

DOES RIPARIAN FOREST RESTORATION THINNING ENHANCE BIODIVERSITY? THE ECOLOGICAL IMPORTANCE OF LARGE WOOD¹

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ABSTRACT: Intact riparian ecosystems are rich in biological diversity, but throughout the world, many have been degraded. Biodiversity declines, particularly of vertebrates, have led to experimental efforts to restore riparian forests by thinning young stands to accelerate creation of large diameter live trees. However, many vertebrates depend on large diameter deadwood that is standing as snags or fallen to the forest floor or fallen into streams. Therefore, we reviewed the sizes of deadwood and live trees used by different vertebrate species to understand which species are likely to benefit from different thinning treatments. We then examined how riparian thinning affects the long-term development of both large diameter live trees and deadwood. To this end, we used a forest growth model to examine how different forest thinning intensities might affect the long-term production and abundance of live trees and deadwood. Our results suggest that there are long-term habitat trade-offs associated with different thinning intensities. Species that utilize large diameter live trees will benefit most from heavy thinning, whereas species that utilize large diameter deadwood will benefit most from light or no thinning. Because far more vertebrate species utilize large deadwood rather than large live trees, allowing riparian forests to naturally develop may result in the most rapid and sustained development of structural features important to most terrestrial and aquatic vertebrates.

(KEY TERMS: riparian ecology; rivers/streams; restoration; forests; fish; fluvial processes; forest management; forest structure; large wood.)

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INTRODUCTION

Throughout much of the world, old, complex, and biologically diverse forested riparian ecosystems have been cleared and replaced by young, structurally simple forests (Naiman *et al.*, 1993; Sala, 2000; Stromberg *et al.*, 2004). In the Pacific coastal states of North America, extensive degradation of riparian forests has led to the decline of numerous aquatic and

terrestrial species that depend upon them, a number of which are now listed under the United States (U.S.) Endangered Species Act (ESA) (Nehlsen *et al.*, 1991; USDA and USDI, 1994). In such forests, much of the decline in biodiversity is due to the loss of four major structural features; large live trees, large snags, large down wood on the forest floor, and large down wood in streams (Bauhus *et al.*, 2010; Bunnell and Houde, 2010; Marcot *et al.*, 2010). Notable among the ESA-listed species that utilize riparian ecosys-

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tems are several salmonids of the genera *Oncorhynchus* and *Salvelinus*, which rely on habitat created by large wood falling into streams; northern spotted owls *Strix occidentalis*, which depend on large live and deadwood for nest sites and habitat for their prey; and marbled murrelets *Brachyramphus marmoratus*, which require large live trees for nesting (USDA and USDI, 1994).

Large living trees and deadwood provide important habitat for a range of other species. Diverse epiphytic communities are found in the crowns of large live trees (Muir *et al.*, 2006), while large snags and down wood provide nesting, roosting, denning, and foraging habitat for numerous birds and mammals (Bunnell *et al.*, 1999; Bunnell and Houde, 2010; Marcot *et al.*, 2010). For numerous aquatic organisms, large wood that falls into streams is essential for the maintenance of habitat because it forms pools, traps, and sorts gravels, increases hyporheic exchange, modulates stream temperature, and provides cover and increased habitat complexity (Beechie and Sibley, 1997; Moore *et al.*, 2005). Large wood that falls to the forest floor provides thermal and moisture refugia for amphibians, habitat for small mammals, and establishment sites for numerous plant species (Harmon and Franklin, 1989; Carey *et al.*, 1999; Kluber *et al.*, 2009). Standing and down wood in various stages of decay creates habitat heterogeneity that supports a complex and diverse fungal community (Norden *et al.*, 2004; Berglund *et al.*, 2005). Large wood ultimately decomposes and helps to provide a humic-rich forest floor with high moisture holding capacity and a biologically complex and diverse soil taxa (Harmon *et al.*, 1986; Coleman and Whitman, 2005). Much of the riparian forest structure needed to maintain biologically diverse aquatic and terrestrial communities is provided by large standing and fallen deadwood.

Rapid biodiversity declines in forested ecosystems have led to experimental efforts to accelerate the development of complex forest ecosystem structure, and in particular to more rapidly create large live and deadwood from young forests (Davis *et al.*, 2006; Puettmann *et al.*, 2009; Bauhus *et al.*, 2010). In the U.S. Pacific Northwest and elsewhere, riparian forest reserves have been established for the primary purpose of recovering species with declining populations (USDA and USDI, 1994). However, many riparian forest reserves are degraded from past land use activities and are now dominated by young, simplified forests. There is an emerging debate as to what types of active and passive management are the best approaches for restoring the structural complexity needed to maintain both terrestrial and aquatic biodiversity as these young forests mature (Beechie *et al.*, 2000; Puettmann *et al.*, 2009; Bauhus *et al.*, 2010; Marcot *et al.*, 2010).

To help resolve this debate, in this article we review and summarize available quantitative data describing the different sizes of large live trees and deadwood that are used by vertebrate species, to better understand which species are likely to benefit from restoration thinning. We then use a forest growth model, Forest Vegetation Simulator (FVS), to simulate how four common restoration thinning intensities (high, medium, low, and no thin) are likely to affect the long-term production of large live trees and large deadwood. We focus our analysis on the sizes of wood important to aquatic and terrestrial vertebrate species found in the Pacific Northwest that are known to use riparian forests, with an emphasis on the structural attributes required by species in population decline.

THE STRUCTURAL HABITAT REQUIREMENTS OF SPECIES THAT UTILIZE RIPARIAN FORESTS

From the perspective of enhancing and maintaining biological diversity in riparian forests, it is helpful to understand the specific structural attributes a given species needs. There has been some effort to understand the specific habitat needs of vertebrate species, while the needs of specific plants, fungi, and invertebrate fauna are not as well known, although data are accumulating (Bunnell *et al.*, 2008; Bunnell and Houde, 2010). However, to date, there has been no synthesis that summarizes how different species utilize specific sizes and types of large wood in riparian forests. To this end, we provide a review of the specific structural components of forests that have been directly linked to usage by vertebrate species. Initially, we used Web of Knowledge, Google, and Google Scholar to search for studies published in peer-review journals examining quantifiable forest structural attributes that are correlated with usage by Pacific Northwest forest vertebrate species. In reviewing the literature, we found that researchers consistently identified one or more of four measurable forest structural attributes that could be related to the habitat requirements of specific species: (1) large down wood in streams, (2) large down wood on the forest floor, (3) large standing snags, and (4) large living trees, often with large limbs and structural irregularities such as cavities and irregular, broken branches, and broken tops. A fifth structural attribute often identified as important for certain species was canopy gaps (e.g., Spies, 1989). However, this attribute was frequently discussed conceptually, and limited quantitative information was available as to the specific size, frequency, and general nature of

canopy gaps that were needed by specific species. Therefore, we limited our review of this attribute to a generalized qualitative discussion, and focused our review effort on identifying studies examining relationships between specific species and the four quantifiable structural attributes of riparian forests previously identified. Many of the studies we examined established relationships between specific forest structural elements and vertebrate species abundance that were not limited to riparian forests, particularly for terrestrial vertebrates, but all of the species we discuss in this review utilize riparian forests.

Table 1 summarizes specific sizes of instream wood, forest floor wood, snags, and live trees associated with certain vertebrate species that we were able to identify in the scientific literature. Each of these attributes and the species associated with them are discussed below.

Trees That Fall into Streams

Salmonids and other aquatic species benefit from the presence of large diameter riparian trees that have fallen into streams. The loss wood inputs from riparian forests is thought to be a major factor in the degradation of freshwater habitat (Gregory *et al.*, 2003; Cluer and Thorne, 2014). Large wood ranging from 15 to 200 cm in diameter and over 2 m in length has been found to structure stream habitat in ways that are beneficial, primarily by forming wood jams, reducing sediment transport, and creating pools (Table 1; Bilby, 1981; Montgomery *et al.*, 1996; Beechie and Sibley, 1997; Fox and Bolton, 2007).

Complex wood jams, that is, the accumulations of many pieces of large wood in streams and rivers, are particularly important because they fundamentally alter transport rates of both sediment and water and in doing so, create complex instream and floodplain habitat (see overview in Cluer and Thorne, 2014). By slowing the flow of water and sediment, complex wood jams help to push water onto floodplains, increasing the dynamic nature of riparian ecosystems and in doing so creating multithreaded channels, mid-channel islands, off-channel habitat, and wetlands which fundamentally enhance riparian species richness by creating a diversity of habitats (Naiman *et al.*, 1993; Walter and Merritts, 2008; Cluer and Thorne, 2014). Thus, arguably, the most important role of riparian forests in terms of enhancing biological diversity is to produce wood of a size distribution and abundance sufficient for large, complex wood jams to form.

Complex wood jams are composed of wood across a wide range of sizes (length and diameter) that is generally commensurate with the size of riparian trees available to fall into streams. Wood jams are com-

posed of a framework of large structural pieces that then serve to trap smaller pieces, which fill in the interstices such that sediment accumulates behind jams and flow is routed around them. However, all wood jams initially require at least one piece which is large enough to be stable during high flows and which forms the initial frame against which other pieces can accumulate (Bilby and Ward, 1989; Fox and Bolton, 2007). The size of such a “key” piece varies with stream characteristics. The size (volume) of the key piece of large wood needed to form stable jams is proportional to the bankfull width for low gradient streams, and wood volume ranges from 1 to 11 m³ for streams up to 100-m wide or measured by diameter or length ranges from 40 to 70 cm or 8 to 24 m, respectively, for streams up to 20-m wide (WFPB, 1995; Fox and Bolton, 2007) but in high gradient headwater streams, at least one piece of large diameter wood (60-200 cm) is needed to form stable wood jams even if the streams are small (Montgomery *et al.*, 1996). Thus, restoration of riparian forests for the purposes of providing wood to streams such that complex jams can form requires consideration of both the size and abundance of large trees.

Individual riparian trees that fall into streams can also provide important habitat for aquatic organisms, primarily by creating cover and helping to form pools. Similar to key pieces, the minimum size of large wood needed to independently form pools can be predicted from the width of the stream, and ranges from 15 to 75 cm diameter for streams ranging in width from 4 to 23 m (Table 1; Beechie and Sibley, 1997).

Standing Snags and Trees That Fall to the Forest Floor

Numerous terrestrial vertebrates that utilize riparian forests are associated with large trees that have fallen completely or partially to the forest floor (a portion of the tree may have also fallen into a stream or remain standing as a snag). The size of tree utilized by such species ranges from 13 cm to >200 cm diameter, with the average diameter of deadwood used ranging from 53 to 123 cm, depending on the species (Table 1). A number of forest vertebrates are also positively associated with the percent cover of all deadwood on the forest floor, often defined as logs >10 cm or >30 cm diameter (Marcot *et al.*, 2010). Large diameter snags or down wood are used in a number of ways that vary by species (Table 1). Such uses include nesting, denning, resting, foraging, and roosting. For example, the widely distributed wood duck *Aix sponsa* requires large riparian snags with cavities for nesting and the loss of such structures is thought to have resulted in population declines (Soulliere, 1988). Several small

TABLE 1. Examples of Species of Pacific Coastal Forests Use of Large Diameter Deadwood and Live Trees in Aquatic and Terrestrial Habitats, with an Emphasis on ESA-Listed Species (salmonids, the northern spotted owl [and its prey base], and the marbled murrelet). Size range numbers refer to bole diameter breast height (dbh), unless otherwise noted (cf. Bunnell *et al.*, 1999; Bunnell and Houde, 2010).

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
<i>Oncorhynchus</i> , <i>Salmo</i> , and <i>Salvelinus</i> (salmonids) and other aquatic species	Instream down wood	Forms pools independently, in the absence of other wood or obstructions	0.15-0.75 m diameter for streams with bankfull widths between 4 and 23 m according to the equation: Diameter = $0.028 \cdot \text{BFW} + 0.0057$	—	—	Beechie and Sibley (1997)
Salmonids and other aquatic species	Instream down wood	Independently stable during large floods. "Key" piece forms jams	Varies with stream size: wood piece volumes from 1.0 to 10.8 m ³ for streams 1-100 m wide.	—	—	Fox and Bolton (2007)
Salmonids and other aquatic species	Instream down wood	Independently stable during large floods. "Key" piece forms jams	Varies with stream size: wood diameters from 40 to 70 cm and lengths from 8 to 24 m for streams 1-20 m wide.	—	—	WFPB (Washington Forest Practices) (1995)
Salmonids and other aquatic species	Instream down wood	Stabilize valley spanning jams in high gradient channels	60-200 cm diameter	—	—	Montgomery <i>et al.</i> (1996)
Salmonids and other aquatic species	Instream down wood	Accumulates on larger "key" pieces to form debris jams	>10 cm dbh, 2 m length	—	—	Bilby (1981), Bilby and Likens (1980), Bilby and Ward (1989)
<i>Strix occidentalis</i> (northern spotted owl)	Riparian down wood	Preferred foraging areas	Foraging positively related to all CWD volumes, and big log (dbh > 50 cm and $L > 8$ m) volumes and densities	—	—	Carey (1995)
<i>G. sabrinus</i> (northern flying squirrel), <i>Neotamias townsendii</i> (Townsend's chipmunk)	Riparian down wood	Preferred habitat for spotted owl prey species	12% cover of large wood	—	—	
<i>Myotis lucifugus</i> (little brown myotis)	Riparian down wood	Roosting	—	55	8	Bunnell and Houde (2010)
<i>Martes pennanti</i> (fisher)	Riparian down wood	Resting	50-200	95		Zielinski <i>et al.</i> (2004)
<i>Martes americana</i> (marten)	Riparian down wood	Denning	—	53	—	Ruggiero <i>et al.</i> (1998)
<i>M. americana</i>	Riparian down wood	Resting	—	66	17	Bull and Heater (2000)
<i>Ursus americanus</i> (black bear)	Riparian down wood	Denning	—	108	17	Bull <i>et al.</i> (2000)
<i>U. americanus</i>	Riparian down wood	Denning	—	123		Davis (1992)
<i>Ensatina escholtzii</i>	Riparian down wood	General habitat	0-800 m ³ /ha, density = $0.11 \cdot (\text{CWD Volume})^{0.66}$	—	—	Butts and McComb (2000)

(continued)

TABLE 1. Continued.

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
<i>Ensatina escholtzii</i>	Riparian down wood	General habitat	91% of observations related to CWD	—	—	Bury and Corn (1988)
<i>Aneides ferreus</i> (clouded salamander)	Riparian down wood	General habitat	84% of observations related to CWD	—	—	Bury and Corn (1988)
<i>Batrachoseps wrightorum</i> (slender salamander)	Riparian down wood	General habitat	64% of observations related to CWD	—	—	Bury and Corn (1988)
<i>S. occidentalis</i>	Snags	Preferred foraging areas	Vol > 142 m ³ /ha, 70% of snag volume was from snags >50 cm dbh. 15 large snags >50 cm/ha in medium and high use areas	86	—	North <i>et al.</i> (1999)
<i>G. sabrinus</i> (northern flying squirrel), <i>Neotamias townsendii</i> (Townsend's chipmunk)	Snags	Preferred habitat for spotted owl prey species	23 large (>50 cm) snag/ha	—	—	Carey (1995)
<i>Myotis californicus</i> (California myotis)	Snags	Roosting	—	56	27	Brigham <i>et al.</i> (1997)
<i>Myotis volans</i> (long-legged myotis)	Snags	Roosting	95% CI = 83-110	97	38	Ormsbee and McComb (1998)
<i>Myotis thysanodes</i> (fringed myotis)	Snags	Roosting	58.5-167	121	41	Weller and Zabel (2001)
<i>M. americana</i>	Snags	Denning	—	55	—	Ruggerio <i>et al.</i> (1998)
<i>M. pennanti</i>	Snags	Resting	66-200	119	—	Zielinski <i>et al.</i> (2004)
<i>Aix sponsa</i> (wood duck)	Snags	Cavity nesting	>31 cm	—	—	Souliere (1988)
<i>Colaptes auratus</i> (common flicker)	Snags	Cavity nesting	36-112 cm	61	11	Mannan <i>et al.</i> (1980)
<i>Dryocopus pileatus</i> (pileated woodpecker)	Snags	Cavity nesting	46-172 cm	78	15	Mannan <i>et al.</i> (1980)
<i>Picoides villosus</i> (hairy woodpecker)	Snags	Cavity nesting	48-172 cm	92	18	Mannan <i>et al.</i> (1980)
<i>Sphyrapicus varius</i> (sapsucker)	Snags	Cavity nesting	56-216 cm	101	17	Mannan <i>et al.</i> (1980)
<i>Sitta canadensis</i> (nuthatch)	Snags	Cavity nesting	74-185 cm	118	28	Mannan <i>et al.</i> (1980)
<i>Oecile rufescens</i> (chickadee)	Snags	Cavity nesting	53-160 cm	103	18	Mannan <i>et al.</i> (1980)
<i>C. auratus</i>	Snags	Foraging	19-167 cm	95	23	Mannan <i>et al.</i> (1980)
<i>D. pileatus</i>	Snags	Foraging	20-185 cm	103	30	Mannan <i>et al.</i> (1980)
<i>P. villosus</i>	Snags	Foraging	13-173 cm	62	20	Mannan <i>et al.</i> (1980)

(continued)

TABLE 1. Continued.

Species	Wood Type	Function	Size Range	Average Diameter (cm)	Average Length or Height (m)	References
<i>Haliaeetus leucocephalus</i> (bald eagle)	Live trees	Nesting	53-277 cm dbh, 21-87 m, for a range of forest types	137	43	Anthony <i>et al.</i> (1982)
<i>H. leucocephalus</i> (bald eagle)	Live trees	Nesting	53-277 cm dbh, 21-87 m, for a range of forest types	137	43	Anthony <i>et al.</i> (1982)
<i>Pandion haliaetus</i> (osprey)	Live trees	Nesting	28-136 cm dbh, 6-33 m	59	23	Swenson (1981)
<i>S. occidentalis</i>	Live trees	Platform nesting	36-179 cm dbh	106	42	Forsman <i>et al.</i> (1984)
<i>S. occidentalis</i>	Live trees	Cavity nesting	74-205 cm dbh	135	38	Forsman <i>et al.</i> (1984)
<i>S. occidentalis</i>	Live trees	Roosting	Range of means: 15-115 cm, varies with location and weather	83	—	Forsman <i>et al.</i> (1984)
<i>S. occidentalis</i>	Live trees	Dispersal habitat	>40% canopy cover of trees >28 cm dbh	—	—	USFWS (2004, 2010)
<i>Brachyramphus marmoratus</i> (marbled murrelet)	Live trees	Platform nesting	Large trees >82 cm dbh comprising >10% of the canopy cover	—	—	Meyer and Miller (2002)
<i>B. marmoratus</i>	Live trees	Platform nesting	Dominated by conifers >50 cm dbh	—	—	Ripple <i>et al.</i> (2003)
<i>B. marmoratus</i>	Live trees	Platform nesting	Mean dbh of trees >77 cm (OR) or >91 cm (CA)	—	—	Meyer <i>et al.</i> (2002)
<i>B. marmoratus</i>	Live trees	Platform nesting	>70% crown closure from trees >53 cm dbh (WA)	—	—	Raphael <i>et al.</i> (2002)
<i>B. marmoratus</i>	Live trees	Platform nesting	High density of trees >80 cm within 50 m of nest	—	—	Rodway and Regehr (2000)
<i>B. marmoratus</i>	Live trees	Platform nesting	49-533 cm dbh, range of means, varies with location	116-278	51-73	Hamer and Nelson (1995)
<i>M. americana</i>	Live trees	Resting	—	61	25	Bull and Heater (2000)
<i>M. pennanti</i>	Live trees	Resting	35-205	125	—	Zielinski <i>et al.</i> (2004)
<i>U. americanus</i>	Live trees	Denning	—	112	24	Bull <i>et al.</i> (2000)
<i>U. americanus</i>	Live trees	Denning	—	159	—	Davis (1996)

mammals, such as the northern flying squirrel *Glaucomys sabrinus* form the prey base for avian predators with declining populations such as the spotted owl and are among the species utilizing riparian forests that are associated with abundant large dead standing and down wood. This presumably is why such avian predators prefer to forage in stands with abundant standing and fallen deadwood (Table 1; North *et al.*, 1999). The fruiting bodies of hypogeous fungi are a food source of northern flying squirrels and are also associated with down logs, suggesting that there are complex, indirect paths through which trees that fall to the forest floor support biologically diverse ecosystems (Amaranthus *et al.*, 1994; Carey, 2000).

Although species associations with specific sizes of large deadwood are known (Table 1), mechanistically speaking, the reasons why a particular species is associated with a particular size class of deadwood are not always well understood (cf. Bunnell *et al.*, 1999). Potential functions provided by large dead terrestrial wood that would not occur in smaller deadwood includes temperature (hot and cold) and humidity refugia which are particularly important to riparian-dependent taxa such as amphibians (Ruggiero *et al.*, 1998; Kluber *et al.*, 2009), large internal cavity volumes for nests and dens (Bull *et al.*, 2000; Zielinski *et al.*, 2004), cavities between the bark and bole (Bunnell *et al.*, 2002), and sustained structural integrity, particularly during advanced stages of decay (Mannan *et al.*, 1980). For some species, the size of the deadwood may not matter so much as the mechanism by which the tree died and what happened to the tree while it was alive. As an example, the slow death of a tree by heart rot creates a large cavity that is useful as a denning site for several species (e.g., black bear *Ursus americanus*, fisher *Martes pennanti*, and marten *M. americana*), suggesting that variation in the mechanisms of tree death is another consideration for the maintenance of biodiversity (Bunnell and Houde, 2010).

A number of vertebrates utilize snags and down wood >100 cm diameter, suggesting that similar to species found in aquatic environments, terrestrial species will also benefit from wood of this very large size (Table 1). However, many of these species will also utilize deadwood 50-100 cm diameter and some will utilize deadwood as small as 10 cm diameter (Marcot *et al.*, 2010).

Large Live Trees

Large live riparian trees are utilized by numerous raptors, including the bald eagle *Haliaeetus leucocephalus*, osprey *Pandion haliaetus*, and the northern spotted owl for nesting and roosting, by pileated woodpeckers *Dryocopus pileatus* for foraging and nesting, and by marbled murrelets for nesting

(Table 1). The marbled murrelet and spotted owl are both ESA listed. These two species prefer to build nests on the limbs or the broken tops of very large diameter live trees (Forsman *et al.*, 1984; Huff *et al.*, 2006). Marble murrelets nest in forests that are dominated by large diameter (>50 cm) live trees, and the diameter of individual trees used as nesting sites averages from 49 cm to >500 cm along the west coast from northern California to Alaska, generally decreasing in size with increasing latitude (Table 1).

Spotted owls also build nests in large diameter live trees, either on the platforms of irregular branches such as those misshapen by mistletoe infections, or in cavities atop the boles of trees with broken tops. Platform nests are found in live trees averaging 106 cm diameter and ranging from 36 to 179 cm diameter, while cavity nests are found in live trees averaging 135 cm diameter and ranging from 74 to 205 cm diameter (Table 1; Forsman *et al.*, 1984). Spotted owls also roost in live trees ranging from 15 to 115 cm diameter, depending on location (Forsman *et al.*, 1984).

Canopy Gaps

Canopy gaps have been identified as a structural attribute important to the maintenance of biodiversity primarily because gaps allow more light to reach the forest floor and this can improve the growth of understory vegetation and increase floristic diversity (Halpern and Spies, 1995; Van Pelt and Franklin, 1999). Trees adjacent to canopy gaps also extend their branches into gaps, resulting in larger diameter branches which should create more sites for the establishment of epiphytes and may benefit species such as the marbled murrelet, which nest on "platforms" created by epiphytes growing on large diameter or irregular branches (Hamer and Nelson, 1995; Naslund *et al.*, 1995). Gap creation in Douglas-fir forests also results in short-term increases in the abundance of some songbirds, but causes declines in others (Hagar, 2009).

The character of canopy gaps is complex and metrics for quantifying the value of different types or sizes of gaps have not been well developed. Although active management may create canopy gaps, it is also noteworthy that canopy gaps naturally develop as trees die and fall and knock down neighboring trees, and that the character of natural gaps may differ from artificial gaps, depending in part on whether tree boles are removed during active management (Van Pelt and Franklin, 1999). If a tree dies naturally and falls over to create a gap, it also creates topographical and substrate heterogeneity (e.g., pit and mound topography) that can help increase floristic diversity (Beatty, 1984; Pollock *et al.*, 1998). When trees die and fall, they also may break tops and branches and scrape the boles of

adjacent trees. This can create irregularly shaped branches and apical and lateral cavities, all of which are habitat features used by a variety of species and are a useful index of biodiversity (Michel and Winter, 2009). Additional research is needed to assess the role of variation in the cause of tree death and tree fall in the creation of canopy gaps essential to the maintenance of biodiversity.

EVALUATION OF FOREST THINNING AS A RESTORATION PRACTICE

In the Pacific Northwest, a commonly applied riparian restoration technique is to thin young forests to help promote the development of complex forest structure. The rationale for such thinning is that it should increase the growth rates of the remaining trees and thus more rapidly develop a forest of large diameter trees (Davis *et al.*, 2006). Thinning young forests may also help to create canopy gaps, another structural attribute of older forests that is often missing in dense young stands (Spies, 1989). If such restoration approaches can accelerate the development of complex riparian forest structure, then the restoration of biologically diverse aquatic and terrestrial communities could also be accelerated (Puettmann *et al.*, 2009; Bauhus *et al.*, 2010).

To demonstrate how the potential effects of such restorative treatments on forest structure could be assessed, we used a forest growth model FVS to examine how the size and abundance of large live and dead trees might be affected over the long term in response to various restoration treatments intended to improve the condition of young, degraded conifer stands typical of Pacific Northwest riparian forests. We projected how these stands would respond to three different levels of active restorative thinning treatments and compared them to a passive, no thin treatment. Details of the forest growth model calibration and parameterization, and initial stand conditions have been previously described by Pollock *et al.* (2012) and are detailed below.

PARAMETERIZATION AND CALIBRATION OF THE FOREST GROWTH MODEL, FOREST VEGETATION SIMULATOR

Site Description of Stands Used in the Simulation

For our analysis, we simulated the growth of planted stands of 30- to 40-year-old Douglas-fir for-

ests in the Coast Range of western Oregon. The geology of the Coast Range consists primarily of marine sandstone and shale, with localized basalt intrusions. The terrain is mountainous and highly dissected. Elevations range from sea level to 1,250 m. The climate is temperate maritime with warm dry summers, and mild wet winters. Most of the peak flows occur in late fall or winter and low flows occur in late summer. The watershed is heavily forested in conifers, with Douglas-fir *Pseudotsuga menziesii* the most abundant species. In these forests, the main successional pathway is characterized by Douglas-fir colonization after fire, Douglas-fir dominance during the first 200-300 years, and then slow succession to a "climax" forest dominated by the shade-tolerant (but fire intolerant) western red cedar *Thuja plicata*, western hemlock *Tsuga heterophylla*, and Sitka spruce *Picea sitchensis* (Munger, 1940). However, because the historic fire return interval in these forests averaged between 180 and 230 years (Long and Whitlock, 2002), many of these stands were continually dominated by Douglas-fir, since stands were often reset by fire prior to succeeding to western hemlock and western red cedar dominance.

Model Parameterization and Calibration

To project long-term changes in stand structure, we used the model FVS and the post-processor Fires and Fuel Extension (FFE) (USFS, 2010c). FVS is a distance-independent, individual tree forest growth model developed by the U.S. Forest Service that has been used to project forest stand development in the Pacific Northwest and most other forested regions of the U.S. (Bragg, 2000; Wilhere, 2001; Crookston and Dixon, 2005). Extensive information concerning FVS, including its development, its use, software downloads, reference documents, and related publications can be found at www.fs.fed.us/fmnc/fvs/. Other forest growth models have been developed to simulate the development of Pacific Northwest forests (e.g., Zelig and Organon), but these have significant shortcomings (Pabst *et al.*, 2008; Hann *et al.*, 2009). Zelig is not publically available, lacks institutional support, and has a complex user interface such that a very small number of scientists understand how to use it. Relative to Zelig, Organon is more widely used, but its growth and mortality parameters are not easily adjusted to calibrate the model to real stand data. On the other hand, most of the growth and mortality parameters in FVS can be adjusted, and this enabled us to calibrate the model against real stand data, as we describe below.

The key parameters affecting the FVS model behavior are tree growth rates and mortality rates.

TABLE 2. Long-Term Annual Mortality Rates for *Pseudotsuga menziesii* in Young, Mature, and Old *P. menziesii*-Dominated Stands in the Pacific Northwest.

Site	Age Start (year)	Age End (year)	Interval (year)	TPH Start	TPH End	Mortality Rate (%)	Source
Mt Hood, nw Oregon	45	109	64	847	306	1.6	Bible (2001)
Gifford Pinchot, sw Washington	50	117	67	557	181	1.7	Bible (2001)
WNF, nw Oregon	54	90	36	464	277	1.4	Munger (1946)
WNF, nw Oregon	54	90	36	529	289	1.7	Munger (1946)
WNF, nw Oregon	54	90	36	469	287	1.4	Munger (1946)
Willamette, nw Oregon	55	137	82	489	208	1.0	Bible (2001)
Hagen RNA, nw Oregon	90	102	12	284	246	1.2	Bible (2001)
RS26, nw Oregon	130	148	18	385	335	0.8	Bible (2001)
Bagby, nw Oregon	270	288	18	127	104	1.1	Bible (2001)
Ohanepecosh, sw Washington	277	288	11	138	126	0.8	Bible (2001)
Munger, sw Washington	400	450	50	53	38	0.7	Bible (2001)
WS202, nw Oregon	460	472	12	89	82	0.7	Bible (2001)

Note: TPH, trees per hectare; WNF, Willamette National Forest; RNA, Research Natural Area; nw, northwest; sw, southwest.

We used a maximum stand density index of 1,250, which is typical for the area, to project competition mortality rates in young stands. We set a minimum background mortality rate of 0.7% for all stands, a somewhat conservative estimate relative to Douglas-fir mortality rates in older stands or thinned stands (Table 2, Munger, 1946; Bible, 2001). Maximum tree height was set at 76 m because that is the typical site potential tree height in the study area.

To ensure that simulated changes in diameter, stand density, and height were consistent with local conditions, the model was calibrated against 66 Douglas-fir dominated reference stands from the area ranging from 23 to 139 years in age.

We also wanted to assess the effects of the different treatments on potential understory tree growth, since understory growth over the course of 200 years may produce some large diameter live and dead trees. To ensure opportunities for understory tree growth, we simulated the planting of seedlings of the shade-tolerant species, western red cedar, western hemlock, and Sitka spruce, at densities of 60 trees/ha every 10 years. We anticipated that most of these would not survive, particularly in the young stands, because of a dense overstory canopy, but that some would begin to survive as the overstory trees began to die and the canopy opened up, consistent with typical successional processes. However, we also expected that the heavier thinning treatments would reduce the overstory canopy sufficient to allow growth of the shade-tolerant species in the understory at a relatively young age, consistent with empirical studies (Comfort *et al.*, 2010).

Initial Stand Conditions

The United States Forest Service (USFS) provided detailed data on seven 30- to 40-year-old Douglas-fir

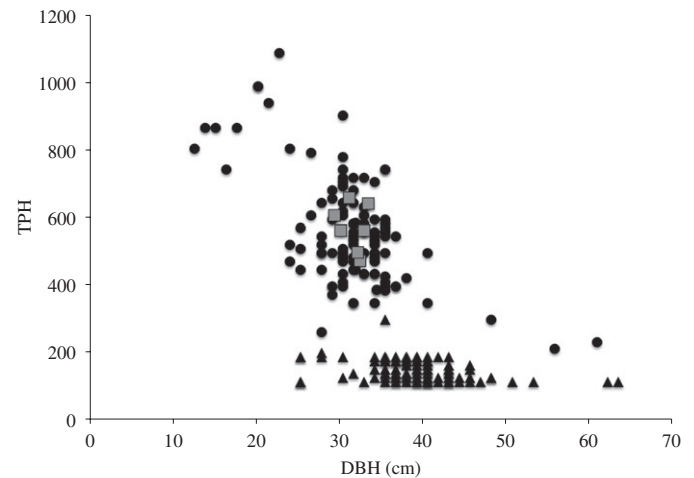


FIGURE 1. Graph Showing Empirical Pre-Treatment Data (black circles) and Proposed (by the USFS, 2010b) Post-Treatment (black triangles) Stand Densities and Average Tree Diameter for the 130 Stands from Which We Modeled Seven for the Purposes of Estimating Long-Term Changes in Large Live Tree and Large Deadwood Production. Gray squares represent the seven stands modeled, and are generally representative of average condition of the larger group of stands, but do not encompass the full range of stand densities.

dominated stands in the Siuslaw River basin from a group of 130 stands that will be thinned for the purposes of restoring forest functions (Figure 1). Most of the stands to be thinned originated 30-50 years ago, when Douglas-fir was planted following clear-cut harvest of the original forest. The average stand age proposed for restorative thinning ($n = 130$) is 35 years ($SD = 9.0$) and ranges from 14 to 64 years. Stand densities currently average 558 trees/ha (range = 210-1087 trees/ha) and post-treatment will average 147 trees/ha (range = 111-296 trees/ha). The proposed treatment is typical of USFS and Bureau of

Land Management plans to restore biologically diverse forests on riparian reserve lands (e.g., USFS, 2010a; BLM, 2011).

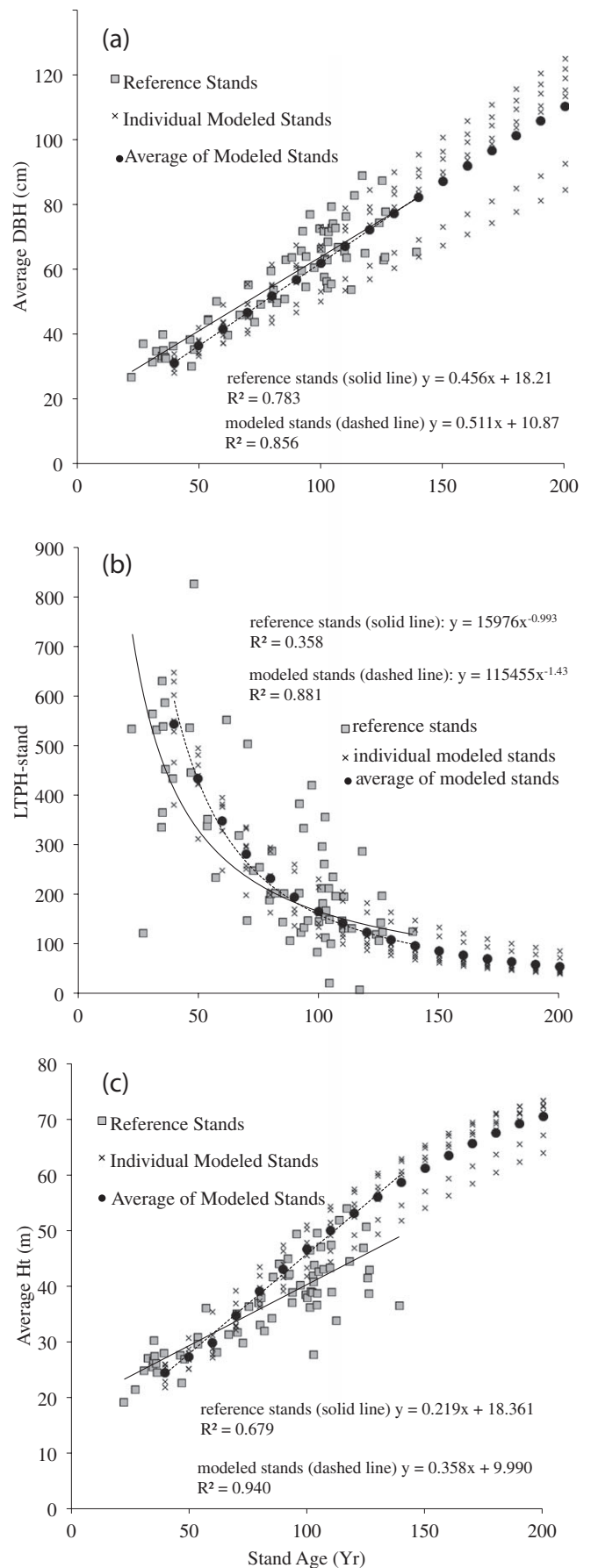
Comparison of our calibrated model outputs with the reference stands showed that our projected changes in diameter, height, and stand density all followed patterns generally consistent with the reference stands, suggesting that the model was appropriately calibrated (Figure 2). The projected changes in average tree height trended toward the higher end of what was observed in the reference stands (Figure 2c) which we attribute to the fact that tree tops in the natural world are often damaged from wind, disease or insects, something that the FVS model does not take into account.

We also compared the thinning treatments with the individual trees in the reference stands used to calibrate the model to verify that all of the treatments produced age-diameter and age-height relationships within the range of natural variation (Figure 3). We found that many trees in the natural environment were growing more rapidly than the trees even in our heaviest thin (Figure 3). This was surprising because the heaviest thin was intended to maximize live tree growth by eliminating any potential for competition.

Caveats

We simulated the growth of stands in the absence of major disturbances. In reality, many stands experience pulses of mortality caused by disturbances such as wind, insect outbreaks, pathogens, and fire. Thus, our mortality estimates are likely lower than what many stands will actually experience. This suggests that recognition of the potential for natural disturbance is important when considering application of restorative treatments. Heavy thins in particular, followed by a disturbance could result in a loss of most of the overstory and delay the creation of a forest with desirable structural attributes (e.g., see Mitchell and Rodney, 2001; Ruel *et al.*, 2001).

FIGURE 2. Graph Showing Comparison of Forest Vegetation Simulator Model Growth Projection of the Seven Modeled Stands (a) Diameter, (b) Stand Density, and (c) Height, Relative to the Static State of 66 Reference Stands 23-139 Years of Age (see Pollock *et al.*, 2012). The static reference stands are represented by gray diamonds, the crosses represent the modeled trajectory of the seven individual stands described in Figure 1, and the black circles represent the median trajectory of the seven modeled stands. Regression lines help to assess the extent to which the range of modeled stands is representative of the empirically observed range of natural conditions.



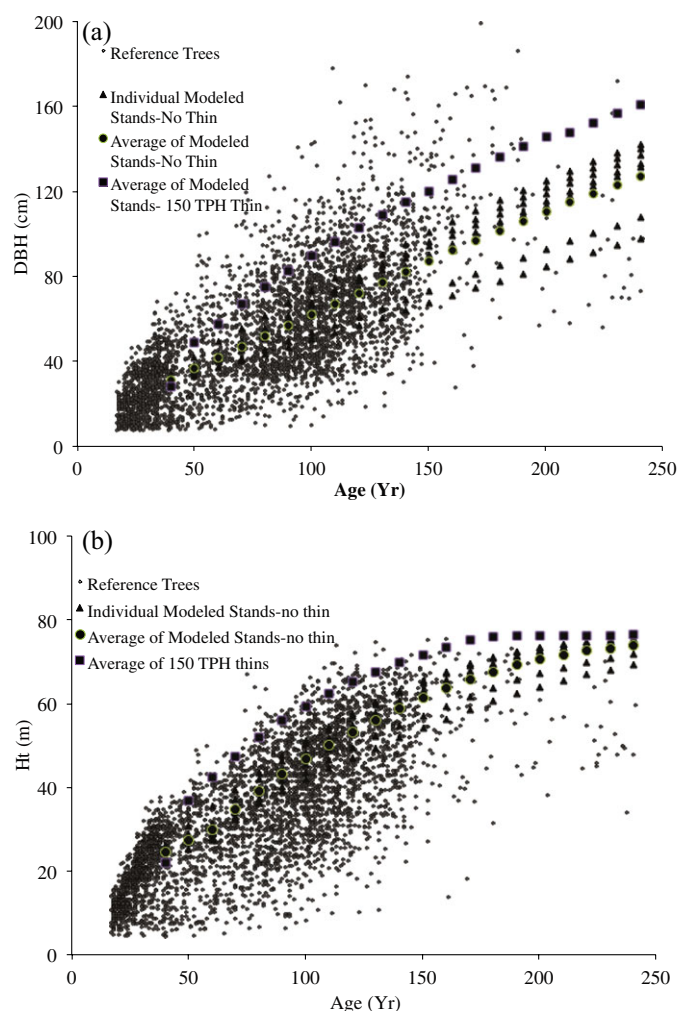


FIGURE 3. Graph Showing the Comparison of the Projected Average Diameter (a) and Height (b) Changes over Time of the Four Simulated Treatments with the Height and Diameter of 3,946 Live Trees in the Area, Ranging in Age from 17 to 250 Years. Tree data were obtained from the USFS Forest Inventory and Analysis database and were limited to productive (site index >120) Douglas-fir-dominated stands that were growing within the coastal region of northwest Oregon. These data help to verify that simulated tree growth in the model was parameterized consistent with growth rates for real live trees.

We found that model projections from the thinning treatments created tree sizes and densities within the natural range of variation. For individual trees, we found that growth rates in the heavy thinning treatment trended toward the upper end of growth rates observed in real stands. This is expected, since the heavy thinning treatments were intended to maximize growth rates of the remaining trees. While such data are reassuring that the model is making reasonable predictions, we note that natural analogues for a stand that has 75% of its overstory removed around age 40 (as was the case for our heaviest thinning treatment) are rare, and forest growth models are not

necessarily calibrated for stands that have developed along such a trajectory.

In addition, stochastic events can change stand developmental trajectories and the input data used to parameterize the initial stand conditions do not contain the variation in tree density inherent in any natural stand. As such, using forest growth models (or any models for that matter) in a relative (rather than absolute) context is useful to compare the results of different treatments under controlled conditions where the effects of changing a limited number of variables can be assessed. While forest growth models are no substitute for empirical data, they are currently still the only tool available for predicting the long-term effects of thinning and as such represent our collective best estimate as to how stands will respond to different management scenarios.

Simulated Restoration Treatments

We projected changes in the average mortality, size, and abundance of large diameter live trees, snags, and down wood of seven 30- to 40-year-old stands that averaged about 600 trees/ha, under three restorative treatments; thinning to 400, 250, and 150 trees/ha (light, moderate, and heavy thins). We then compared these to a projection of the stands if left untreated (no thin). Because the restoration thinning is intended to accelerate the development of large diameter trees, all the thinning scenarios removed the smaller diameter trees until the target density was reached, such that the largest trees remained. We assumed that all thinned trees were removed from the site and did not include them in mortality counts. Every 10 years in the simulation, we categorized the live and dead trees by diameter classes; 30-50 cm, 50-100 cm, and >100-cm-diameter breast height. We used these categories because they were representative of size class categorization used to assess live and dead tree habitat value for a variety of taxa (see Table 1).

RESULTS

Deadwood Production

Tree mortality is the number of trees dying in any given decade, and represents the combined production rate of snags and down wood. The thinning treatments minimally affected the timing of the peak in mortality, but substantially affected the magnitude (Figure 4). The peak in mortality rates for trees

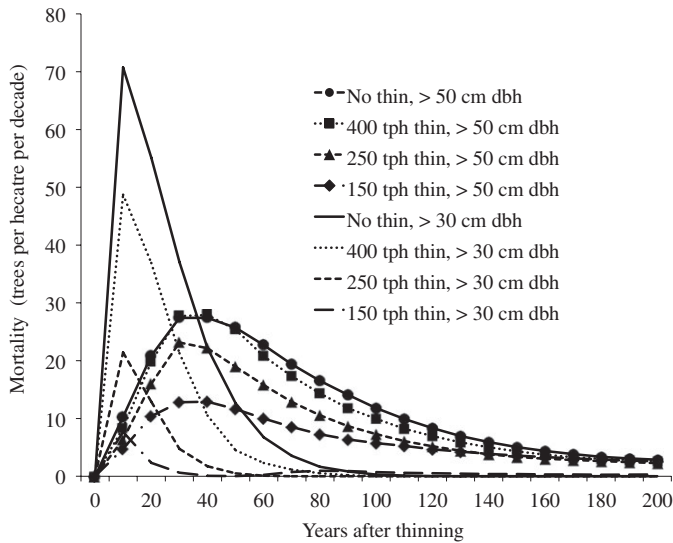


FIGURE 4. Graph Showing Projected Average Mortality Rates (number of trees dying per decade) of Trees >30 cm Diameter and Trees >50 cm Diameter, for each of the Four Simulated Treatments. The 10-year mortality rate of trees >100 cm diameter is low for all treatments throughout the length of the simulation and is not shown in the figure.

>30 cm diameter occurred about 10 years post-treatment and ranged from 8 to 71 trees/ha/decade, with the rate inversely proportional to the intensity of the thin. The peak mortality rate for trees >50 cm occurred about 30 years post-treatment and ranged from 13 to 28 trees/ha/decade, again with the rate inversely proportional to the intensity of the thin. Mortality rates for trees >100 cm were extremely low throughout the simulation (not shown on Figure 4).

The cumulative dead tree production varied considerably among each of the thinning treatments for the >30 cm and >50 cm size classes, while difference in cumulative mortality of trees >100 cm was minimal (Figures 5a and 5b). Over the course of the simulation, the most intensively thinned stands produced a third as many mortality trees >30 cm (145 vs. 461) and half as many mortality trees >50 cm (127 vs. 250) relative to the unthinned stands (Figures 5a and 5b). In contrast, the heaviest thin produced slightly more mortality trees >100 cm, a cumulative average production of 42 mortality trees >100 cm for the heaviest thin, relative to 37 mortality trees >100 cm for the unthinned stands (Figure 5a).

Relative to the no thin scenario, thinning reduced the mortality peak of boles in the 30-50 cm and 50-100 cm size classes that occurred 10-60 years post-treatment in the passively managed stands, with the reduction in mortality proportional to the intensity of the thin (Figure 4).

In summary, thinning minimally increased the production of large diameter deadwood >100 cm, while causing substantial losses in deadwood 30-

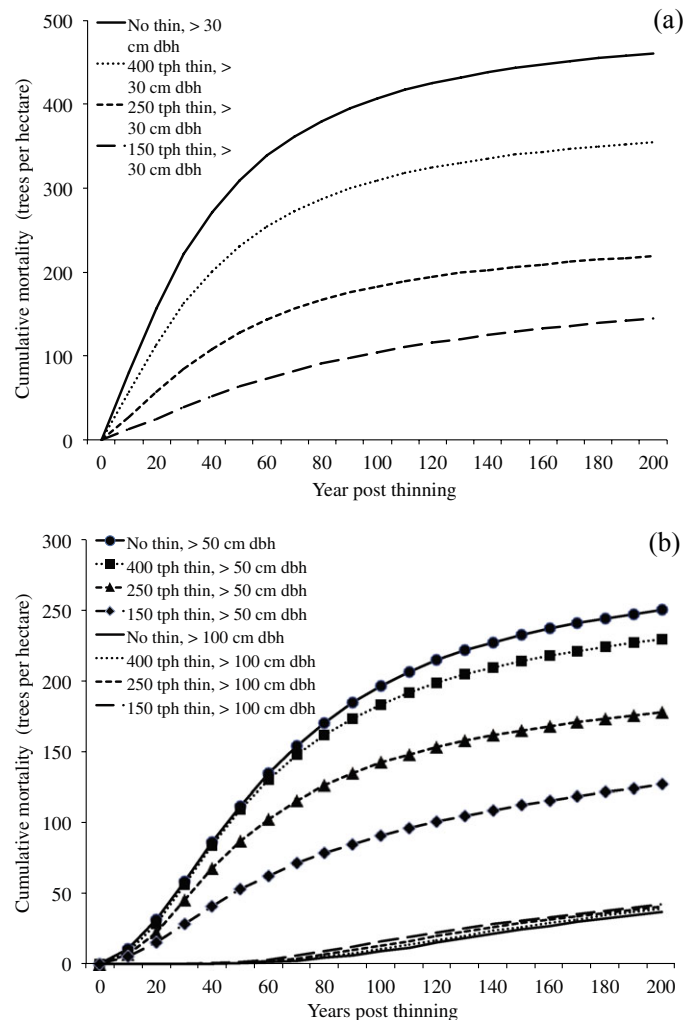


FIGURE 5. Graph Showing Cumulative Mortality over Time for Each of the Four Simulated Treatments. Cumulative mortality provides an index of the total production of deadwood over the course of the simulation and is useful to compare relative production rates of the different treatments for different size classes of wood. Cumulative production of dead trees >150 cm was close to zero for all treatments and is not shown in the figure.

50 cm and 50-100 cm diameter, with no acceleration in the production of these size classes (Figure 5). This suggests that the thinning regimes we examined are not an effective approach for increasing the abundance of ecologically functional deadwood. The no thin scenario produced substantially more deadwood across a wide range of sizes useful to a variety of vertebrate species (Table 1).

Live Trees

Relative to the no thin alternative, thinning initially accelerated the development of large diameter, live trees >100 cm (Figure 6). For example, 100 years post-treatment, the heavily thinned stand contained

34 trees/ha > 100 cm, *vs.* 18 trees/ha for the no thin treatment. However, from 100 to 200 years post-treatment, the number of >100 cm live trees begins to decline in the heavy thinning treatment, such that by year 200, it had the fewest trees >100 cm of all the treatments. Live trees >150 cm begin to show up in the stands 140-160 years post-treatment, but the densities of this size class are very low (9-11 trees/ha) in all the treatments 200 years post-treatment. Heavy thinning caused a 10-year acceleration in the development of live tree densities >50 cm relative to the unthinned stands (Figure 6). However, the higher initial tree densities in the unthinned stand ultimately enabled it to produce more live trees >50 cm than the thinned stands, beginning 30-60 years post-treatment. For trees >30 cm, density generally declined as the intensity of the thinning increased, and this trend was maintained throughout the treatment. The exception was that in the heavy thinning treatment, the growth of understory trees began to produce additional trees in this size class beginning around year 100 (Figure 7a). By year 200, the heavily thinned stand had a broad distribution of tree sizes from 20 to 160 cm, whereas the growth of understory trees in the other treatments was minimal and trees <60 cm diameter were generally absent (Figure 7b).

DISCUSSION

Consideration of the structural attributes that different species utilize and the effect that different res-

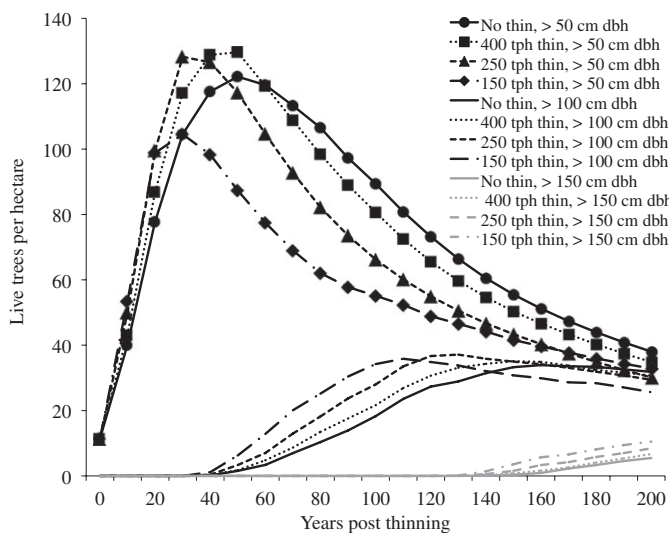


FIGURE 6. Graph Showing the Changes in the Abundance of Large Diameter Live Trees over Time for Each of the Four Simulated Treatments. Relative to deadwood production, the beneficial effect of thinning is more apparent when comparing live trees.

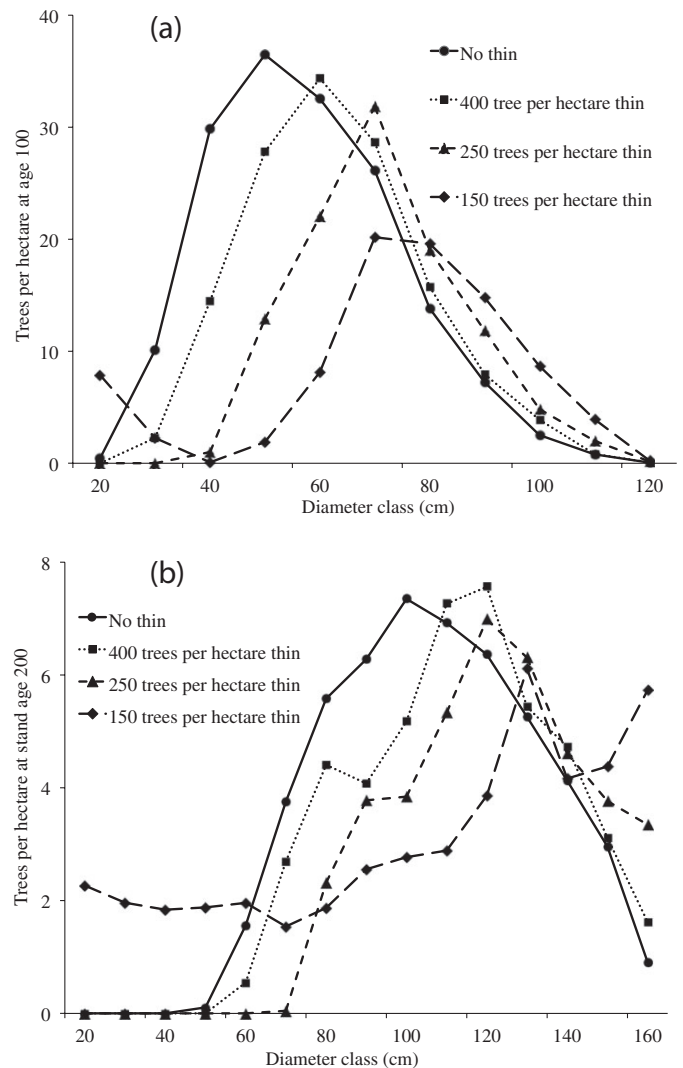


FIGURE 7. Graph Showing the Size Distribution of Live Trees at Age 100 and Age 200 for Each of the Four Simulated Treatments.

toration treatments have on the abundance of these structural attributes suggests that passive management may often be the treatment that will best enhance biological diversity in degraded riparian forests, but that in some cases thinning may be beneficial. We identified four quantifiable structural attributes of forested riparian ecosystems that are frequently associated with specific habitat needs of vertebrates. Of these structural attributes, three of them (trees that fall into streams, trees that fall onto forest floors and standing snags) are composed of large deadwood, and most species we examined utilize one or more of these structure types. This suggests that the key driver creating biologically diverse forested riparian ecosystems is a steady supply of large deadwood.

We provided examples, using a forest growth model, as to how different restoration efforts might affect the supply of large deadwood and large live

trees. Our results suggest that there are tradeoffs associated with both passive and active management, and that different treatments will result in substantial differences in forest structure that will persist over the long term. For the forest stands we examined, as thinning levels increase, forest development predictably trends toward a more open stand with a low number of overstory trees that attain very large sizes, an understory that develops more rapidly, and substantially reduced large diameter deadwood production (Figures 5-7). In contrast, unthinned stands produce abundant large diameter deadwood, but the growth rate of overstory trees and understory development is reduced.

Since different species have a variety of needs in terms of the size and abundance of large live trees and large deadwood (Table 1), we suggest that from a restoration perspective, there is no one "ideal" management regime, but that a range of passive and active management options should be considered for the purposes of creating biologically diverse riparian ecosystems, commensurate with the structural attributes needed by the species of concern. However, we note that for the scenarios examined, more large deadwood that is useful to vertebrates (Table 1) was produced across all size classes when the stands were left unthinned. This suggests that restoration thinning should generally be limited to situations where large deadwood is already abundant, or where the needs of the few species that need very large (>100 cm diameter) live trees outweighs the needs of the many species that utilize large deadwood.

In particular, for providing deadwood to streams, this suggests that for the purposes of facilitating the formation of complex wood jams to benefit the myriad species that utilize the diversity of habitat formed by such jams (e.g., salmonids), a passive management approach that allows for large deadwood production across a range of sizes may be most appropriate.

In contrast, the largest live trees were produced from the heaviest thinning treatment, but this treatment produced the least amount of large deadwood. Thus, such a treatment would be expected to benefit species that utilize very large live riparian trees, but not large deadwood (e.g., marbled murrelets). Examination of Table 1 suggests that deadwood >30 cm diameter creates habitat that is used by many species, but that deadwood >50 cm provides even more habitat benefits, and that maximizing the production of deadwood >50 cm diameter may be a suitable management target if the goal is to benefit the most vertebrates. There were far fewer species that preferred live trees or deadwood >100 cm, but larger diameter dead trees will take longer to decompose, extending the length of time that habitat benefits are provided.

From a restoration perspective, it may also be desirable to directly introduce wood to streams and riparian areas to ensure that there is adequate deadwood in the short term. Even unthinned riparian forests will provide deadwood to forests and streams at a relatively slow rate, and restoration of riparian and instream wood loads to levels that create complex habitat may take decades without active wood placement. Direct placement could also compensate for the loss of instream and riparian wood delivery that will occur if riparian stands are actively thinned.

While our results suggest that passive management will often lead to the most rapid development of large diameter trees and deadwood used by a wide range of species, this interpretation may be limited to the range of stand densities, ages, and forest types that we examined in our study (see Figure 1). Many degraded riparian forests throughout the Pacific Northwest and elsewhere contain stands with smaller and more densely crowded trees that may be dominated by species other than Douglas-fir. The purpose of this study was to assess what structural attributes are used by different species that utilize riparian forests and to provide a simple example of how different management approaches will emphasize the development of different structural attributes important to the maintenance of biological diversity. Future research should examine stands across a wider range of ages, densities, and forest types to develop a more comprehensive understanding as to the conditions where active management can help to restore species-rich riparian forest ecosystems.

Finally, while specific structural attributes of forest ecosystems have been correlated with certain species, it is uncertain how such species will respond to treatments designed to recreate these features. There is always the possibility that in our attempt to create a structural attribute we think is important, we eliminate another attribute that is equally important, but unrecognized. One example is that attempts to restore spotted owl habitat by heavily thinning to accelerate the development of large diameter nesting trees could actually delay spotted owl recovery by reducing production of the large down wood utilized by the species it preys upon (Forsman *et al.*, 1984; Carey, 1995; North *et al.*, 1999). Similarly, heavily thinning stands to accelerate the development of marbled murrelet nesting trees also create open stands with a dense understory that is ideal habitat for a number of corvid species that prey on marbled murrelet nest eggs (USFWS, 2010). Riparian thinning efforts to create long-term supplies of very large diameter instream wood that can initiate complex wood jam formation (e.g., key pieces) are also likely to reduce the supply of large diameter wood that will create pools (Beechie and Sibley, 1997; Beechie *et al.*,

2000; Fox and Bolton, 2007). Thus, we suggest that any efforts to actively restore riparian forests for the benefit of certain species should be treated as scientific experiments and proceed cautiously, skeptically, and with robust pre- and post-treatment data collection efforts. Hypothesized effects of thinning on riparian forest structure and the use of that structure by targeted species should be tested against empirical data.

CONCLUSIONS

The importance of large deadwood as habitat for many aquatic and terrestrial species has been extensively studied over the last three decades, yet there is little comprehensive understanding of how multiple aspects of forest structure contribute to maintaining biologically diverse aquatic, riparian, and upland ecosystems. Our analysis suggests that species rely on different sizes of the key structural attributes of large deadwood in streams, large deadwood on the forest floor, large snags, and large live trees. Different active and passive restoration treatments will have long-term effects on the abundance of these structural elements. For the forests we examined, passive management resulted in the most rapid development of deadwood 30-100 cm diameter, whereas heavy thinning most rapidly developed live trees >100 cm diameter. Other forest types in different climates may produce different results. In the example we provided, passive management created dense forests that produced large volumes of large diameter deadwood over extended time periods as overstory tree densities slowly declined. In contrast, heavy thinning immediately created an open forest that allowed a low-density stand of large diameter overstory trees and an understory of shade-tolerant species to more rapidly develop. Because these size classes of live and deadwood support different biological components of forest ecosystems, tradeoffs in the abundance and production rates of different large diameter live and deadwood size classes should be considered when weighing different management options. Light or medium restoration thins may be an option that provides some increase in diameter growth of live trees, while minimizing production losses of large diameter deadwood. Large deadwood and large live trees are not the only structural attributes needed to maintain biologically diverse riparian ecosystems, but the decline of numerous species has been attributed to the lack of these features. Management strategies that seek to create a range of large live and dead tree densities across the landscape will help to hedge against uncertain outcomes related to unanticipated

disturbances, unexpected species needs, and unknown errors in model assumptions. Over the long term, careful monitoring of active and passive treatments can determine if restored riparian ecosystems are being used by the targeted species. Such monitoring will help guide management toward developing biologically diverse riparian ecosystems.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article that includes spreadsheets of the forest growth model inputs and outputs necessary to reproduce the results of this study.

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