The floodplain large-wood cycle hypothesis: A mechanism for the physical and biotic structuring of temperate forested alluvial valleys in the North Pacific coastal ecoregion

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ABSTRACT

A 'floodplain large-wood cycle' is hypothesized as a mechanism for generating landforms and influencing river dynamics in ways that structure and maintain riparian and aquatic ecosystems of forested alluvial river valleys of the Pacific coastal temperate rainforest of North America. In the cycle, pieces of wood large enough to resist fluvial transport and remain in river channels initiate and stabilize wood jams, which in turn create alluvial patches and protect them from erosion. These stable patches provide sites for trees to mature over hundreds of years in river valleys where the average cycle of floodplain turnover is much briefer, thus providing a future source of large wood and reinforcing the cycle. Different tree species can function in the floodplain large-wood cycle in different ecological regions, in different river valleys within regions, and within individual river valleys in which forest composition changes through time. The cycle promotes a physically complex, biodiverse, and self-reinforcing state. Conversely, loss of large trees from the system drives landforms and ecosystems toward an alternate stable state of diminished biogeomorphic complexity. Reestablishing large trees is thus necessary to restore such rivers. Although interactions and mechanisms may differ between biomes and in larger or smaller rivers, available evidence suggests that large riparian trees may have similarly fundamental roles in the physical and biotic structuring of river valleys elsewhere in the temperate zone.

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1. Introduction

Biota structure their own physical environments in such diverse systems as coral reefs, kelp forests, and prairies (Jones et al., 1997). Such feedbacks are increasingly documented between the forms and dynamics of rivers and plants (Bennett and Simon, 2004; Corenblit et al., 2007) and animals (e.g., Naiman et al., 2000; Beschta and Ripple, 2011). In particular, recent studies show how large riparian trees and fluvial wood in temperate forest river valleys in North America, Australia, New Zealand, and Europe interact with water and sediment in structuring rivers and floodplains in forested environments (Gregory et al., 2003).

In the temperate Pacific coast evergreen forest biome of North America (Fig. 1), hereafter referred to as the 'Pacific coastal ecoregion,' recent studies document feedbacks between forest structure and ecology, fluvial geomorphic processes and landforms, and aquatic ecology. Dominant tree species in the conifer and mixed conifer-deciduous river valley forests (Table 1) grow to 1–4 m in diameter and 60 m high (Franklin and Dyrness, 1973; Burns and Honkala, 1990) and play

prominent physical and biotic roles (Fig. 2). Once delivered to rivers and streams, wood from the largest trees directly influences fluvial processes and landforms; and the effects of logs and stable fluvial wood jams have been shown to be particularly important (Gurnell et al., 2002; Montgomery et al., 2003). These processes and landforms, in turn, play a role in structuring terrestrial and aquatic ecosystems.

An understanding of how large wood affects fluvial processes and riverine ecosystems in the Pacific coastal ecoregion has emerged in largely separate bodies of research. Synthesizing these into a hypothesized model of biophysical landscape development would contribute to emerging theory on coupled physical-ecological systems (e.g., Stallins, 2006; Renschler et al., 2007) and facilitate identifying gaps in understanding. It also provides a way to generalize research results from rivers in different ecoregions and to examine how factors such as differences in forest composition and channel dimensions affect the role of wood in shaping valley-bottom processes. Formally hypothesizing a model also has potentially considerable practical importance for river restoration. At least $1B USD is spent annually on stream restoration in the United States (Bernhardt et al., 2005). In the Pacific Northwest, many restoration projects focus on use of artificial wood jams and forest planting as part of a strategy implicitly premised on a model of biophysical landscape development. However, this model has not been explicitly formulated and

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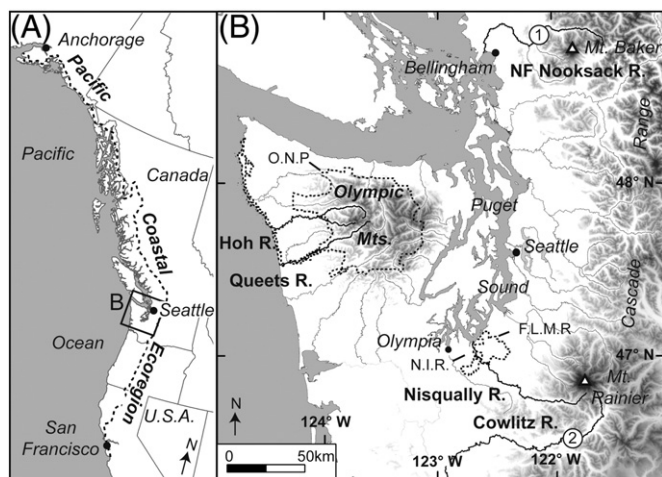*E-mail address:* bcollins@uw.edu (B.D. Collins).

Fig. 1. (A) Location of the temperate Pacific coastal ecoregion of North America. (B) The Queets and Hoh Rivers are largely protected within Olympic National Park (ONP). The lower Nisqually River is protected by inclusion in the Fort Lewis Military Reservation (FLMR) and the Nisqually Indian Reservation (NIR). See Table 1 for basin and discharge characteristics.

doing so provides an opportunity for current restoration efforts to serve as controlled field experiments for testing and refining the model.

Here we synthesize studies from the geomorphological and ecological literature with additional data and propose a 'floodplain large-wood cycle' as a mechanism for the development of fluvial landforms and forest patch dynamics in which the growth of large riparian trees leads to a self-reinforcing state. The model predicts that removing these large trees simplifies fluvial landforms and dynamics and thereby reduces the complexity of associated communities and ecosystems. That the presence or absence of certain species or sizes of trees could cause divergent trajectories toward alternate, self-reinforcing states has fundamental implications for river restoration.

2. Rivers, forests, and wood in alluvial valleys of the Pacific coastal ecoregion

The results of three research topics are summarized below: wood transport and wood budgeting (Hyatt and Naiman, 2001; Latterell and Naiman, 2007); wood jams, channel dynamics, and landform development (Abbe and Montgomery, 1996; Collins and Montgomery, 2002; Abbe and Montgomery, 2003; O'Connor et al., 2003; Brummer et al., 2006; Montgomery and Abbe, 2006); and the role of dead wood in forest development (Fetherston et al., 1995; Balian and Naiman, 2005; Latterell et al., 2006; Van Pelt et al., 2006; Latterell and Naiman, 2007).

2.1. Wood sources and residence time

Trees fall into rivers as migrating channels eat into floodplains, terraces, or valley sides. Latterell and Naiman (2007) found that bank erosion associated with lateral erosion by the Queets River contributed 82% of large wood > 1.0 m in diameter. Most (76%) large wood was recruited from mature forest patches (72% from standing trees and 4% from buried wood) or from remnant logs previously deposited on pioneer bars or developing floodplains (18%; Table 1 in Latterell and Naiman, 2007).

Some of this fluvial wood is exported from the system immediately, but most deposits in the river, on river bars, or in the floodplain forest. Deposited wood is eventually reentrained by lateral channel erosion, to be redeposited, remain stable for a period of time, and then become reentrained and redeposited in downstream locations prior to disintegrating or export. Most of this deposited wood remains in the river valley for only a few decades before disintegrating or being exported. Latterell and Naiman (2007) estimated that 50% of large logs deposited in the Queets River are transported downriver within five years. Hyatt and Naiman (2001) estimated that fluvial wood has a mean residence time of 30 years; conifer species [Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western redcedar (*Thuja plicata*)] were depleted more slowly than hardwood species [red alder (*Alnus rubra*), black cottonwood (*Populus balsamifera trichocarpa*), and bigleaf maple (*Acer macrophyllum*)].

However, some wood remains in the system for long periods. Wood can remain in streams for at least 200 years in coastal redwood forest (Keller and Tally, 1979), and can remain buried in wood jams for more than a millennium; wood found buried in jams in the Queets River was up to 1400 years old (Hyatt and Naiman, 2001; Montgomery and Abbe, 2006). Of particular importance in explaining this long residence time are pieces of wood so large that they remain lodged in the river channel where they can catalyze a number of physical and ecological processes and effects.

2.2. 'Key pieces' and wood jams

Wood large enough to remain stable (i.e., resist re-entrainment by the river) in the active channel can function as a stable 'key piece' (e.g., Keller and Swanson, 1979; Nakamura and Swanson, 1993; Abbe and Montgomery, 1996) by initiating and stabilizing a wood jam (Fig. 2), which forms as smaller pieces accumulate upstream on the stable key piece or pieces. Stable key pieces that initiate jams are generally large diameter, long pieces of wood, typically with an attached root ball (Abbe and Montgomery, 1996; Braudrick and Grant, 2000; Abbe and Montgomery, 2003), derived from the largest valley bottom trees (e.g., Collins and Montgomery, 2002). For example, two studies of fluvial wood in the Queets River found key piece basal diameters averaged 1.4 m ($n = 61$; Fetherston, 2005) and 1.8 m (range = 0.76 to 3.4 m,

Table 1
Characteristics of the Queets and Nisqually Rivers in western Washington State.

Region	River	Drainage area (at USGS gage, km²)	Mean annual discharge at USGS gage, m³s⁻¹	Maximum discharge of record, m³s⁻¹	Dominant large-diameter species [a]
Western Olympic Mountains (WA)	Queets	1190 (1152[b])	124	3766	*Picea sitchensis* *Tsuga heterophylla* *Acer macrophyllum* *Populus balsamifera trichocarpa*
Western Cascade Mountains (WA)	Nisqually	1890 (1339[c])	37	1416	*Pseudotsuga menziesii* *Thuja plicata* *Acer macrophyllum* *Populus balsamifera trichocarpa*

[a] Sources: Queets River, Van Pelt et al. (2006); Nisqually River, Collins and Montgomery (2002).
[b] Gage 12040500 (50-year record), river kilometer 12.
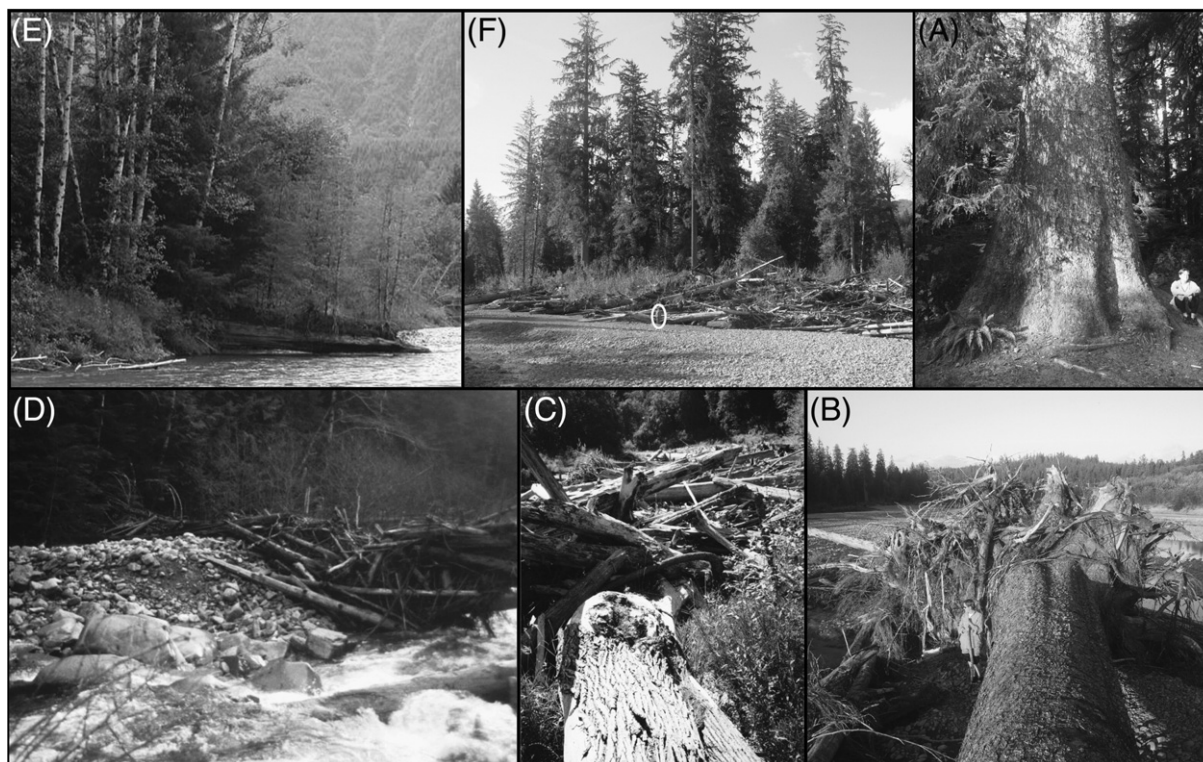[c] Gage 12089500 (49-year record), river kilometer 35.

Fig. 2. In river valleys of the Pacific coastal temperate forest, trees regenerate on alluvium and on dead wood. Conifer species (A; here a Sitka spruce, *Picea sitchensis,* in the South Fork Hoh River valley) commonly grow to diameters up to 4 m. These large trees fall onto the forest floor, creating sites for conifer establishment, or if recruited into the river, become large fluvial wood, which may remain in place or be transported and redeposit in the river. Wood pieces large enough to remain stable, typically also having large rootballs (B; a *P. sitchensis* log in the Queets River), can function as a "key piece" by instigating wood jams (C; a black cottonwood, *Populus trichocarpa,* functions as a key piece in the Nisqually River by instigating the accretion of a wood jam extending 260 m upstream). These jams can accrete sediment and form elevated alluvial patches (D; stream in western Cascade Range) that become sites of forest colonization (E; on this island in the Hoh River conifers in photo right are growing on a "nurse log" formerly buried in alluvium and to photo left red alder, *Alnus rubra*, regenerate on alluvium). These patches can eventually become islands that resist fluvial erosion for several hundreds of years (F; depicted is the upstream end of a forested island surrounded by active channel of the South Fork Hoh River). The longevity of these patches, which are embedded in a patchwork of considerably younger floodplain forest and channel surfaces, allows conifers to mature (A; tree is located on the forested island shown in the previous panel). Each of these stages can be found in each river.

$n = 287$; Montgomery and Abbe, 2006). In the Nisqually River (Fig. 1) of Washington's western Cascade Range, 79 key members in 38 wood jams averaged 1.0 m in diameter; in a 2000 field sample of the Nisqually valley forest, only 1% of 1275 trees exceeded 1.0 m in diameter (Collins and Montgomery, 2002).

2.3. Wood jam 'hard points'

Brummer et al. (2006) summarized data from several rivers that showed how jams, by creating locally lower shear stresses, can cause sediment to accrete either downstream or upstream, creating alluvial patches elevated 1 to >4 m above the surrounding floodplain (Fig. 2E). These elevated patches, either singly or by coalescing with other jam-induced patches, become nuclei around which islands form (Fetherston et al., 1995; Abbe and Montgomery, 1996; O'Connor et al., 2003). These elevated alluvial patches function as stable 'hard points' (Figs. 2G and 3B) that can resist future river erosion for up to many hundred years (Abbe and Montgomery, 2003; O'Connor et al., 2003; Fetherston, 2005; Latterell et al., 2006; Montgomery and Abbe, 2006; Van Pelt et al., 2006).

These patches contribute to a floodplain topography characterized by a diversity of elevations, termed a 'patchwork floodplain' (Montgomery and Abbe, 2006) (Fig. 4). Such floodplain topography, and the mechanisms that create it, have received far less study than mechanisms of lateral channel erosion, bedload sediment deposition below the bankfull stage, and overbank sedimentation, and the associated processes of meander migration and avulsion that produce scroll-bar topography, oxbows, and abandoned channels (Fig. 3).

Stable topographic patches are augmented by wood and wood jams that accumulate on, and protect from erosion, the upstream side of the patch (e.g., Fig. 2F). These stable patches can divert flow, split it into an anastomosing river pattern (Fig. 3B), and cause and mediate channel-switching avulsions (Sedell and Froggatt, 1984; Harwood and Brown, 1993; Nanson and Knighton, 1996; Collins and Montgomery, 2002; Abbe and Montgomery, 2003; Jeffries et al., 2003; O'Connor et al., 2003; Wohl, 2011). This morphological complexity translates into greater hydrologic diversity, contributing to diverse surface water environments, degrees of connectivity with the main channel, and development of spatially variable surface-subsurface hydrologic exchange (Malard et al., 2002).

Retrospective studies of channel morphology in rivers from which large wood has been removed from the system provide additional, indirect evidence in support of these effects. Numerous examples are found throughout the region in which riparian logging and wood removal coincides in time with the transformation of a multiple-channel system characterized by forested islands to a much wider, braided channel (e.g., Millar, 2000) (Figs. 5 and 3C). However, temporal correlation cannot illuminate the relative importance of direct wood removal, the loss of wood recruitment from the riparian forest, or the loss of root strength from riparian deforestation.

Removing wood has been shown to establish completely different river-forming processes (Abbe et al., 2003). Archival studies (e.g., Sedell and Froggatt, 1984; Collins et al., 2002) and comparison of relatively undisturbed systems with systems from which large trees have been removed demonstrate that channel pattern can shift from anastomosing to braided or meandering, simplifying the structure and abundance of physical habitats and widening the active channel.
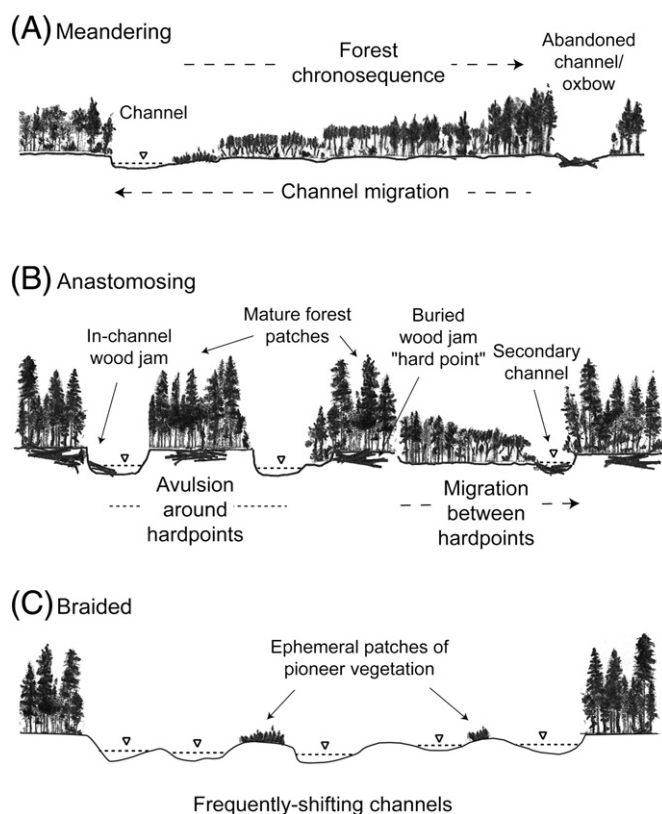
Fig. 3. Cross-sectional views of three idealized models of floodplain landform and forest development in moderate-gradient river valleys of the North Pacific coastal ecosystem. (A) In a system dominated by the lateral migration of channel meanders, erosion at the outside of bends and deposition on the inside of bends, and eventual meander cutoffs, result in scroll-bar topography, oxbow ponds, and sloughs associated with channel avulsion. Forest succession initiated on newly accreted sediments and continued lateral migration leads to a chronosequence of surface and forest ages. The maximum forest age is limited by the rate at which the river meanders across the floodplain. (B) Stable alluvial patches instigated by wood jams can resist lateral channel erosion for hundreds of years, providing sites for conifer forests to establish and mature. River channels avulse around stable patches and migrate [as in panel (A)] between patches. Maximum forest age is limited by patch stability. The result is a patchwork floodplain of multiple channels and elevations and greater diversity in forest patch age. (C) Braided rivers are characterized by multiple, frequently-shifting channels. Mature forest vegetation is restricted to the channel margins. Ephemeral patches of pioneer vegetation may grow on in-channel bars.

2.4. Forest patch structure

These wood-catalyzed mechanisms for forming floodplain landforms and influencing channel dynamics can, in turn, shape patterns of forest development. In floodplains dominated by laterally eroding rivers, forests initiate on newly accreted sediments on the inside of outward-migrating meander bends. Continued lateral accretion leaves behind a chronosequence of surfaces and associated forests (Fig. 3A). Later modification by avulsion and lateral erosion creates a patchwork of different age surfaces and forests, but the maximum patch age is limited by the rate at which a river migrates across its floodplain.

In contrast, on floodplains having stable hard points, the maximum forest patch age is limited by the length of time such patches can resist erosion. Because they can resist erosion for centuries, stable patches function as riparian refugia where forests can mature (Fetherston et al., 1995; Abbe and Montgomery, 1996; Latterell et al., 2006; Van Pelt et al., 2006) and grow trees much older than the surrounding floodplain matrix (Abbe and Montgomery, 1996; Fetherston, 2005; Latterell et al., 2006) (Figs. 3B and 4). The persistence for up to several hundred years of floodplain forest patches created by stable log jams makes these stable patches a primary source of wood large enough to function as future key pieces. For example, Latterell et al. (2006) recorded an average of 35 trees per hectare that could potentially contribute key pieces with a

diameter >1.0 m from 'mature fluvial terraces,' their term that we equate with elevated alluvial patches formed by logjam-induced aggradation, *sensu* Montgomery and Abbe (2006); they recorded none from floodplain or pioneer bar surfaces.

The longevity of such patches can be several times greater than a floodplain's erosional turnover rate. For example, in the Queets River, *P. sitchensis* is the dominant key piece forming species, followed in importance by *P. menziesii* and *T. heterophylla* (Fetherston, 2005). There, trees require at least 100–200 years to grow large enough to create stable key pieces (Fetherston, 2005; Montgomery and Abbe, 2006). Yet the mean disturbance interval, defined by the recurrence interval for channel migration across the Queets floodplain, is approximately 100 years (O'Connor et al., 2003; Montgomery and Abbe, 2006).

The net result is greater diversity in forest patch age ['forest floodplain mosaic' (Fetherston et al., 1995), 'dynamic patch mosaic' (Latterell et al., 2006)]. By creating conditions favorable for growth of large trees, stable forest islands provide a source for wood large enough to initiate future stable jams and erosion-resistant forest patches, creating a positive feedback for producing large trees (Fetherston et al., 1995; Abbe and Montgomery, 1996; O'Connor et al., 2003; Latterell et al., 2006; Montgomery and Abbe, 2006). The topographic, hydrologic, and forest patch diversity translate directly or indirectly into greater biotic diversity, nutrient storage and availability, and quantity and diversity of habitats (Table 3).

3. The "floodplain large-wood cycle"

As a mechanism for contributing to the ecological and geomorphological complexity of forested river valleys of the Pacific coastal ecoregion, we hypothesize the existence of a "floodplain large-wood cycle" (Fig. 6). The floodplain large-wood cycle concept integrates the research, summarized above, on the role of wood in structuring fluvial processes and landforms with research on riparian forest development, largely from the Queets and Nisqually Rivers, supplemented by studies from other rivers (Tables 2 and 3).

The floodplain large-wood cycle (Fig. 6) begins with logs that are large enough to remain stable within the active channel. These logs initiate wood jams that grow into stable protected patches, where trees colonize in a low-shear zone, often elevated by sediment deposition induced by the jam. Pioneer deciduous trees colonize bare mineral soil, and the key pieces of jams act as nursery logs for trees selectively colonized by conifers (Fetherston, 2005). The presence of stable wood jams favors maturation of all large tree species, making the trees that grow on these stable patches a primary source of wood large enough to function as future key pieces. The amount of wood from mortality and tree fall stored on the forest floor within these patches increases with forest stand age (Latterell et al., 2006; Van Pelt et al., 2006), so that stable island patches also "store" potential key pieces on the forest floor. Stable forest patches instigated or protected by jams generate mature forests that can produce wood pieces large enough to function as key pieces, thus perpetuating the cycle and making it tend toward a self-reinforcing state.

By creating stable alluvial patches, or "hard points," and favoring the development of mature forest stands (Fig. 3B), the floodplain large-wood cycle functions in tandem with lateral river migration and meander cutoff avulsions (Fig. 3A). These latter processes create alluvial patches (bars or abandoned channels) on which forest succession also takes place (Fig. 6). However, unlike the trees in the stable patches created by the floodplain large-wood cycle, the rate at which the river migrates across the valley limits the maximum forest patch age and thus the age and size of trees and the amount of fluvial wood large enough to remain stable in the river. The erosional process of channel migration is integral to jam development because it delivers to the river the wood that forms the bulk of wood jams by accreting onto stable key pieces (Fig. 6).

Fluvial wood not large enough to stabilize in channels, or large enough to stabilize but that does not instigate stable jams, also influences forest development. Wood too small to remain stable in the river
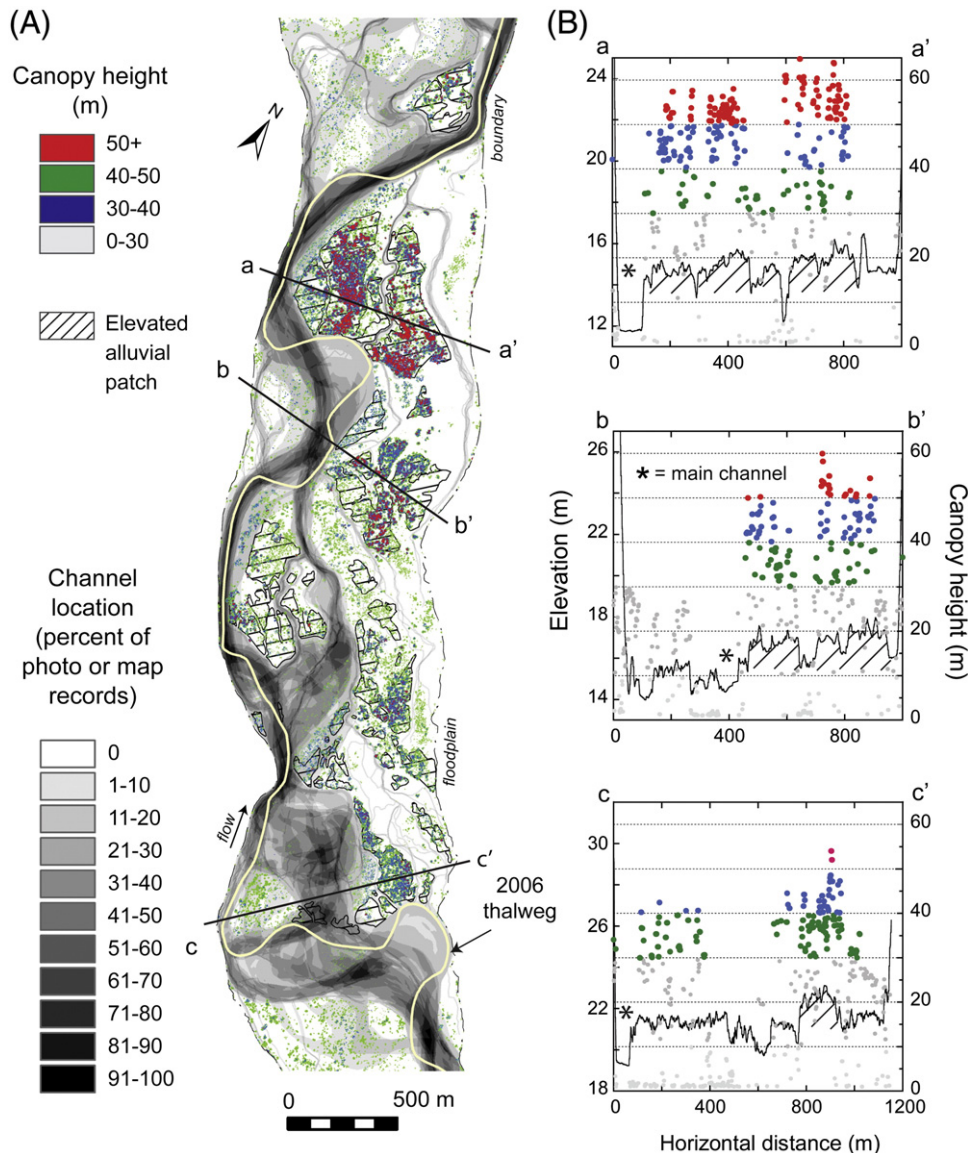
Fig. 4. Channel occupation history, valley topography, and forest canopy height, Nisqually River floodplain, river kilometers 9–15. Map shows (1) the percent of years the active channel (area within bankfull limit including low flow channel and gravel bars) has occupied locations on the floodplain; from 17 sets of aerial photos and maps from 1853 to 2006; (2) elevated alluvial patches, most of which have resisted lateral erosion since at least 1853; and (3) tree heights [tree height classes in panel (B) correspond to colors in panel (A)], measured as the difference between first and last return in lidar data. Three transects of ground elevation and canopy height show the topography associated with multiple channels and elevated alluvial patches, and the ground elevations associated with groves of tall tree. The river appears to have been deflected by or to split around these stable patches. Patches of tall trees are also generally found on these elevated patches. An exception is the patch on the left-hand side of transect c–c′; here trees have established in the period between 1873 and 1933 and have since been protected by flow-deflecting wood jams.

deposits on alluvial patches as individual pieces or transient accumulations, promoting tree regeneration by accreting fine sediments and additional wood. For species that preferentially regenerate on wood, wood pieces and unstable accumulations can serve as nurseries for seedlings. For example, Fetherston (2005) found that 99% of *P. sitchensis* and *T. heterophylla* seedlings regenerated on fluvially organized wood in a 25-ha area of the Queets River floodplain; large percentages of *P. sitchensis* and *T. heterophylla* seedlings have also been found to grow on downed logs in coastal Olympic Peninsula forests (McKee et al., 1982; Stolnack and Naiman, 2010).

In regions where the dominant large tree species are conifers that preferentially regenerate on wood, the cycle includes a positive reinforcement for regeneration of conifers and development of large trees (Fig. 6). Jams can also favor regeneration and growth of *P. menziesii*, which can colonize moist cobble substrates in abandoned channels protected from annual inundation (Van Pelt et al., 2006) and protected from disturbance by log jams.

Different trees species can function in the floodplain large-wood cycle in different ecological regions. Tree life history traits such as dimensions (e.g., maximum height, maximum diameter, growth form), life span, growth rates, shade tolerance, flood tolerance, and reproductive strategies can affect the species' role in the cycle between rivers within a region, between regions, and with changes in forest composition through time.

Because channel depth and width largely determine the size of wood that will remain stable within a channel (Abbe and Montgomery, 1996, 2003), the dimensions of trees relative to dimensions of particular rivers create river-specific differences in how a species functions in the floodplain large-wood cycle. For example, in the Queets River in a study of key, racked, and loose pieces in 32 jams, the ratio of tree bole diameter (D_b) to bankfull depth (h) of $D_b/h > 0.5$ distinguishes key members from other pieces (Abbe and Montgomery, 2003). Ratios of wood length (L) to bankfull width (w) for key members vary from $L/w > 0.5$ for channels < 50 m, with the lower limit approaching
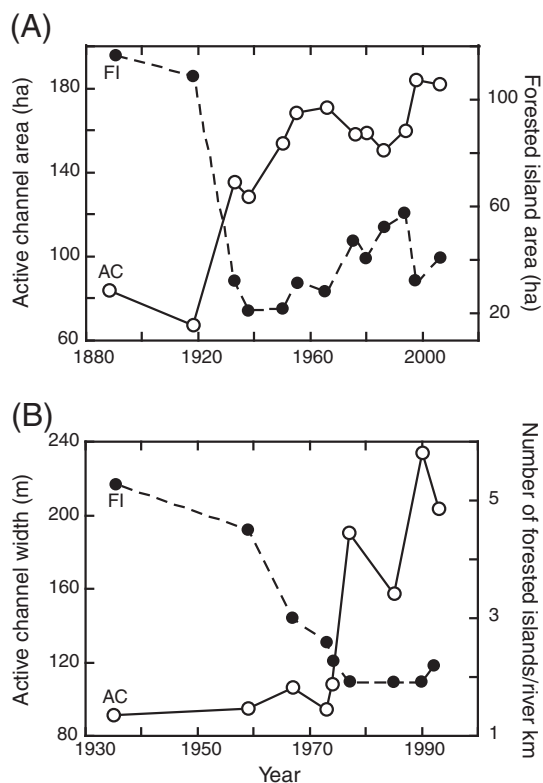
Fig. 5. Channel change through time in two river valleys after floodplain logging and in-channel wood removal. (A) Change in area of active channel and forested islands, 1888–1998, in the North Fork Nooksack River, Washington (Fig. 1), river kilometers 60–65 (point '1,' Fig. 1). Forest was logged between 1918 and 1933. Forest patches since then have been ephemeral, generally not persisting more than 10–20 years. (B) Changes in channel width and forested island frequency in the Cowlitz River, upstream of Packwood, Washington, river kilometers 205–209 (point '2' in Fig. 1). The majority of forest islands appear to nucleate around stable wood jams. In 1935–1995, the channel more than doubled in width, and the number of forested islands declined by more than half. Possible mechanisms include timber removal, which significantly reduced recruitment of the largest trees, and active removal of in-stream wood. [Sources: panel (A), Collins unpublished data; panel (B), modified from Abbe et al., 1997].

one in smaller channels and zero in larger channels. Shape also influences the stability of wood within channels: attached rootballs effectively increase D_b/h (Abbe and Montgomery, 2003). Species-specific density and channel substrate also influence wood stability (Abbe et al., 2003). Variation in growth rate between and within ecological regions and valley-specific channel migration and avulsion rates can further influence the relative role of different species in the cycle.

Contrasts between the Nisqually River (in the Puget Lowland) and the Queets River (in the western Olympic Peninsula) (see Table 1) illustrate how differences in reproduction, growth rates, and successional characteristics of dominant large tree species, in combination with river dimensions and land use changes, affect how elements of the floodplain large-wood cycle differ in importance between rivers and through time. In the Queets River, *P. sitchensis* is the dominant key-piece-forming species [with lesser numbers of *P. menziesii* and *T. heterophylla* (Fetherston, 2005)], and trees require 100–200 years to grow large enough to create stable key pieces (Fetherston, 2005; Montgomery and Abbe, 2006). In coastal humid temperate valley forests, *P. sitchensis* reproduces primarily on large wood (McKee et al., 1982; Fetherston, 2005). Because the average floodplain turnover is less than the length of time necessary for trees to grow large enough for the wood they contribute to the river to function as key pieces, the capability of *P. sitchensis* to produce wood large enough to function as key pieces makes it dependent on stable forest patches created by the floodplain large-wood cycle.

Table 2
Direct effects of the floodplain large-wood cycle on physical processes.

Trait	Process	Sources
Pools	Wood pieces and wood jams (instigated by large "key pieces") increase the number and depth of pools in a river.	Montgomery et al. (1995), Abbe and Montgomery (1996), Beechie and Sibley (1997), Collins et al. (2002)
Floodplain inundation	Local aggradation behind stable logjams raises the bed-surface elevation of channels and increases the potential for floodplain inundation.	Abbe and Montgomery (1996), Buffington et al. (2002), Brooks et al. (2003), Brummer et al. (2006)
Island formation	Fluvial wood and wood jams cause islands to form by inducing sediment deposition, providing sites for plant colonization, and providing regrowth from living wood.	Abbe and Montgomery (1996, 2003), Gurnell and Petts (2002)
Forest island 'hard points'	Wood jams create and protect land patches that resist fluvial erosion for up to hundreds of years. These patches provide sites for forest trees to grow to ages exceeding the recurrence interval for channel migration across the floodplain.	Fetherston et al. (1995), Abbe and Montgomery (1996, 2003), O'Connor et al. (2003), Montgomery and Abbe (2006)
Anastomosing channel pattern	Wood jams create an anastomosing channel pattern by splitting and diverting flow and by mediating avulsion frequency.	Sedell and Froggatt (1984), Harwood and Brown (1993), Collins and Montgomery (2002), Abbe and Montgomery (2003), Sear et al. (2010), Wohl (2011)
Maintain perennial secondary channels	Wood jams at upstream end of secondary channels inhibit main-channel avulsion and maintain flow into the secondary channel.	Sedell and Froggatt (1984), Collins and Montgomery (2002), Montgomery and Abbe (2006)
Mediated channel avulsion	Wood jams mediate (both cause and limit) channel avulsion.	Collins and Montgomery (2002), Abbe and Montgomery (2003)
Valley-scale water, sediment, and wood routing	Large wood jams expand the area exposed to fluvial flooding, sediment, and wood and subject to the creation and maintenance of wetlands.	Triska (1984), Collins et al. (2002), Brooks et al. (2003), Abbe and Montgomery (2003)

In the Nisqually River, by contrast, the broadleaf deciduous black cottonwood (*P. trichocarpa*) is the dominant key piece in jams (Collins and Montgomery, 2002). It reproduces on moist, bare, unshaded mineral substrates (Scott et al., 1996). The functional size of key pieces (diameter on average 1.0 m) is less in the smaller Nisqually River than in the Queets River, and *P. trichocarpa* can attain this size within 80 years (Collins and Montgomery, 2002), making the production of potential key pieces from *P. trichocarpa* in the Nisqually River less dependent on stable forest patches. However, public land survey records show that, before selective logging of conifers in the Nisqually River forest in the late nineteenth century, *T. plicata* and *P. menziesii* were more common than they are today (Collins and Montgomery, 2002) and presumably they accounted for a larger proportion of key pieces than now. In the Nisqually River valley forest, these two conifer species grow to 1 m diameter in 220 years and 150 years, respectively (Collins and Montgomery, 2002), making them more dependent on stable patches. At present, *P. trichocarpa* plays an indirect role in the maturation of *T. plicata* and *P. menziesii* by creating key pieces for wood jams, which trap wood on which conifers can establish, and by inducing deposition of alluvial wedges, which can become protected, elevated surfaces on which conifers can mature. If

Table 3
Direct and indirect effects of the floodplain large-wood cycle on ecosystem diversity and productivity.

Trait	Process	Sources
Biodiversity		
Forest patch age diversity		Fetherston et al. (1995), Latterell et al. (2006)
Biotic diversity associated with wooded islands	Greater biotic diversity and biocomplexity is associated with wooded island reaches.	Fetherston et al. (1995), Brown (1997), Ward et al. (1999), Arscott et al. (2000), Gurnell et al. (2000), Gurnell and Petts (2002)
Biodiversity associated with wood	Aquatic wood and wood accumulations create unique substrate or habitat; provides source of nutrients and energy; creates habitat unit complexity; creates a diversity of habitats; retains organic matter and sediment.	Gurnell et al. (2000), Wondzell and Bisson (2003)
Physical salmonid habitat	Wood jams provide more and deeper pools, cover, and trap spawning gravels; by influencing development of multiple primary and secondary channels, jams create more diverse habitats.	See (Table 1)
Productivity		
Forest productivity	Mature forest patches within floodplain contribute disproportionately large fraction of total annual tree production.	Balian and Naiman (2005)
Biogeochemical processes		
Aquatic nutrient retention	Large wood stabilizes wood jams, which increases retention and extends the residence time of organic material in alluvial valleys. Wood retains particulate organic matter and carcasses of anadromous fish.	Cederholm et al. (1989), Bilby et al. (1996), Collins et al. (2002), Bilby (2003)
Floodplain carbon storage	Wood jams stranded in (and incorporated into) the floodplain by channel migration provide a carbon sink and can remain in floodplains for hundreds of years; large wood can endure for an order of magnitude longer in freshwater–riparian ecosystems than in comparable above-ground terrestrial ecosystems. Backwater associated with wood jams stores carbon.	Murphy and Koski (1989), Nanson et al. (1995), Gippel et al. (1996), Hyatt and Naiman (2001), Guyette et al. (2002), Montgomery and Abbe (2006)
Supply of carbon to hyporheic foodweb and hyporheic invertebrates	Decomposing wood jams stranded in floodplain and stored in backwater behind wood jams provide carbon to hyporheic zone. Wood is associated with higher levels of hyporheic invertebrates.	Coe (2001), Crenshaw et al. (2002), Hester and Doyle (2008)
Nutrient uptake	Wood debris exhibits high nitrate and phosphate uptake per unit surface area; net uptake is related to frequency and volume of wood debris.	Aumen et al. (1990), Valett et al. (2002)
Habitat		
Floodplain conifer seedbed	Some conifer species reproduce preferentially on wood.	Franklin and Dyrness (1973), McKee et al. (1982), Christy and Mack (1984), Harmon and Franklin (1989), Fetherston (2005)
Riparian vertebrate and bird habitat	Fluvial wood and wood accumulations create habitat structure, shelter, and habitat patches; increase food resources.	Harmon et al. (1986), Steel et al. (2003)
Terrestrial invertebrate habitat	Terrestrial wood debris provides food, habitat, shelter, hibernation sites, and nesting sites for invertebrates.	Harmon et al. (1986)
Aquatic invertebrate habitat	Wood provides habitat and food for invertebrates; organic and inorganic matter accumulating on or behind wood provides food for invertebrates; wood-influenced channel structures create invertebrate habitats.	Harmon et al. (1986), Benke and Wallace (2003)

T. plicata and *P. menziesii* regain dominance in the future, they likely would form a larger proportion of key pieces.

4. Discussion

4.1. Large tree species as foundation species

The floodplain large-wood cycle increases diversity of physical and ecosystem structural components and processes and affects plant, animal, and microbial species diversity and abundance at multiple scales, including the valley-scale pattern (Table 3; Fig. 7). Consequently, we propose that species of valley bottom trees that can grow large enough to remain stable in rivers function as "foundation species" (*sensu* Dayton, 1972). Large trees affect a wide range of fundamental biotic and abiotic attributes of forested floodplain ecosystem structure and function, having local effects on habitat (e.g., creating conditions for regeneration of conifers; directly creating salmonid habitat), define community structure (e.g., by creating biotic and geomorphic diversity and complexity), and affect fundamental ecosystem processes (e.g., creating positive feedbacks that favor a particular landscape and ecosystem trajectory).

We further suggest that in Pacific coastal forested river valleys, large trees, through the mechanisms of the floodplain large-wood cycle, can be viewed as a "switch" that shapes the trajectory of physical process and landforms and that influences the assembly of

forested alluvial valley bottoms. Ecosystems shaped by foundation species tend to be dominated by a small number of strong interactions, and such systems are relatively susceptible to switching between alternative stable states following perturbations to those interactions (Ellison et al., 2005). While the web of causality set in motion by the presence of large riparian trees in Pacific coastal forested valley systems is complex, it is based on a few simple interactions, the dominant one being the stability of large trees when they fall into the river. Numerous examples exist from other systems of sudden, drastic switches to contrasting ecosystem states resulting when foundation species are eliminated or introduced, including in lakes, coral reefs, woodlands, deserts, and oceans (Scheffer et al., 2001).

We also propose that large wood provides core resilience to the system and that removing large riparian trees from rivers switches the trajectory toward an alternate domain (Fig. 8). Evidence from Pacific coastal river valleys supports the idea that river systems can enter an alternate, less complex and less productive state in response to the removal of large wood. Removing wood has been shown to establish completely different river-forming processes (Abbe et al., 2003). Archival studies (e.g., Sedell and Froggatt, 1984; Collins et al., 2002) and comparison of relatively undisturbed systems with systems from which large trees have been removed demonstrate that channel pattern can shift from anastomosing to braided or meandering, simplifying the structure and abundance of physical habitats, and that such channels become more mobile. In addition, numerous
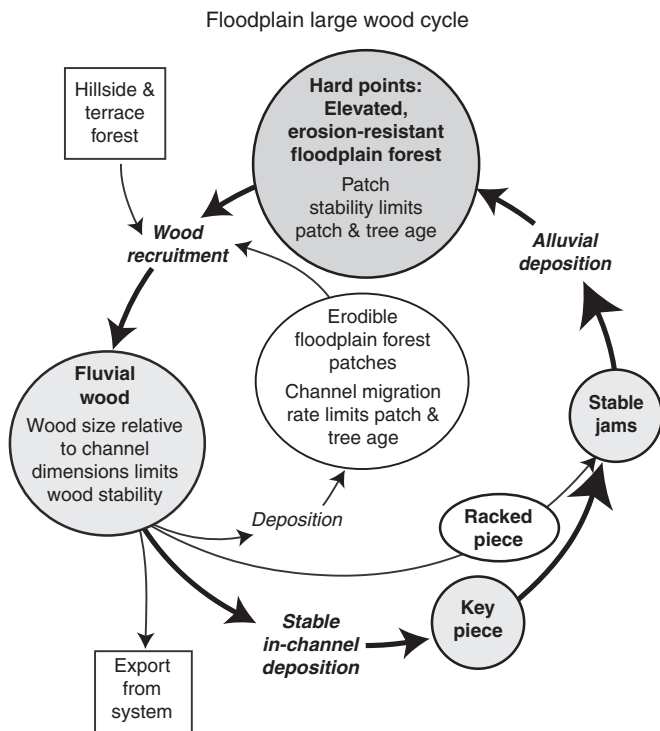
Floodplain large wood cycle

Fig. 6. Diagram of the floodplain large-wood cycle in forested river valleys of the North Pacific coastal ecoregion.

studies document ecological contrasts between rivers that have a mature riparian forest to which the river is laterally connected and rivers that lack such a forest and large fluvial wood.

4.2. Generality of mechanism

The phenomena described above can be observed in many rivers in the North Pacific coastal ecoregion having intact valley-bottom forests and intermediate slopes and discharges and having channel patterns variously classified as 'Type 5 anastomosing' rivers (Nanson and Knighton, 1996), 'wandering' rivers (Church, 2002), or 'island-braided' (Beechie et al., 2006). Further investigation might demonstrate a wider geographic applicability to the large wood cycle model. More generally, there is need for expanded understanding of the roles wood plays in other regions to test the foundation species idea and to elucidate other mechanisms of biotic feedbacks on river systems. Examples from three continents summarized below suggest that large wood is fundamental to structuring riverine landscapes in other temperate biomes, albeit through different mechanisms than the hypothesized large wood cycle presented here.

Large lowland rivers in the European broadleaf temperate forest biome now have a single thread with relatively simple channel form and little floodplain connection. However, paleolandscape reconstructions (Brown and Keough, 1992) and historical maps and records (see Table 1, Gurnell and Petts, 2002) show that wooded islands and anastomosing channels were once common, and wood dynamics may have been important to the Holocene environmental history of European rivers (Francis et al., 2008). In one of the few still-forested lowland rivers in Europe, wood accumulations partition flow (Harwood and Brown, 1993), creating jams and multiple channels that increase aquatic habitat diversity (Brown, 1997). Research in the Tagliamento River, Italy, shows how trees, dead and living wood, and other plant propagules interact with the local topography and fluvial sediment in building islands and shaping the mosaic of vegetation patches (Gurnell et al., 2001). Research on the Tagliamento River led to the suggestion that trees in this setting

Alternate stable states

Higher complexity & diversity ⟵ ⟶ Lower complexity & diversity

1. Diversity of stable main and perennial secondary channel habitats	1. Braided, unstable main channel and shifting, ephemeral secondary channels
2. Abundant, high quality edge habitat	2. Low quality of edge habitat
3. Large trees entrained by river at eroding banks	3. Riparian forest recruitment limited to small wood
4. Stable jams at flow splits and secondary channel inlets	4. Unstable pieces and accumulations of fluvial wood
5. Deep scour pools associated with stable jams	5. Few, shallow pools
6. Forest age and species patch diversity, including mature conifer patches on stable "hard points"	6. Low forest patch age and species diversity, dominantly ephemeral, young stands of pioneer tree species

Fig. 7. Alternate stable states illustrating effects on fluvial landforms and forests of removing large riparian trees. Panel to the left shows the Hoh River (river kilometers 65–68) and to the right is the Cowlitz River (river kilometers 207–210), both from 2009 images. Flow direction is from image top to bottom.

be considered as ecosystem engineers because of their role in landform and ecosystem development (Gurnell and Petts, 2006). In contrast to the model described in this paper for the North Pacific coastal ecoregion in which tree species grow to be very large and can resist decay for centuries, the willow and alder trees that dominate the Tagliamento River's riparian forest do not grow to be large and decay rapidly. Consequently, islands formed by dead wood and the trees that sprout from it are relatively transient features (Gurnell et al., 2009) and should give rise to a
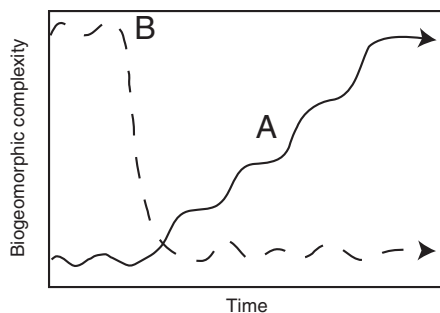
Fig. 8. Generalized trajectories of riverine landscape development. The introduction of large riparian trees (A) triggers a trajectory to a stable state having relatively high biogeomorphic complexity. Loss of large riparian trees (B) sends the system to a transitional state that can lead to an alternate stable state of diminished biogeomorphic complexity.

more dynamic, rapidly shifting mosaic compared to that created by the long-lasting hardpoints described in this paper.

In the temperate deciduous forests of North America, historical sources document channel-filling "raft" jams that often dramatically altered river valleys (for review see Abbe and Montgomery, 2003). For example, a complex of jams extending 257 km on the Red River in Louisiana and Arkansas created a mosaic of anastomosing channels and lakes (Triska, 1984). These "rafts" started as individual snags and small jams (Guardia, 1933) contributed by species that include the broadleaf deciduous American sycamore (*Platanus occidentalis*) and American tulip tree (*Liriodendron tulipifera*) (Guardia, 1933; Triska, 1984). After the jams were removed, the river incised, simplified to a single channel, and tributary lakes drained.

In the Colorado Front Range, Wohl and Cadol (2011) observed that multithread channels only occur in streams flowing through remaining patches of old-growth forest because of the large-diameter wood recruited from these forests and the resulting stable wood jams. Tree-fall can initiate complex behavior that results in a self-enhancing feedback between wood recruitment and channel geometry because hydrostatic forces that mobilize jams increase more slowly in low-gradient, unconfined channels, facilitating jam persistence (Wohl, 2011). Because patches of old-growth forest were likely larger and more common prior to nineteenth century timber harvest, such old-growth-associated multithread channels were likely more wide-spread historically than at present, with consequences that include decreased carbon retention in stream systems (Wohl, 2011).

In the warm temperate rainforest of southeast Australia, Brooks et al. (2003) documented how removal of forest vegetation increased channel depth 360%, slope by 240%, channel capacity by 700%, and rate of lateral channel migration by up to 150-fold. Wood is now flushed through the enlarged river channel, altering river-forming processes. In this new persistent, self-reinforcing state, nutrient and water exchange from the floodplain and the river have been radically altered and habitat complexity dramatically simplified (Brooks et al., 2003). While these examples illustrate the generality of wood's importance to biophysical processes throughout the temperate zone, the large wood cycle as described here may be specific to conifer-dominated biomes.

4.3. Implications for river and forest management and restoration

For managing the remaining river valleys that have mature forests and large wood, the importance of large riparian trees suggests the need to protect remaining islands of large trees that function as 'wood hotspots' (Latterell and Naiman, 2007). Research is needed to understand better how different perturbations of varying severity relate to thresholds of system resilience beyond which trajectories change (Fig. 6). For example, forest clearing, in-channel wood removal, and bank armoring—a combination of modifications common to

the history of many rivers—are a severe perturbation likely to exceed the system's resilience. In contrast, the selective removal of large trees from the Nisqually River in the late nineteenth century suggests that temporarily reducing the abundance of some of the dominant large tree species, but otherwise leaving the forest and channel unchanged, may not exceed the system's resilience if the forest contains other species that can produce large trees.

Collins and Montgomery (2002) presented a conceptual model for a coupled river and riparian forest restoration that emphasizes conditions for developing large trees in riparian forests and for reestablishing river mobility to recruiting trees to the channel. In this context, engineered log jams (Abbe et al., 2003) can play a role as a short-term measure and for starting the restoration process, even though in the long term a self-sustaining restoration depends on there being a supply of large floodplain trees and on the river being free to erode laterally and to recruit large trees to the channel. A number of valley- and reach-scale restoration projects in North Pacific coastal rivers use engineered log jams specifically to accelerate the process of recovery (e.g., Abbe and Brooks, 2011). The wood cycle hypothesis predicts that, absent such intervention, recovery would otherwise be delayed by the time required to grow large key member trees, anywhere from 50 to 300 years, depending on the river system.

Most temperate, forested river valleys have already been transformed by human activities. As an explanation of the historical simplification of riverine environments, the anthropogenic removal of large trees is a complementary and, in some cases, alternate mechanism to direct anthropogenic landscape alteration (e.g., by dams, levees, and river training). The two mechanisms commonly occurred in concert, complicating interpretation of their relative importance. Nonetheless, differentiating these mechanisms is important for river restoration, to know whether achieving a self-sustaining river depends on restoring large trees.

Research from other landscape systems shows that anthropogenic factors and biophysical feedbacks can maintain systems in a 'persistent alternative state' not readily restored simply by reestablishing physical conditions or disturbance regimes alone (Suding et al., 2004); some systems may require restoring species that have critical roles (e.g., ecosystem engineers, Byers et al., 2006). We suggest that many Pacific coastal alluvial valleys represent such a system, and that restoring large trees is essential to restoring physical form and process and associated ecosystem complexity.

5. Conclusions

(i) In many forested or formerly forested riverine environments of the Pacific coastal ecoregion of North America, dominant, large-growing tree species—through the mechanism of the floodplain large-wood cycle—are foundation species because they trigger interactions that define a trajectory toward a geomorphologically and ecologically stable state characterized by resilience. (ii) This idea may prove applicable to many of the world's temperate forested river valleys and provide an alternative or complementary explanation for historical simplification of riverine environments. (iii) Particular attention to tree species capable of growing to large dimensions, the trajectories triggered by their presence or their removal, and the factors that maintain system resilience are important for river restoration and management.

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