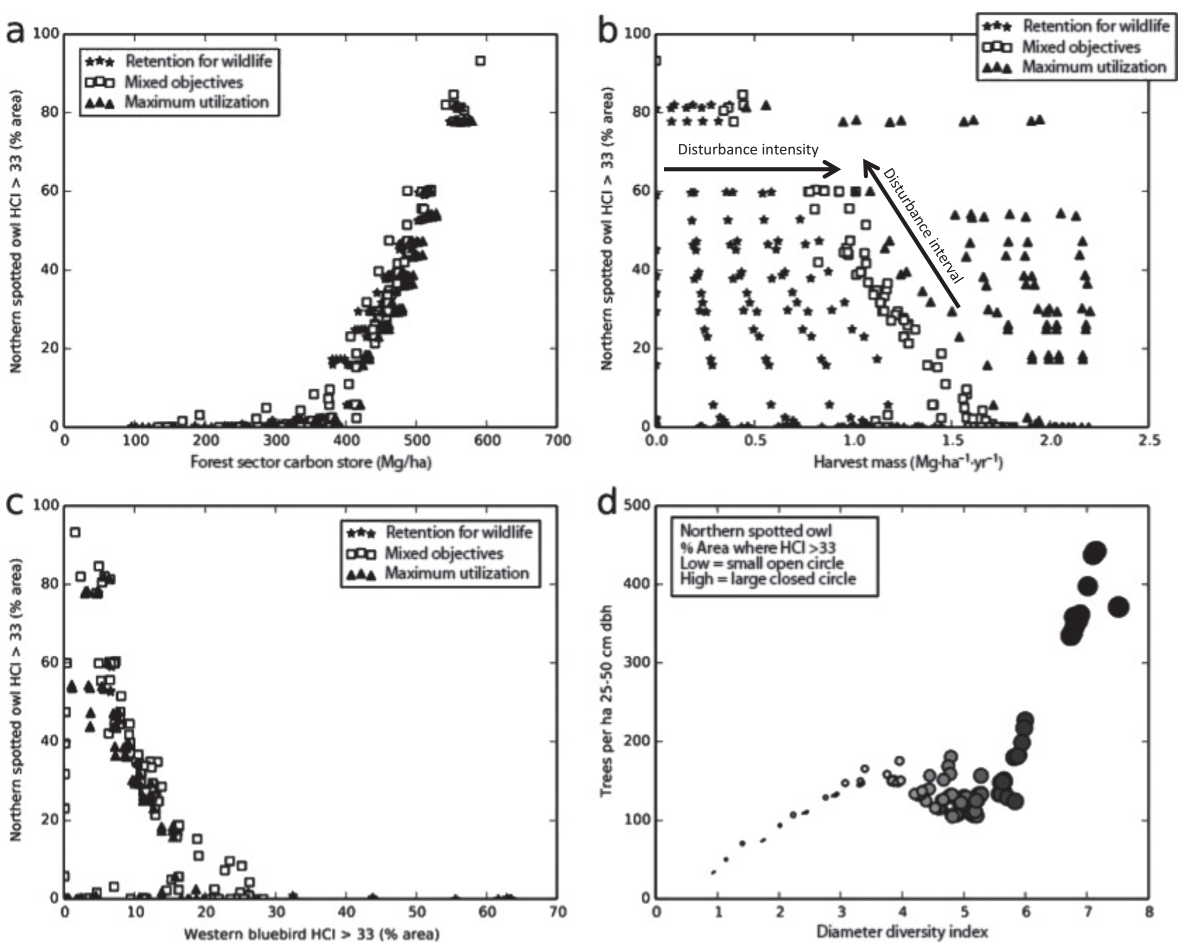

FIG. 2. Joint production possibilities for Northern Spotted Owl and (a) forest sector carbon store, (b) harvest mass, and (c) Western Bluebird resulting from individual simulated management scenarios identified by general management emphasis group. Panel (d) shows the relationship between diameter diversity index and trees/ha 25–50 cm dbh (breast height is 1.37 m).

Joint production relationships involving habitat for Northern Spotted Owl and other species ranged from competitive for Western Bluebird (Fig. 2c) to mostly neutral for Pacific marten (*Martes caurina*) and complementary for the Olive-sided Flycatcher and red tree vole (Appendix S5). In some cases, these relationships can be explained by differences or similarities in the forest conditions preferred by individual species. For example, Western Bluebirds prefer early-seral forest including snags for nesting combined with open canopy, such as occur in recently burned or logged areas with snags. Although snags are important to both Western Bluebird and Northern Spotted Owl habitats, the different canopy cover requirements of these species prevent managing for high percentages of both within the same area (Fig. 2c). The influence of forest stand age on Northern Spotted Owls was shown in owl habitat responses to both large trees (25–50 cm dbh) and diameter diversity index, an indication of more complex forest structures (Fig. 2d). In particular, Northern Spotted Owl habitat increased (larger dots) when forest conditions included >150 trees (25–50 cm dbh) per ha and diameter diversity indices above five.

Western Bluebird.—Western Bluebird habitat (HCI >0.33) and forest sector carbon were competitive at the outer boundary of joint production, largely because greater levels of forest ecosystem carbon are stored in older closed canopy forests that are not preferred habitat by Western Bluebirds (Fig. 3a). Western Bluebird habitat ranged from 0% of the landscape at forest sector carbon stores of about 600 MgC/ha to 65% of the landscape at carbon stores of 100 MgC/ha. However, the complexity of Western Bluebird habitat requirements led to an irregularly shaped joint carbon–bluebird production possibilities space, with some interior combinations appearing infeasible. This infeasible region largely resulted from open areas lacking snags. For most scenarios, the aggregate landscape area suitable for Western Bluebirds did not exceed 30%. The highest habitat levels occurred in the retention for wildlife scenarios featuring frequent disturbance and retention of

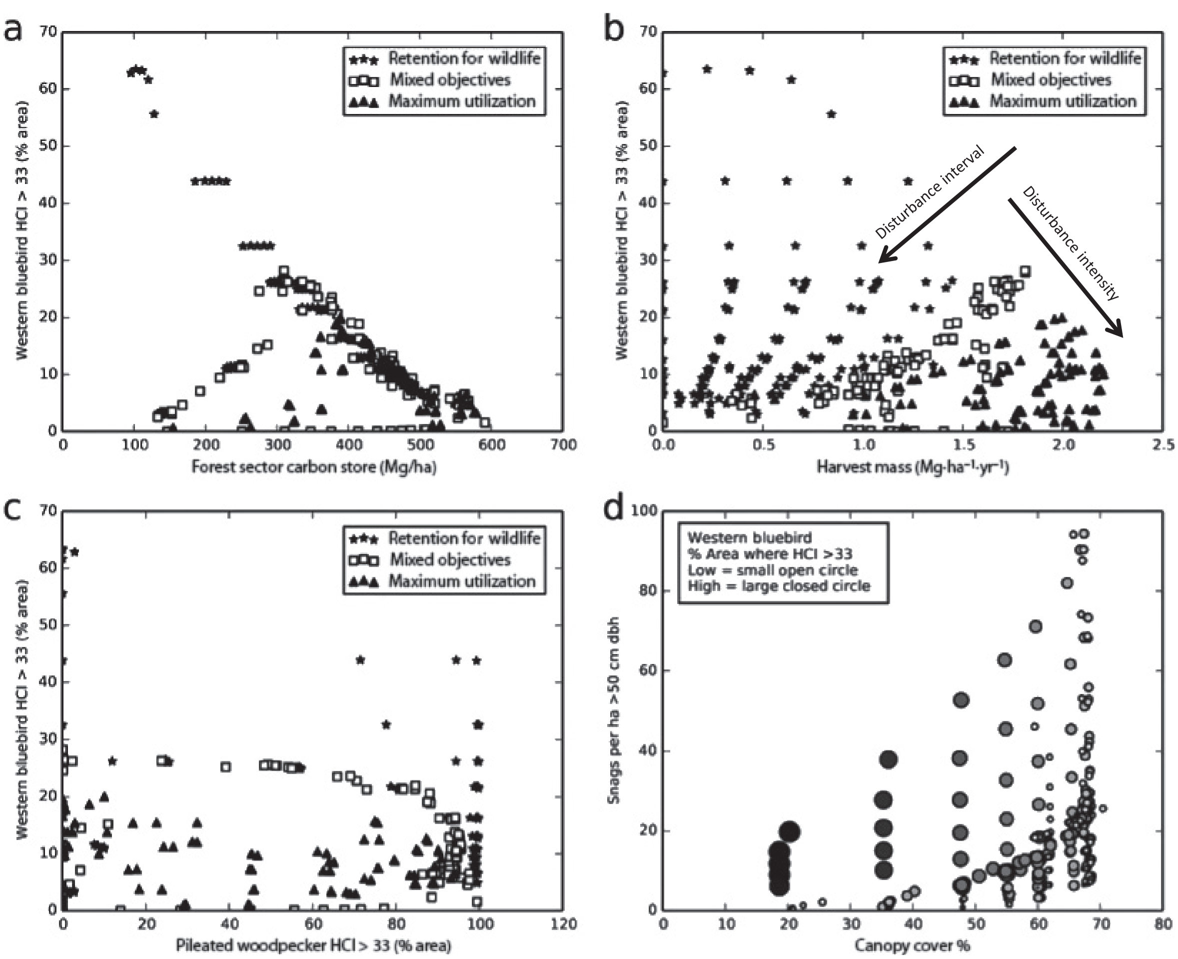

FIG. 3. Joint production possibilities for Western Bluebird and (a) forest sector carbon store, (b) harvest mass, and (c) Pileated Woodpecker resulting from individual simulated management scenarios identified by general management emphasis group. Panel (d) shows the relationship between canopy cover and snags/ha >50 cm dbh.

deadwood at harvest. Absent these scenarios, Western Bluebird habitat peaked at forest sector carbon levels between 250 and 350 MgC/ha but still varied from 0 to about 25% of the landscape, indicating a strong management influence involving harvest interval and dead wood creation and utilization.

Western Bluebirds also were largely competitive in production with timber harvest and strongly influenced by disturbance interval and utilization levels, specifically harvest intensity, which affects snag availability for nesting (Fig. 3b). Western Bluebird habitat achieved its highest landscape percentage, about 64%, in a no-harvest, frequent-prescribed-fire scenario that maintained both open forest conditions and snags. Western Bluebird habitat was lowest (near 0%) in scenarios featuring long rotations and high harvest intensities, which created little early successional vegetation and eliminated snags. The significant influence of harvest intensity can be seen in the clustering of scenarios by the three general management groups, with Western Bluebird habitat most prevalent under retention for wildlife scenarios and less prevalent under maximum utilization scenarios (Fig. 3b).

Joint production involving Western Bluebird with other species indicated mostly competitive relationships with Olive-sided Flycatcher, Pacific marten, red tree vole, Northern Spotted Owl, and a compound relationship with mule deer (*Odocoileus hemionus*; Appendix S5). The combined influence of harvest intensity and canopy cover is evidenced by the joint production relationship between Western Bluebird and Pileated Woodpeckers (*Dryocopus pileatus*), which was somewhat competitive to neutral (Fig. 3c). Although bluebirds and woodpeckers both use dead trees for nesting, Western Bluebirds also require open canopy conditions, while Pileated Woodpeckers prefer closed canopy conditions. The highest percent of Western Bluebird habitat (>50%) occurred when disturbances were relatively frequent, creating large areas of young and open forests but leaving many dead trees, conditions that are too open for woodpeckers. When disturbances were less frequent, bluebirds found moderate amounts of habitat (>25%) and Pileated Woodpeckers found moderate to high amounts of habitat, depending on how many snags were present in the forest. The highest extent of Western Bluebird habitat is coincided with the lowest levels of canopy cover (<40%) when at least some (>0) snags were present (Fig. 3d). When snag numbers fell to near zero, owing to high harvest intensity, for example, Western Bluebird habitat declined dramatically. The starkness of this snag-threshold response diminished as canopy cover increased to where Western Bluebird habitat declined as a result of either increased scarcity of open canopy or shortage of snags.

Olive-sided Flycatcher.—Olive-sided Flycatcher habitat (HCI >0.33) was mostly complementary with forest sector carbon (Fig. 4a), varying from about 20% to 95% of the landscape at forest sector carbon stores above 400 MgC/ha. It was absent below forest sector carbon stores of 100 MgC/ha. The greater width of the carbon–Olive-sided Flycatcher complementary relationship, relative to the narrow relationship between carbon and Northern Spotted Owl habitat, for example, likely owes to Olive-sided Flycatcher's preference for high-edge contrast between tall stands used for nesting vs. open areas used for foraging. Olive-sided Flycatcher habitat was largely neutral to timber harvest, with habitat prevalence ranging from 0% to 90% across the full range of harvest volumes simulated (Fig. 4b). Examination of individual management scenarios indicated that Olive-sided Flycatcher habitat was more prevalent with longer disturbance intervals. Olive-sided Flycatcher habitat appeared to be little influenced by harvest intensity, a key factor influencing harvested timber volume.

Joint production possibilities involving Olive-sided Flycatcher and other species showed a mix of relationships: neutral for Pacific marten and Pileated Woodpecker, complementary for mule deer and red tree vole, competitive for Western Bluebird, and compound for Northern Spotted Owl (Appendix S5). For example, joint production outcomes for Olive-sided Flycatcher and red tree vole suggested general complementary across all three management groups (Fig. 4c), reflecting Olive-sided Flycatcher preference for taller trees and red tree vole preference for older trees. When the landscape area of Olive-sided Flycatcher habitat was above 40%, red tree vole habitat was less responsive to further increases in flycatcher habitat. This change in relationship likely involves differences in the relationships between the habitats for these species to stand biomass, age, and canopy cover. With canopy cover >60%, Olive-sided Flycatcher habitat remained fairly high (>0.25) across edge contrasts (Fig. 4d), indicating greater flexibility in patch sizes for nesting and foraging as long as the spatial arrangement (juxtaposition) of stands maintained high contrast. We note, however, that we did not address connectivity in our analyses and that without consideration of connectivity for low mobility species, such as the red tree vole, our estimates could be overly optimistic.

Discussion

Our results show the potential trade-offs associated with managing Western Cascades forests to store carbon and how these trade-offs are influenced by ranges of management variables and ecological conditions. Joint production possibility sets for wildlife species vary in shape from competitive to complementary to compound (Table 3), reflecting the niche breadth and habitat component needs of the individual species examined. The joint production possibilities sets enable identifying the theoretical limits of jointly produced forest management outcomes and can be used to define the long-term potential of managing forests to produce multiple ecosystem

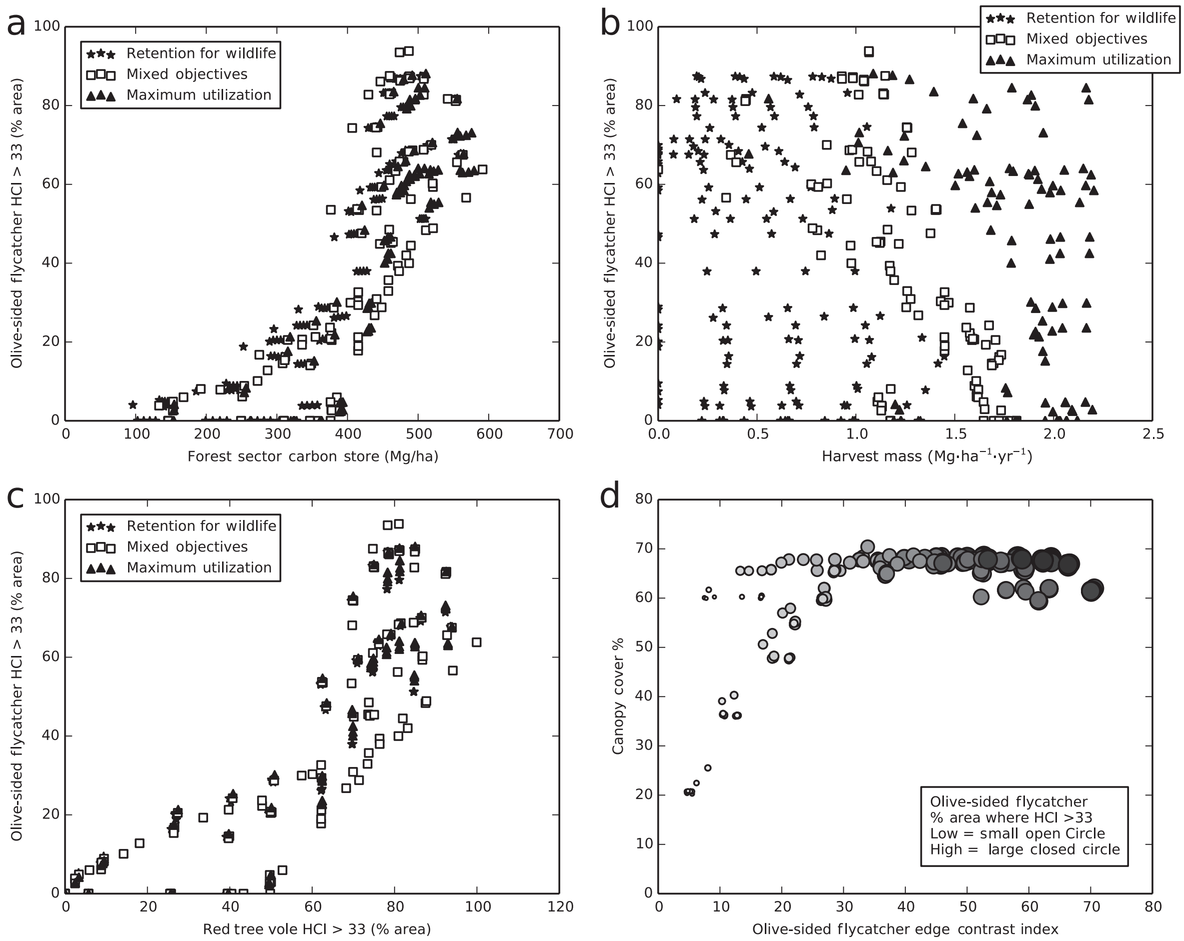

FIG. 4. Joint production possibilities for Olive-sided Flycatcher and (a) forest sector carbon store, (b) harvest mass, and (c) red tree vole resulting from individual simulated management scenarios identified by general management emphasis group. Panel (d) shows the relationship between edge contrast index and canopy cover.

services within and across multiple ownerships. While these limits may be currently unachievable owing to current economic, political, or social constraints, they can be used to define the long-term potential of managing forests to produce multiple ecosystem services within and across multiple ownerships. Although our simulations involved just a small portion of the Western Cascades landscape, our study area is fairly representative of the vegetation, ownership patterns, climate, and topography of the region, where Douglas-fir and western hemlock are dominate tree species. We feel that the differences we found among joint production outcomes resulting from the different management regimes we simulated, if not necessarily their absolute values, are likely representative.

We found that harvested timber generally increased with higher levels of harvest intensity, with peak harvests varying by management group and rotation, a pattern consistent with the findings of other studies (e.g., Curtis 1995, Garman et al. 2003). Likewise, forest ecosystem carbon increased with disturbance interval due to associated increases in landscape NPP and forest sector turnover time, also consistent with past studies (e.g., Harmon and Marks 2002, Seidl et al. 2007, Hudiburg et al. 2009, Nunery and Keeton 2010, Schwenk et al. 2012). However, our results also suggest that the joint production possibilities arising from forest management regimes currently typical on industrial forest lands (e.g., 40- to 80-yr rotations with some tree retention for wildlife) likely represent but a small fraction of the ecologically feasible outcomes in the Western Cascades region. Results from several of the management scenarios we simulated suggest the possibility of storing additional carbon without significantly reducing harvested timber. Current industrial management, of course, reflects economic factors and regulatory constraints that tend to encourage relatively short rotation intervals (e.g., Talbert and Marshall 2005) and high levels of timber removal, subject to streamside forest protection and tree retention for wildlife mandated by the Oregon Forest Practices Act (Oregon Department of Forestry 2014). However, management regimes on other ownerships (e.g., federal,

Table 3. General relationships for output pair combinations at the outer limit (frontier) of joint production possibilities.

Species	Forest sector carbon	Timber harvest	Mule deer	Northern Spotted Owl	Olive-sided Flycatcher	Pacific marten	Pileated Woodpecker	Red tree vole	Western Bluebird
Forest sector carbon		~	~	+	+	~†	~	+	~
Timber harvest	~		0†	0†	0†	−	−	0†	−†
Mule Deer	~	0†		−	−	0	0	~	~
Northern Spotted Owl	+	0†	−		~	0†	~	+	−
Olive-sided Flycatcher	+	0†	−	~		0†	0†	+	−
Pacific Marten	~†	−	0	0†	0†		+	0†	−
Pileated Woodpecker	~	−	0	~	0†	+		0†	~†
Red Tree Vole	+	0†	~	+	+	0†	0†		−
Western Bluebird	~	−†	~	−	−	−	~†	−	

Notes: Predominant relationship between output pair across all management scenarios simulated denoted as complementary (+), competitive (−), or neutral (0). Relationships that feature combinations of these within specific ranges are denoted as compound (~).
†Denotes output pairs whose relationship within individual management emphasis groups may differ substantially from the predominant relationship across all management scenarios simulated. In the case of Northern Spotted Owls and timber harvest, for example, the relationship across all management scenarios simulated appears neutral. However, within each of the individual management emphasis groups (retention for wildlife, mixed objectives, and maximum utilization) the relationship is negative. Refer to Appendix S5 to examine relationships among each pair of individual outputs.

state, and non-industrial private) are characterized by a wider range of management variables and often involve longer rotations (including no harvest) and lower utilization intensities at harvest.

We found that adding salvage of dead timber only at the time of live tree harvest increased the amount of timber harvested but did not change the parabolic relationship between stored carbon and timber harvest found among no-salvage scenarios. However, adding salvage at fixed and more frequent intervals, such as in the maximum utilization scenarios, increased timber harvest over the long-term, particularly with long harvest intervals of over 100 yr, while not necessarily reducing stored carbon. This is because salvage timber volumes routinely removed at more frequent intervals do not decline as do salvage timber volumes removed only at live-tree harvest. Once tree mortality is at a maximum, the average amount of timber volume routinely salvaged remains relatively constant. On the shortest salvage intervals, virtually all wood produced by the forest is removed, leading to higher average timber harvest over the long-term. However, the forest ecosystem carbon consequences of salvage are less dramatic than the effect of harvesting live timber volumes, in part, because dead wood comprises a fairly small share of total forest ecosystem carbon (10–15%). We are not aware of any previous studies that have reported the effects of different salvage strategies on wood and carbon.

Our results also suggest that managing Western Cascades forests to store forest sector carbon can be roughly complementary with the production of habitat for Olive-sided Flycatcher, Pacific marten, Pileated Woodpecker, Northern Spotted Owl, and red tree vole, while the implications for mule deer and Western Bluebird are more diverse (Table 3). Other studies have found similar complementarity between increased carbon storage and habitat for species that thrive in late (vs. early) successional forest conditions (e.g., McCarney et al. 2008, Schwenk et al. 2012). However, we also found that ranges of joint production possibilities involving carbon and Olive-sided Flycatcher, Northern Spotted Owl, and red tree vole appear to be fairly narrow, while the ranges of joint production possibilities involving Pacific marten and Pileated Woodpecker appear broader and more compound-shaped. These ranges varied among species as a function of each species' habitat breadth and the ecological conditions produced by the management scenarios simulated. At forest sector carbon levels between 400 and 450 MgC/ha, for example, habitat prevalence for Northern Spotted Owl varied from 0% to 30%, compared to 0–100% for Pacific marten and Pileated Woodpecker. Such differences in ranges likely are related to the influence of dead wood. For species that rely on both live and dead wood (e.g., Pileated Woodpecker), there may be more ways to produce habitat for a given level of carbon than for species that rely primarily on live forms of carbon (e.g., Northern Spotted Owl).

We note several primary caveats concerning our analysis. First, our analyses were limited by assumptions, information, and variables included in our component sub-models. For example, we did not include natural disturbances, such as wildfire and climate change, in our simulations, to focus on simulating only the deliberate actions of forest managers. The feasibility of our predicted outcomes thus must be weighed against uncertainties posed by wildfires and climate change. Second, we have ignored costs and revenues associated with simulated management scenarios, such as might be included in an optimization analysis, focusing instead on defining what might be ecologically feasible for the study area landscape. However, nothing precludes us from including costs and revenues in future analyses. Third, we have simulated management uniformly across the landscape, when a more typical arrangement would include a mix of ownerships and management agencies pursuing diverse economic and policy goals. We chose to simulate a uniform approach to define the influence of specific management variables and scenarios on joint production possibilities over the long-term, to define what is feasible at a landscape scale. Testing scenarios in multi-ownership landscapes could reveal joint production possibilities superior to those we have found in our homogenous simulations.

We also caution that we have not examined possible consequences of error propagation in our linked ecosystem–habitat models. Ideally, analysts would evaluate the different types of uncertainty in integrated modeling (e.g., Hamilton et al. 2015). Although theoretically possible, we felt that uncertainty analysis was impractical in this case, evaluating the effects of 100s of different parameter value combinations, for example, and believe that it constitutes a separate research question. We did, however, qualitatively assess our approach based on what we know about the different models, their uses, and the purpose of our study. Our evaluations of LandCarb indicated that it approximates live and dead biomass dynamics fairly well for this study area (Appendix S4). Our habitat capability models have previously been evaluated using sensitivity analysis and, in some cases, empirical validation as described in the methods. Our evaluations of our statistical approach for linking LandCarb output with the habitat capability models indicated that the best data fit occurs for live structure variables (e.g., tree cover, tree size, and large tree density) and the poorest fit and most error for variables related to sang and small tree densities (Appendix S2). Most of the regression models that link LandCarb outputs to the habitat capability models were statistically significant. We are confident that the errors and uncertainties are not large enough to invalidate our major assumptions, given that we are using them to compare relative differences among management regimes. However, we do caution against using absolute values from the production relationships identified. For example, our finding that western bluebirds have a complex joint production relationship with timber, carbon, and other species makes ecological sense. Its habitat depends primarily on canopy cover and dead wood, which are not strongly correlated across a range of disturbance regimes. However, the absolute thresholds that define these relationships are subject to uncertainty and errors that warrant further study.

We note that the joint production outcomes identified by our steady-state simulations may not necessarily be achievable in practice. Maintaining the same management regime for centuries is unlikely given economic, political, and social dynamics, natural disturbances, and climate change. Carbon stored in wood products can take an exceedingly long time to achieve a steady state. Moreover, our analysis assumed that each species we examined could recover from situations in which other biological processes, such as dispersal and reproduction, might be at times potentially limiting. In reality, such processes can interact with landscape conditions to create bottlenecks that prevent habitat use by a given species. However, our steady-state values provide a common reference for comparing the relative effects of different management regimes on carbon, timber, and habitat, and can be useful for testing prevailing assumptions about the degree to which various ecosystem services can be produced in combination with others on a given landscape. Ultimately, the degree to which the joint production outcomes can be achieved should also be examined based on realistic time-frames, natural disturbance regimes, climate change, and the possibility of biological bottlenecks. In ongoing research, we are examining the pre-steady-state time trajectories, or "transient" values, of timber and habitat outcomes to determine whether particular joint production outcomes might actually be possible given natural disturbances such as wildfire. It is conceivable that the transition periods toward particular steady states might be so variable and long that they, rather than the steady-state condition itself, will define what is ecologically and socially feasible.

Following a century of change in the way federal forests are managed and valued by the public, policymakers and managers still struggle with how to evaluate the effects of managing for one valued ecosystem service vs. another. Continued divergence of management into forest reserves on federal lands and intensively managed plantations on private industrial lands (e.g., Spies et al. 2007*a*) suggests an increasing need to better understand interactions and trade-offs at landscape scales. This need becomes all the more pressing as public forests in the USA increasingly are viewed by policymakers and the public as a major component in any overall strategy to mitigate climate change via carbon sequestration and storage (e.g., Skog et al. 2014). In addition to supporting the eventual development of isocost curves (Bowes and Krutilla 1989) to examine the economic feasibility of particular carbon, timber harvest, and habitat outcomes, combined models and analysis such as ours potentially can be used qualitatively by forest managers to test assumptions about the influence of different management regimes on carbon storage and other valued ecosystem services, and to facilitate discussions with stakeholders and the public concerning national forest plan revisions, among other uses. The time, expertise, and computing resources necessary for completing analyses such as these likely bars their use in routine forest planning and management applications. We feel, however, that such approaches can be useful both in research for identifying and examining interactions between key ecosystem services of interest and in application for facilitating discussions among managers, stakeholders, and the public about key trade-offs associated with public forest management.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.1358/suppinfo

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.6qr6j