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REVIEW

Linking instream wood recruitment to adjacent forest development in landscapes driven by stand-replacing disturbances: a conceptual model to inform riparian and stream management

Kyle D. Martens, Daniel C. Donato, Joshua S. Halofsky, Warren D. Devine, and Teodora V. Minkova

Abstract: Instream wood plays an important role in stream morphology and creation of fish habitat in conifer forests throughout the temperate zone. In some regions, such as the US Pacific Northwest, many streams currently have reduced amounts of instream wood due to past management activities (timber harvest, wood removal, etc.). These reductions exist against a backdrop of naturally dynamic amounts and distributions of instream wood, which likely fluctuate over time based in part on the stage of development (disturbance and succession) in adjacent riparian forests. Despite many studies on both forest development and instream wood accumulation, the linkages between these processes have not been fully described, particularly as they relate to stream restoration needs. In this paper, we combine literature on forest development, disturbance, and processes that drive instream wood recruitment to more explicitly connect the temporal dynamics of stream wood inputs with the dynamics of adjacent riparian forests. We use moist forests of the Pacific Northwest as an exemplary system, from which to draw broadly applicable patterns for landscapes influenced by stand-replacing disturbance regimes. This conceptual model highlights a U-shaped pattern of instream wood recruitment, in which instream wood is highest after a stand-replacing disturbance and during the old-growth stage, and lowest through the middle stages of forest development (currently the most abundant stages in many landscapes as a result of past forest management practices). This mid-successional period of scarce wood is likely exacerbated in streams with a history of wood removal. The U-shaped pattern suggests that, without higher-than-average levels of disturbance, many streams in landscapes dominated by mid-successional second-growth forests (∼30–80 yr old) will be deficient of instream wood until forest stands are over 200 years old. As such, the balance between the predominant riparian conservation strategy of passive restoration (e.g., unharvested riparian reserves) and the alternative of active restoration (e.g., wood additions and (or) riparian stand treatments) should be carefully considered, depending on management objectives, site context, and potential tradeoffs over time.

Key words: forest development, instream wood, second-growth forests, riparian, passive restoration.

Résumé : Le bois des cours d'eau joue un rôle important dans la morphologie des cours d'eau et la création de l'habitat des poissons dans les forêts de conifères de toute la zone tempérée. Dans certaines régions, telles que le Nord-Ouest Pacifique aux États-Unis, de nombreux cours d'eau présentent actuellement des quantités réduites de bois en raison des activités de gestion passées (récolte de bois, enlèvement du bois, etc.). Ces réductions s'inscrivent dans un contexte de quantités et de distributions naturellement dynamiques du bois dans les cours d'eau, qui fluctuent probablement dans le temps en fonction du stade de développement (perturbation et succession) des forêts riveraines adjacentes. Malgré de nombreuses études sur le développement forestier et l'accumulation de bois dans les cours d'eau, les liens entre ces processus n'ont pas été entièrement décrits, en particulier en ce qui concerne les besoins de restauration des cours d'eau. Dans cet article, les auteurs combinent la littérature portant sur le développement, les perturbations et les processus forestiers qui entraînent le recrutement de bois dans les cours d'eau afin de relier plus explicitement la dynamique temporelle des apports en bois dans les cours d'eau à la dynamique des forêts riveraines adjacentes. Ils utilisent les forêts humides du Nord-Ouest Pacifique comme système type, à partir duquel il est possible de tirer des modèles largement applicables pour les paysages influencés par des régimes de perturbation renouvelant les peuplements. Ce modèle conceptuel met en évidence un modèle en U du recrutement de bois dans les cours d'eau, dans lequel le bois dans les cours d'eau est le plus abondant après une perturbation renouvelant un peuplement et pendant le stade de peuplement ancien, et le plus faible pendant les stades intermédiaires du développement forestier (actuellement les stades les plus abondants dans de nombreux paysages en raison des pratiques de gestion forestière passées). Cette période de rareté du bois de milieu de succession est probablement exacerbée dans les cours d'eau ayant des antécédents d'enlèvement du bois. Le schéma en U suggère que, sans des niveaux de perturbation plus élevés que la moyenne, de nombreux cours d'eau des paysages dominés par des forêts de seconde venue en milieu de succession (∼30–80 ans) seront déficitaires en bois dans les cours d'eau jusqu'à ce que les peuplements forestiers aient plus de 200 ans. En tant que tel, l'équilibre entre la stratégie de conservation riveraine prédominante de restauration passive (par exemple, les réserves riveraines non exploitées) et l'alternative de restauration active (par exemple, les ajouts de bois ou les traitements des peuplements riverains) doit être soigneusement examiné, en fonction des objectifs de gestion, du contexte du site et des compromis potentiels au fil du temps. [Traduit par la Rédaction]

Mots-clés : développement forestier, bois de cours d'eau, forêts de seconde venue, riverain, restauration passive.

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K.D. Martens, J.S. Halofsky, and W.D. Devine. Washington State Department of Natural Resources, 1111 Washington Street SE, Olympia WA 98504, USA.
D.C. Donato and T.V. Minkova. Washington State Department of Natural Resources, 1111 Washington Street SE, Olympia WA 98504, USA; School of Environmental & Forest Sciences, University of Washington, Seattle WA 98185, USA.

Corresponding author: Kyle D. Martens (email: kyle.martens@dnr.wa.gov).

Introduction

Instream wood plays an important role in determining the characteristics of streams (Fetherston et al. 1995). It can direct flow, influence stream velocity, and scour stream beds, helping to create a diversity of conditions (Montgomery et al. 2003). Instream wood also allows for sediment storage and movement (Bilby and Ward 1989) while providing cover to protect stream inhabitants against predation (Allouche 2002). Many species of fish, amphibians, and macroinvertebrates have evolved to take advantage of stream conditions created in part by instream wood. In the Pacific Northwest of North America, ranging from northern California into Alaska, salmonids rely on these conditions to complete most freshwater stages of their life cycle. While the importance of instream wood (Bilby and Ward 1989; Fausch and Northcote 1992; Beechie and Sibley 1997), and the role of riparian forests as a source of that wood, is widely recognized there has been relatively little work detailing how the link between instream wood recruitment and forest successional dynamics can inform contemporary stream restoration efforts (see Beechie et al. 2000; Rot et al. 2000; Benda and Sias 2003; Czarnomski et al. 2008).

Intensive and widespread anthropogenic influences on streams and their associated riparian forests across the US Pacific Northwest have left many streams altered from pre-European settlement conditions (i.e., before the mid-1800s). These changes have negatively affected many of the native species of salmon (Nehlsen et al. 1991; Fausch et al. 2002; Gustafson et al. 2007). Salmon populations within the Pacific Northwest have fallen to 6%–7% of their historic levels due to many factors (Gresh et al. 2000) including, but not limited to, widespread changes to the landscape as a result of forest harvests. Prior to European settlement, most forests in the Pacific Northwest were in the later stages of development and dominated by old-growth forests (Strittholt et al. 2006; Donato et al. 2020). Since settlement, many of these forests have been harvested at least once or converted to other uses (agriculture and urbanization; Everest and Reeves 2007; Alig and White 2007). This has shifted many landscapes, previously dominated by older forests, into younger-aged forests (Cohen et al. 1995; Wallin et al. 1996; Donato et al. 2020).

One of the more significant effects of intensive forest management has been on accumulations of instream wood. Historical forest practices often required instream wood to be actively removed from streams, and (or) used splash damming to transport wood downstream via channel-scouring flash floods, leaving many streams deficient of instream wood (Bilby and Ward 1991; McHenry et al. 1998; Roni et al. 2015; Wohl 2014). In addition, before the implementation of unharvested riparian reserves or buffers, riparian forests were often clear-cut up to or through streams, temporarily leaving them without a source of instream wood (Richardson et al. 2012). Since widespread application of riparian forest reserves, beginning as early as the 1960s, many riparian forests of the Pacific Northwest have been left to recover on their own through passive restoration (Martens et al. 2019). A critical question about the effectiveness of this restoration approach is how long it will take for instream wood to recover to predisturbance levels.

While there is currently a consensus that widespread reductions of instream wood have occurred throughout the Pacific Northwest (Murphy and Koski 1989; Ralph et al. 1994; Mellina and Hinch 2009; Roni et al. 2015), the amount and characteristics of instream wood required to support salmon recovery is relatively unknown (Fox and Bolton 2007). The amount and size of instream wood throughout a watershed is not only a function of watershed geomorphology, but also of forest age and composition, rate of recruitment, and stream retention (Hassan et al. 2005; Wohl et al. 2019). Even in the absence of human influences, it is likely that instream wood would cycle through periods and areas of greater and lesser accumulations based on the adjacent riparian forest's stage of development and disturbance history (Hedman et al. 1996; Bragg 2000; Benda and Sias 2003), among other factors. Currently, however, there is limited information on the relationships among forest development, forest disturbance, and instream wood recruitment.

An improved understanding of these linked forest–stream dynamics is needed to place current conditions in a broader context and to better predict stream habitat recovery as forests redevelop after past harvests. The goal of this review is to synthesize information on forest succession, disturbance, and instream wood to develop a conceptual model linking instream wood recruitment to widely used, management-relevant forest development stages. We then discuss the potential implications of these links for stream restoration and riparian forest management.

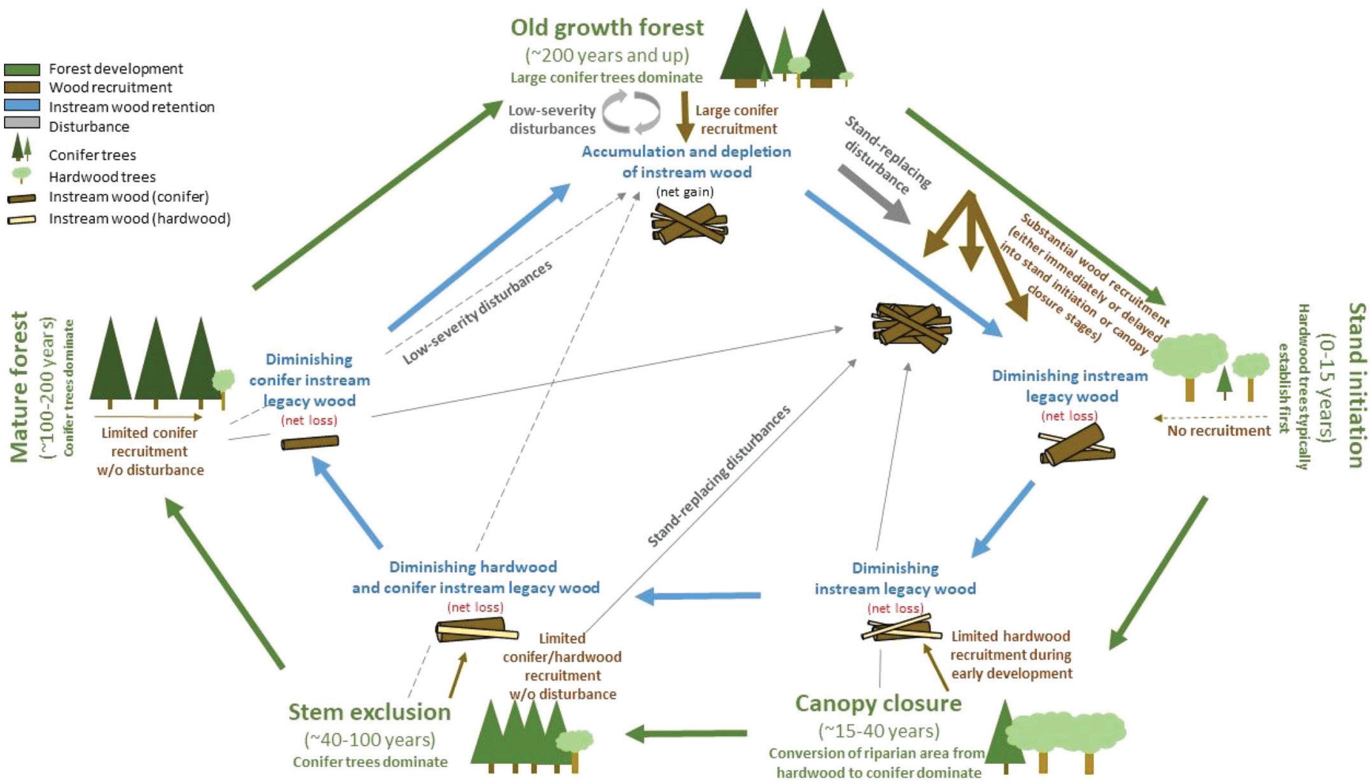
Conceptual model of instream wood recruitment based on adjacent riparian forest development

Our instream wood model draws on information from forest development, wood recruitment, instream wood retention and both stand-replacing and low-severity disturbances to understand how wood accumulates over time (Fig. 1). The model builds on prior work that showed generalized trends with, or comparisons among, forest age classes (Beechie et al. 2000; Bragg 2000; Benda and Sias 2003; Meleason et al. 2003; Czarnomski et al. 2008), but more explicitly addresses the effects of forest disturbances (e.g., fire, wind) and ties directly to designated forest successional stages relevant to forest management (e.g., Franklin et al. 2002). Its foundation is the natural development of long-lived conifer forests (derived from mostly upland forest studies that may slightly deviate from riparian forests), using five distinct stages of forest development relevant to instream wood accumulation. We use moist forests of the Pacific Northwest as a focal example of landscapes driven by cycles of major stand-replacing disturbances, as well as intervening low-severity/background mortality events. The model focuses on the key process of recruitment of instream wood (at the stream-reach scale)—the foundation on which virtually all other instream wood dynamics operate (e.g., reach- and network-scale processes such as storage, decay, and transport; discussed below). We also acknowledge that forests operate at the reach level, whereas streams are influenced by both reach and upstream influences. The model is most relevant to smaller streams where upstream influences are not as apparent as in larger streams. We imagine that this model is most relevant for first- to fourth-order streams (Strahler 1957) or streams with widths within approximately one potential tree height (typically 46–61 m in moist conifer forests). Its relevance likely diminishes for larger rivers where wood retention patterns are inherently different and more likely to be influenced by an accumulation of upstream conditions. While the concept of the instream wood recruitment model was developed using the example of conifer-dominated forests, the model is likely generally applicable to other types of forests driven by comparable disturbance regimes.

Riparian forest disturbances

Forest disturbances, natural and anthropogenic, are at the heart of the instream wood recruitment model. Stand-replacing (high-severity) events such as wildfires and windstorms "reset" stand dynamics to the stand initiation phase, whereas low-severity events such as individual or small-group mortality promote and maintain old-growth conditions (Franklin et al. 2007). The timing and amount of disturbance will determine the amount of time a forest stand remains within a stage of development and thus the amount of wood potentially available to a stream. Disturbances ultimately drive the most critical variations in forest stand structure and species composition (Oliver 1980). These disturbances are largely unpredictable, and the amount of disturbance in a watershed can lead to large variation in instream wood accumulations.

Fig. 1. Instream wood recruitment model identifying the mechanisms for instream wood accumulations over five stages of forest development (stand initiation, canopy closure, stem exclusion, mature forest, and old growth forest) with low-severity and stand-replacing disturbances. The figure follows forest development (green), wood recruitment (brown), instream wood accumulations (blue), and disturbance (grey) processes over time. Dashed grey lines represent low-severity disturbances and solid grey arrows represent larger stand-replacing disturbances.



Within the instream wood recruitment model, we incorporated both stand-replacing and low-severity disturbances. In the former, most if not all trees within a stand are killed and vegetation recolonizes the site via seeding or sprouting. Oliver (1980) defined this level of disturbance as "those which knock over or kill all living tree stems in an area large enough to ensure that most trees beginning growth after the disturbance do not encounter competition from surrounding undisturbed trees". These types of disturbances typically result from wildfires, major windstorms, landslides, large floods, or timber harvests. Historically, stand-replacing natural disturbance events were infrequent and, without human influence, may have occurred only once every 200–500 years in a given stand (Franklin et al. 2007; Donato et al. 2020). In disturbances in which most or all trees are knocked over during the event (e.g., wind or volcanic eruption), there will be an immediate major input of wood to streams, whereas in those that leave most trees standing for a period of time (e.g., fire or disease), dead trees will fall either gradually or episodically. The type of stand-replacing disturbance can also influence the species that follow. For example, a common conifer pioneer in the Pacific Northwest following a stand-replacing wildfire is Douglas-fir (*Pseudotsuga menziesii*). Conversely, following a major wind disturbance that topples overstory trees, there may be a release of suppressed shade-tolerant trees, already present in the understory, such as western hemlock (*Tsuga heterophylla*; Franklin et al. 2002).

Low-severity disturbance is smaller in scale but occurs at higher frequencies than stand-replacing disturbance. These disturbances normally involve the death of individual trees or small groups of trees, leaving the forest mostly intact (Franklin et al. 2007). They "vary in type, intensity, size, frequency, and homogeneity" (Franklin et al. 2002). Examples of low-severity disturbances are lightning strikes, small or low-severity fires, small windthrow events, small landslides, endemic insects or diseases, and stream erosion. If a stand is subject to a higher frequency of low-severity disturbances, it can reduce the amount of time required to reach the later stages of forest development by opening the main canopy and promoting additional canopy layers (Oliver 1980). However, recurring disturbances, such as regular flooding events, can create a shifting mosaic of accumulating and depleting alluvial deposits that maintain early-seral conditions (Tabacchi et al. 1998; Van Pelt et al. 2006). In riparian forests, the types of low-severity disturbances differ somewhat from those often found in upland forests. Riparian forests are more likely to experience debris flows, floods, and bank erosion than upland forests (Moore and Richardson 2012), and may also be more protected from wind-related disturbances due to their location (e.g., lowest elevations) on the landscape (Harcombe et al. 2004). The severity of disturbance will determine whether a stand will maintain its current rate of development, accelerate its development, or, if severe enough, reset to the stand initiation stage.

Most forest disturbances result in wood recruitment to the forest floor or adjacent stream. Windstorms and insect outbreaks leave ~100% of tree bole mass on site. Even high-severity wildfires tend to consume no more than ~20% of aboveground biomass, and <5% of the large bole biomass, leaving virtually all the large wood near streams to immediately or eventually recruit to the stream (Campbell et al. 2007; Donato et al. 2013). In contrast, the primary disturbance that removes tree boles from the site is that of forest harvest (Franklin et al. 2002).

Riparian forest development and wood recruitment

Stand initiation

After a stand-replacing disturbance, the first stage of forest development in our model is stand initiation, also referred to variously as "early-seral" or "pre-forest" conditions (e.g., Swanson et al. 2014). This stage occurs after a large natural disturbance or forest harvest and before tree canopy closure. During this period, a forest regenerates without constraints (e.g., shading) from existing trees (Winter et al. 2002). Quick-growing vegetative species become dominant as they hold an advantage over slower-growing species (Oliver 1980). Typically, early successional hardwoods, such as red alder (*Alnus rubra*), and shrubs establish first along with the first conifers, especially in wetter riparian forests. The length of the stand initiation stage will vary depending on the intensity of disturbance, type of disturbance, patch size (vis-á-vis effects on seed source proximity), growth rate of colonizing species, regenerating mechanisms, seed crop and weather, density of seed predators, competition between shrubs and trees, and the degree to which silvicultural activities accelerate the dominance of trees over other vegetation in managed stands (Oliver 1980). The stand initiation stage may persist for one to several decades (Freund et al. 2014), continuing until small trees provide shading to the ground or stream (Franklin et al. 2002). Recruitment of instream wood can begin or peak during this stage following disturbances that left dead trees standing initially (e.g., fire) depending on the snag longevity of local tree species. Secondary or repeat disturbances in this stage, such as recurrent fires or floods, would reinitiate stand development but may not result in significant input of instream wood, unless snags still standing from the first disturbance are weakened or toppled.

Canopy closure

The second stage of forest development is canopy closure. The timing of canopy closure varies widely in uplands from 10 to 50 or more years after disturbance but in riparian forests has been observed as early as 15 years after disturbance (Hicks et al. 1991; Johnson and Jones 2000). This stage manifests when trees become the dominant form of vegetation (Franklin et al. 2002). During this stage, streams transition from higher to lower levels of light. In riparian forests, this stage can be dominated by conifers (particularly in the lowest order streams) or, often, pioneer hardwoods such as red alder. The latter generally dominate a site ~40–60 years before transitioning to dominance by more shade-tolerant, longer-lived conifers. Disturbance-generated wood is typically still abundant in the canopy closure stage, albeit with a diminishing or decaying trend. During the hardwood–conifer transition there may be a period of time with increased canopy openness (and presumably increased hardwood tree recruitment; Gregory et al. 1987); however, Kaylor et al. (2017) did not find evidence of canopy openness 30 to 100 years after harvest. This may be the result of a slow conversion process from hardwood to conifer trees rather than a rapid conversion. Low-severity disturbances during this forest development stage create canopy gaps, allowing younger conifer and hardwood trees to establish and recruiting hardwood logs into the stream.

Stem exclusion

Stem exclusion is the third stage of forest development. This stage typically spans the period ~40–100 years following the originating disturbance (Franklin et al. 2002). During this stage, trees have established to a point where competition for light is limiting the recruitment of new trees. Young conifers are now dominant. This stage is characterized by extreme competition between trees within the same cohort (Franklin et al. 2002). Low-severity disturbances will typically not allow for new trees but only increase growth in the existing trees (Oliver 1980). The forest canopy is very dense and blocks most of the light into the stream; there is very little understory vegetation (Warren et al. 2016). Larger trees outcompete smaller trees, resulting in increased mortality (Rot et al. 2000). This dynamic results in the smallest trees being recruited into streams. Moreover, the wood generated by the stand-replacing disturbance has attenuated considerably due to decay, fragmentation, and transport. Frequent and (or) extensive low-severity disturbances can reduce the length of the stem exclusion stage, accelerating succession toward later stages. High-severity disturbances would restart the stand initiation stage.

Mature forest

The fourth stage of forest development is mature forest. This stage typically spans the period ~100–200 years following the originating disturbance (Franklin et al. 2002). Dominant trees attain their maximum height and crown spread during this period (Franklin et al. 2002). The canopy remains dense, but scattered gaps and sufficient time allow the initiation of a shade-tolerant understory. The mean diameter of mature stands is often the highest of all stages of development, as young saplings and poles are not yet sufficiently abundant to strongly influence the mean. Mature forests often have relatively low volumes of downed wood, as the disturbance-generated pulse is largely decayed away, while the mortality rate of large trees is not yet high enough to supply new large logs to streams or the forest floor (Spies and Franklin 1991). Canopy opening, understory establishment, and dead wood recruitment increase in the latter portions of the mature stage. Low-severity disturbances, such as small windthrow events, within this stage can accelerate development toward old-growth conditions and produce large pieces of instream wood. Larger disturbances will reinitiate the stand initiation stage and generate pulses of large instream wood.

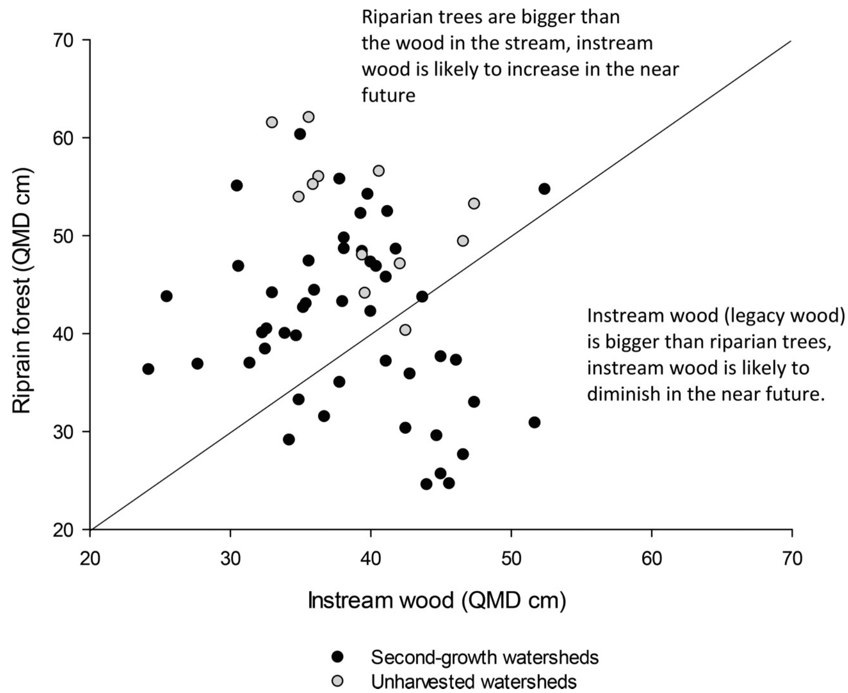
Old growth

The final stage of development is the old-growth stage. In this stage, low-severity disturbances create gaps that facilitate tree recruitment in the under- and mid-stories. There is a wide range in tree diameters, a continuum from very small to very large trees, and the canopy is vertically contiguous from the ground to the dominant treetops. A substantial portion of old-growth trees have "decadence" features such as broken tops, cavities, heart rot, and reiterated trunks. Spies and Franklin (1991) found that the amount of trees with broken crowns was almost three times the amount found in both mature and younger forests. Down wood volumes again reach high levels during this stage. Old-growth conditions are not necessarily tied to a particular forest age, instead being associated with sufficient structural development (Van Pelt 2007); however, typically these conditions begin to show around 200–250 years, and continue to evolve for another 300–500 years in the absence of a stand-replacing disturbance. Van Pelt et al. (2006) found that old-growth conditions developed quicker (within 200 years) in riparian forests when compared with upland forests. During this stage, low-severity disturbances can recruit large pieces of instream wood, whereas severe disturbances generate the greatest pulse of large wood of any stage.

Instream wood accumulation—general processes

Instream wood at any given time is the result of gains through tree mortality, disturbances, and any upstream inputs and losses through downstream transport, decay, fragmentation, and in some cases, past forest management practices (e.g., direct removal). In addition, process domains influence wood accumulations. Process domains are ecologically significant areas characterized by distinct geomorphic processes driven by geological, climatic, and topological influences (Montgomery 1999). For example, some areas within a watershed are more likely to accumulate wood (e.g., shallow, low-gradient sections of streams), whereas others are more likely to transport wood (e.g., deeper, higher-gradient sections of streams; Wohl et al. 2019). Broadly, instream wood represents some combination of both past and present forest conditions at the stream reach and network scales. Because of the inherent time lags between forest development, instream log recruitment, and subsequent decay/loss of instream wood, adjacent riparian forests largely represent the future potential, rather than

Fig. 2. The relationship between the quadratic mean diameter (QMD; cm) of riparian forests (within 60 m of stream banks) and that of instream wood in 60 watersheds (50 watersheds that have been harvested at least once and 10 watersheds that have never been harvested) on the western Olympic Peninsula of Washington state.



the current condition of instream wood. For example, Martens (unpublished data) found no significant relationship between instream wood diameter and riparian forest tree diameters across 60 sites on Washington State's Olympic Peninsula (Fig. 2; X^2 = 20.00, df = 16, P = 0.220). One interpretation of this lack of correspondence is that current instream wood levels likely reflect inputs derived from forests of past decades rather than contemporary forests. This would suggest that, in watersheds with larger-diameter riparian trees and smaller-diameter instream wood, wood conditions are likely to improve with recruitment. Conversely, streams with smaller-diameter riparian trees compared with instream wood are likely to diminish in habitat quality, other factors and inputs being equal, until the riparian forest matures. Thus, the relationship between adjacent riparian forests and instream wood is likely a good indicator of future potential rather than solely current conditions.

Instream wood additions (tree mortality)

Inputs of wood from forests are of course the foundation of instream wood dynamics. Inputs may be episodic, as those generated from large forest disturbances, or chronic, as those generated by background tree mortality rates. The pulses of instream wood generated by stand-replacing disturbances can range from immediate to protracted, can include small to large pieces depending on the structure of the disturbed forest, and can influence instream wood levels for many decades. For background mortality (i.e., that from competition, endemic insects or disease, etc.) annual rates are typically under 2.5% of the tree population across all successional stages in the Pacific Northwest (Reilly and Spies 2016). Commonly, mortality rates range from 0.8% to 1.5% depending on successional stage (Edmonds et al. 1993; Martin and Benda 2001; Van Mantgem et al. 2009). The proportion of instream wood recruited by background mortality varies among streams; examples from the literature indicate contributions as low as 23% of total instream wood (Murphy and Koski 1989) to as high as 65% (Johnston et al. 2011). The relative role of background mortality in overall instream wood budgets likely varies with the nature of the local disturbance regime, being highest when disturbances are especially infrequent or small.

Instream wood retention

Wood transportation, fragmentation, and decay are the main factors driving instream wood retention in the different stages of riparian forest development. Process domains and biotic factors such as the size and species of wood can affect wood retention. King et al. (2013) found the average residence time of a piece of wood to be 20 years in a study on smaller streams, whereas Hyatt and Naiman (2001) found that 80% of wood pieces are lost from a channel within 50 years in the much larger Queets River (Washington, USA). Even with these relatively short retention times within a reach, individual pieces of wood have the capability of lasting much longer (Naiman et al. 2002). Murphy and Koski (1989) found wood retention was related to diameter, with smaller pieces (10–30 cm) lasting less than 110 years and pieces greater than 60 cm lasting up to 226 years. Hyatt and Naiman (2001) found instream wood pieces could last for up to 1400 years depending on burial dynamics. Shorter residence times are likely from process domains that encourage instream wood movement while longer times are likely in domains that resist instream wood movement. Regardless of the process domain, wood retention is likely to be longer when it is composed of larger pieces of coniferous wood (Fetherston et al. 1995; Naiman et al. 2002; Benda et al 2003; Collins et al. 2012), produced during the later stages of forest development (Beckman and Wohl 2014).

Transport

While the development stage of adjacent forests is an important factor in recruiting instream wood, decoupling can occur due to a variety of processes, including downstream wood transport. Wood transport is a function of the size of a stream, size of wood, and amount of flow. Larger streams with higher amounts of flow are more likely to transport wood than smaller streams (Naiman et al. 2002). As such, wood in smaller streams is more likely to be from local sources, whereas wood in larger streams is likely to be some combination of local and upstream conditions. Wood transport is also affected by obstructions such as wood jams or larger pieces of instream wood. The amount of burial, stream depth, length of the piece, bracing against other objects, and the presence or absence of rootwads all factor into whether pieces of wood are transported downstream (Merten et al. 2010). In general, when more or larger pieces of wood are present, the stream is more likely to accumulate and hold wood (Braudrick et al. 1997; Martin and Benda 2001). Merten et al. (2013) determined smaller logs recruited in earlier stages of forest development would likely not persist as long as larger logs from later stages of development. Martin and Benda (2001) found that pieces of wood in small, jam-rich streams travel on average 200 m, whereas pieces in larger channels with few jams moved around 2500 m. Of all the factors influencing wood retention in a stream, transport has by far the greatest potential influence on losses or gains (Merten et al. 2013). Downstream transport has the potential to partially decouple reach-scale instream wood from its adjacent riparian forest. In transport reaches (either chronically or resulting from a major flood event), instream wood becomes a function of network-scale forest conditions as much or more than immediately adjacent forest conditions. The role of a given riparian stand in wood dynamics (i.e., the model presented here) thus depends on process domains, including transport capacity of streams within the larger stream network and the condition of riparian stands (Czarnomski et al. 2008; Wohl et al. 2019).

Fragmentation and decay

Another mechanism of instream wood reduction is fragmentation and decay. These two processes likely work together, as pieces are more likely to break apart as they age and decay. Merten et al. (2013) found that fragmentation (7.3%) was responsible for more loss of mass in instream wood than decay (1.9%) over a year. Fragmentation depletes wood by creating shorter pieces that are more susceptible to transport. Fragmentation is more likely to occur on initial impact with the stream and in higher velocity streams (transporting reaches). Wood is more susceptible to fragmentation if it is long and thin, braced against other pieces, or partially buried (Merten et al. 2013). Higher gradient streams, often with increased velocities, are also more likely to experience wood fragmentation than lower gradient streams (accumulating reaches). This may at least partially explain why gradient has been negatively associated with instream wood accumulations (Fox and Bolton 2007; Wohl and Cadol 2011). In addition to fragmentation considerations, some tree species are more resistant to decay than others. For example, hardwood trees decay quicker than conifer trees of the same diameter (Bilby et al. 1999).

Linking instream wood accumulation and riparian forest development

Instream wood accumulations are a function of both recruitment and retention. Changes in wood accumulations at a given time are likely a result of differences in background tree mortality rates during different stages of forest development, the intensity and timing of disturbance, and differences in retention based on the size and species of wood. The seminal studies on coarse wood abundance in forests have found the highest accumulations in early and late developmental stages, and lowest in the middle stages (e.g., Spies et al. 1988). This dynamic is often referred to as a U-shaped pattern over time. Spies et al. (1988) found that stands less than 80 years old had moderate levels of downed wood, stands between 80–120 years old had the lowest amount of wood, and stands between 400–500 years old had the highest levels of downed wood. The low point appears to last beyond 120 years, as Franklin et al. (2007) found depressed wood amounts for a 150- to 200-year period of middle succession.

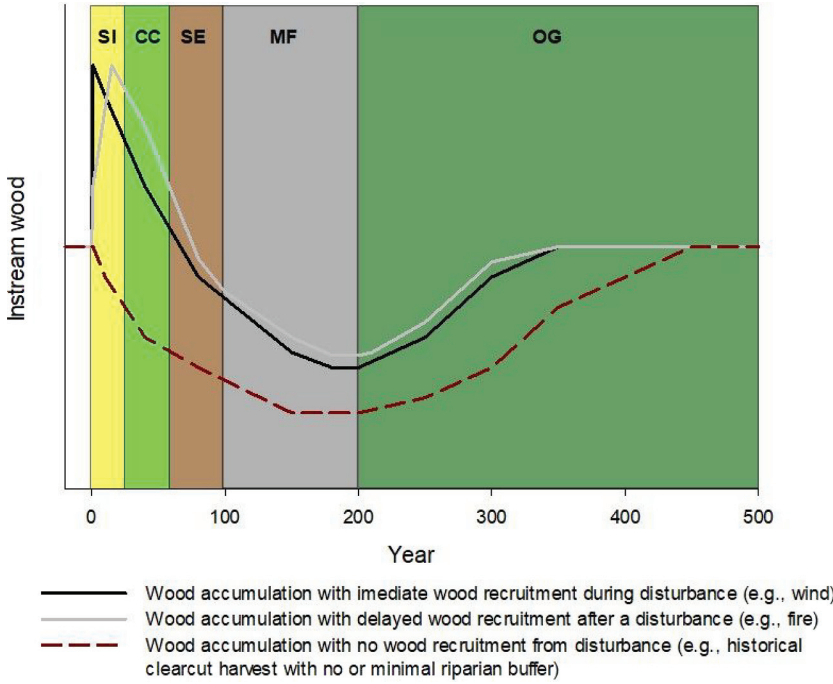
While the U-shaped pattern of downed wood accumulation was first observed in the conifer-dominated forests of the Pacific Northwest, it has also been identified in the eastern Hemlock forests of the Southern Appalachian Mountains (Hedman et al. 1996), the evergreen broad-leaved forests in Eastern China (Yan et al. 2007), and in the balsam fir–black spruce forest of Newfoundland (Sturtevant et al. 1997). To date, most studies providing evidence for this U-shaped pattern of downed wood have focused on wood in terrestrial ecosystems, where processes of decay and fragmentation predominate, rather than transportation. However, a number of studies have, to varying degrees, described this same pattern for instream wood accumulations (e.g., Hedman et al. 1996; Bragg 2000; Benda and Sias 2003). While Acker et al. (2003) found substantial variation within mature and old-growth forests, the site with the least amount of instream wood was found in a mature forest, and the highest amount was found in an old-growth forest. The large variation among their sites was likely due to the amount of low-severity disturbances or the type of process domain at each site.

The mechanisms behind the U-shaped pattern of wood accumulation are likely the result of both changes in recruitment and stream retention associated with forest development. Recruitment following stand-replacing disturbance results in high accumulations of wood in the early successional stages. This material is predominantly "legacy" wood derived from the predisturbance stand, with virtually no input yet from the new stand, which is composed of small sapling trees and nontree vegetation. Most of this legacy wood would be lost from the stream within a few decades (Hyatt and Naiman 2001; King et al. 2013), with some lasting into the mature to old growth stages (Murphy and Koski 1989; Hyatt and Naiman 2001). As riparian forests develop through the canopy closure stage, wood recruitment would likely only come from hardwood and small conifers that, as instream wood, are susceptible to transport, fragmentation, and decay, resulting in a net loss of instream wood (Bilby et al. 1999; Beach and Halpern 2001; Merten et al. 2013). In the stem exclusion stage, wood is recruited primarily from smaller conifer trees that were outcompeted by larger trees (Rot et al. 2000), providing more recruitment than the previous stages but still resulting in a net loss of instream wood. The mature forest stage continues to have limited recruitment of wood from tree mortality (Spies and Franklin 1991), also resulting in a net loss of instream wood. Finally, the old-growth stage of development is sustained by gaps created through low-severity disturbances and tree mortality (Spies and Franklin 1991); the creation of these gaps would recruit large trees to the stream creating a net gain of instream wood with higher longevity in streams.

The U-shaped pattern of wood accumulation can be altered through both disturbance type and frequency. Under long-term disturbance regimes, instream wood is either recruited all at once (e.g., windstorms or volcanic eruptions) or gradually, if trees are killed but remain standing as snags (e.g., fires or insect epidemics). If all trees are inputted into the stream at once, a stream would be subjected to low input levels during the ensuing early to middle stages of forest development (Fig. 3). If a stand-replacing disturbance results in gradual wood recruitment that may result after a large wildfire or insect epidemics, the decrease in wood accumulations may not be as severe and result in a shallower U. Where past forest harvest practices removed the riparian forest, thereby removing current and (or) potential future instream wood inputs, little recruitment resulted from the disturbance, leaving only diminishing pieces of legacy wood creating a deeper U. Collins et al. (2012) found that these reductions in instream wood could drive ecosystems to an altered state of reduced biogeomorphic complexity.

Other changes affecting the shape of the U would derive from the frequency of disturbances. With higher frequencies of low-severity disturbances in the stem exclusion or mature forest stages, there would be an upward shift in the bottom of the U, lessening the depletion of wood (Fig. 4). On the other hand, a relatively short

Fig. 3. The U-shaped distribution of instream wood accumulation under a one-time stand-replacing disturbance with three wood recruitment scenarios (immediate, delayed, and no recruitment). SI, stand initiation; CC, closed canopy; SE, stem exclusion; MF, mature forest; and OG, old growth.



interval between stand-replacing disturbances could delay a site from reaching old-growth conditions and limit wood inputs to smaller pieces. Beechie et al. (2000) identified an increase in instream hardwood (alder) during the hardwood–conifer transition period (20–80 years) in the canopy closure stage that would suggest more of a W-shaped pattern rather than a U-shaped pattern. Thus, while we focus on a U-shape, we also recognize the potential for a W-shaped pattern where the middle increase in wood occurs 20–80 years after stand initiation under this hardwood–conifer pathway. More research is needed on instream wood accumulations during the hardwood–conifer transition period. Overall, the range of disturbance types and frequencies will determine the amount of time and to what degree instream wood accumulations would be subjected to lower wood levels during the middle stages of forest development.

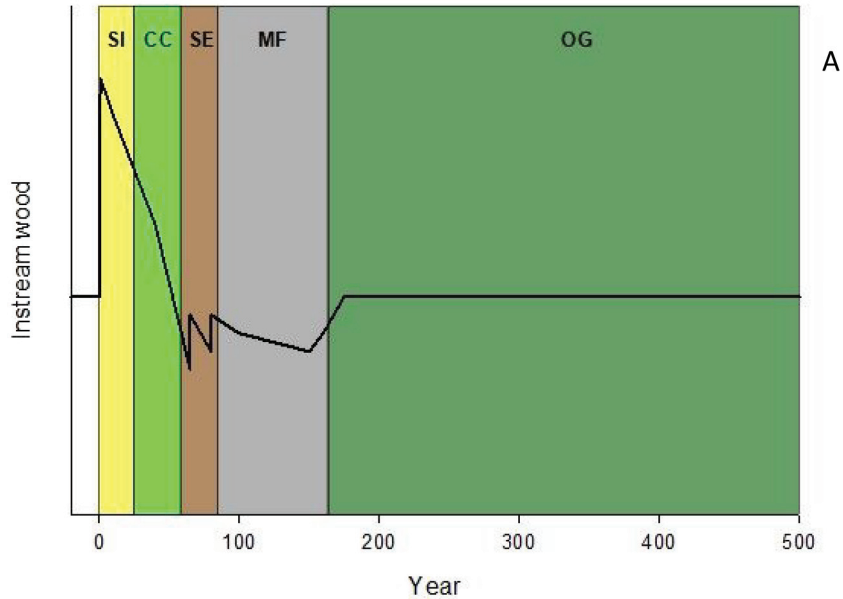
Implications for riparian forest management

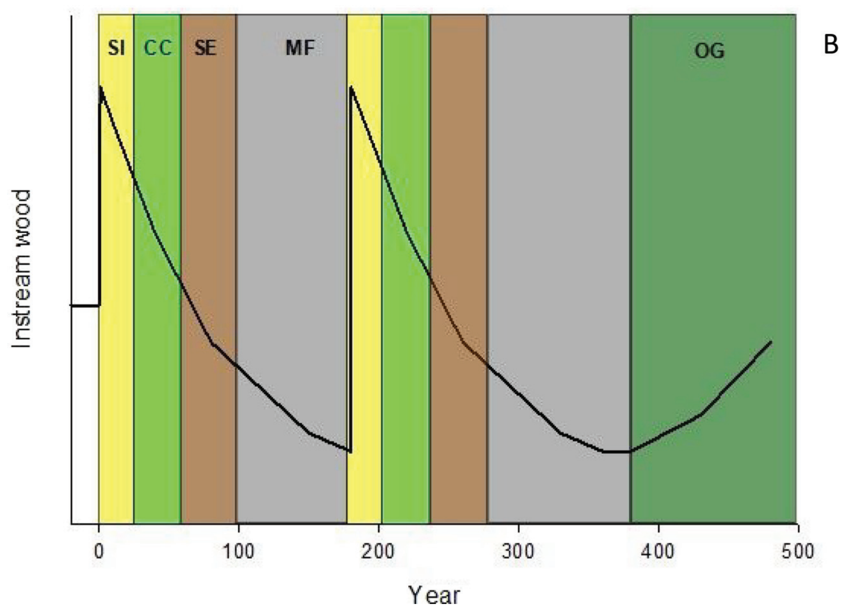
Many managed forests of the Pacific Northwest are in the early to mid-stages of forest development from the intensive and extensive forest harvesting that began during the 20th century. It has been estimated that two-thirds of the land area in the Pacific Northwest at the time of European settlement was in old-growth conditions and that 72% of these forests have been significantly impacted or converted to earlier developmental stages (Strittholt et al. 2006). More recent estimates suggest that late-successional forests covered approximately 70% of the western Cascade Range of Washington state, ranging between ~45%–90% over time, based on the occurrence of large wildfires (Donato et al. 2020). The current landscape contains ~30% late-successional forest, meaning a shift to a regional landscape dominated by the earlier stages of development. As a result, many of these forests and associated streams are experiencing the bottom of the U-shaped pattern of wood accumulation. Furthermore, many of these streams with diminished levels of instream wood also experienced instream wood removal, splash damming, or forest harvest related landslides (that can either deliver wood at the end of a landslide or scour a stream removing wood in the path of the landslide; Cederholm and Reid 1987; Bilby and Ward 1991; Gomi et al. 2001; Roni et al. 2015). These areas not only have less wood due to their current forest developmental stage, but also lack the legacy wood that would lessen the impact of depletion, i.e., a doubling down of wood depletion in some streams (Fig. 3). This likely leads to further declines in fish habitat quality even though most streams are protected through riparian reserves (Naiman 1992; Thomas et al. 2006).

Recovery from instream wood depletions is likely to take significant time, especially in watersheds where instream wood was intentionally removed as a forest management practice (FEMAT 1993; Everest and Reeves 2007). A logical and low-risk way to reach and maintain preharvest levels of instream wood is to allow riparian forests to advance to the old-growth stage and let natural disturbances determine instream wood levels. This has already begun, as most riparian forests adjacent to fish-bearing streams are managed with unharvested riparian reserves to protect streams from the impacts of forest harvest (e.g., increases in stream temperatures, increased sedimentation, and reductions in wood recruitment). The practice of using natural processes of forest development for recovery will eventually restore instream wood levels toward more characteristic ranges, but recovery will take a long time. Murphy and Koski (1989) estimated that instream wood recovery would take more than 250 years in the conifer forests of Alaska. In addition, Stout et al. (2018) estimated that recovery of instream wood levels would take over 250 years in the King River in Australia. The timeline of the U-shaped wood dynamic in Pacific Northwest forests (Spies et al. 1988) suggests a similar multi-century recovery horizon.

The long timeline for natural recovery may create additional risk to the many threatened and endangered species inhabiting these streams. This has led to considerations of using a combination of active and passive restoration rather than passive restoration alone (Reeves et al. 2018). Active restoration options for improving instream wood could include instream wood placements and (or) riparian manipulations (typically through riparian

Fig. 4. Instream wood accumulations with higher than average level of low-severity disturbances with immediate wood recruitment (e.g., wind) (A) and earlier than average stand-replacing disturbance with immediate wood recruitment (B). SI, stand initiation; CC, closed canopy; SE, stem exclusion; MF, mature forest; and OG, old growth.





thinning) to accelerate forest development. Instream wood additions would provide immediate habitat improvements, while thinning could expedite the timeline for developing late-successional stands that sustain higher levels of large wood inputs. While there can be immediate (increased aquatic production) and accelerated (instream wood recruitment) benefits from thinning, the magnitude and long-term ecological effects of habitat creation will likely vary by the tree diameters and amount of wood removed, rather than left onsite, during a thinning operation (Wilzbach et al. 2005; Benda et al. 2016; Reeves et al. 2018).

Yet, given limited resources, where should managers focus active restoration? One prioritization strategy is to compare the diameters of both instream wood levels and standing riparian trees to help determine the need for recovery (Fig. 2). If riparian trees are smaller than the diameter of wood in the stream reach, instream wood conditions are not likely to improve (i.e., recruit more large pieces) in the near future. On the other hand, if riparian trees are larger than the wood in the stream, the volume of instream wood is likely to increase over the next few decades. Another prioritization question is whether to focus active restoration on sites that are likely to recover sooner (e.g., late in the stem exclusion or early in the mature forest development stages) or in areas that are likely to see further reductions in instream wood accumulations (e.g., early or middle part of stem exclusion). Adding wood to an area that is likely to recover within a couple of decades may help reach sustainable levels quicker. On the other hand, working in areas that are likely to decline in habitat quality for several decades may prevent further salmon or other priority fish species declines. However, there has been much debate on whether wood additions have been successful for restoring stream functions and salmonid populations (Stewart et al. 2009; Jones et al. 2014; Roni et al. 2015). To ensure a greater chance of successful restoration, process domains should also be considered when prioritizing active restoration. Focusing restoration on accumulating reaches would likely be more successful than working in transporting reaches. For small streams, for which smaller wood can provide pool-forming functions, thinning mid-successional stands may only serve to reduce the population of potential logs (Beechie et al. 2000), unless trees are directly tipped into and left in streams. In contrast, near larger streams for which larger wood is needed to form pools, thinning may be effective in accelerating the growth and input of larger-diameter trees and logs (Beechie et al. 2000).

Another consideration in whether, and where, to prioritize active over passive restoration is riparian forest site context and potential ancillary impacts. Any silvicultural entry has potential impacts to a site, including skidding or yarding corridors, soil disturbance or compaction, and damage to small trees and understory vegetation. Riparian sites are generally considered more susceptible to many of these impacts than are uplands. However, even riparian sites vary in susceptibility, and a given site's context, such as soil condition or relative likelihood of landslides, must be weighed alongside the relevant stream (and salmonid population) condition and restoration need. Overall, more work is needed to determine when it is better to actively improve habitat above current levels, specifically in what combinations of forest development, site, stream, and fish population conditions.

Further complicating decisions on active versus passive restoration of streams is the changing climate. While the frequency and intensity of future wind events is uncertain, area burned is projected to increase as summers become warmer and drier across moist forests in the Pacific Northwest (Littell et al. 2010; Rogers et al. 2011; Halofsky et al. 2018). Landslide risk may also increase in the fall, winter, and spring if the amount and duration of snowpack declines and the frequency and intensity of heavy rain events increases (Mauger et al. 2015). Given wildfire and landslide projections, it is likely that the amount of instream wood will increase as these disturbances become more frequent. Yet, the unknown timing and location of such disturbances, in combination with the large stream network area still lacking wood and containing primarily younger-aged forests, all lend support to a possible role for active restoration in promoting fish habitat under a less certain future.

Conclusions

Forest development plays an important role in determining the conditions of instream fish habitat. This simple statement is all too often overlooked when evaluating steam recovery. A better understanding of the mechanisms through which forest succession and disturbance interact with instream wood dynamics will improve our assessment of current stream habitat conditions and the timeline for their recovery. Since many of the riparian forests of the Pacific Northwest (and similar regions globally) are currently in the early stages of forest development, they are still going through a period with declining instream wood levels as a result of past forest practices. As such, some restoration activities may only be preventing further declines rather than improving current conditions. Despite the widely used no-touch riparian reserves, a form of passive restoration, the decline of instream wood will likely continue to occur until riparian forests are over 200 years old or until naturally disturbed. Given this likely continued deterioration of instream wood accumulations across the region, conducting active riparian restoration where feasible and consistent with other management objectives may be advisable to accelerate recovery and prevent further declines in fish populations.

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