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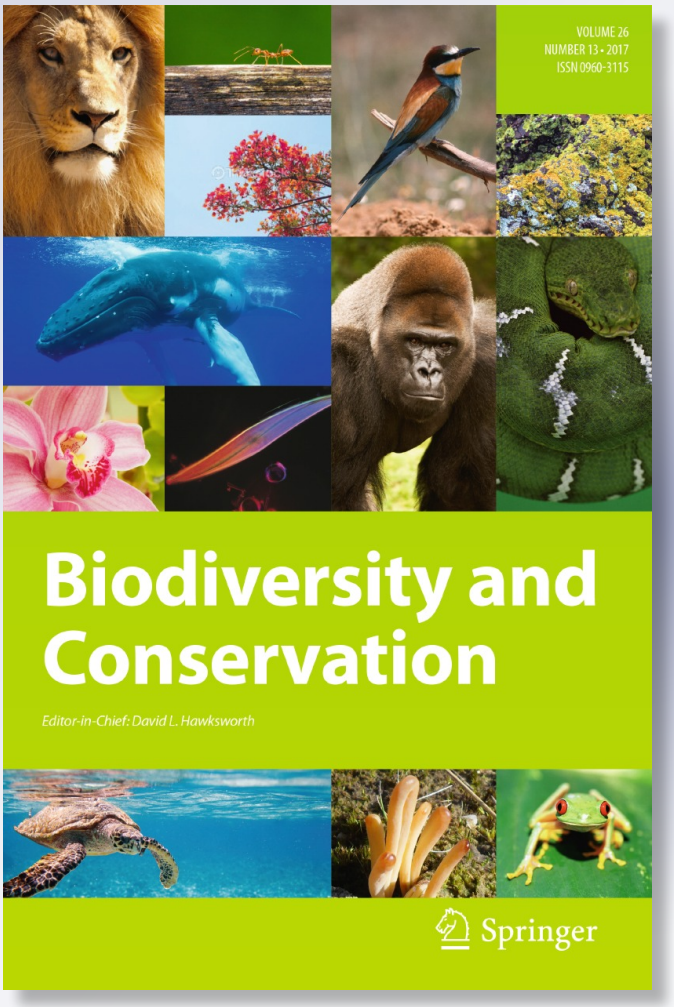

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ORIGINAL PAPER

Aquatic biodiversity in forests: a weak link in ecosystem services resilience

Brooke E. Penaluna[1] · Deanna H. Olson[1] · Rebecca L. Flitcroft[1] · Matthew A. Weber[2] · J. Ryan Bellmore[3,4] · Steven M. Wondzell[1] · Jason B. Dunham[3] · Sherri L. Johnson[1] · Gordon H. Reeves[1]

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Abstract The diversity of aquatic ecosystems is being quickly reduced on many continents, warranting a closer examination of the consequences for ecological integrity and ecosystem services. Here we describe intermediate and final ecosystem services derived from aquatic biodiversity in forests. We include a summary of the factors framing the assembly of aquatic biodiversity in forests in natural systems and how they change with a variety of natural disturbances and human-derived stressors. We consider forested aquatic ecosystems as a multi-state portfolio, with diverse assemblages and life-history strategies occurring at local scales as a consequence of a mosaic of habitat conditions and past disturbances and stressors. Maintaining this multi-state portfolio of assemblages requires a broad perspective of ecosystem structure, various functions, services, and management implications relative to contemporary stressors. Because aquatic biodiversity provides multiple ecosystem services to forests, activities that compromise aquatic ecosystems and biodiversity could be an issue for maintaining forest ecosystem integrity. We illustrate these concepts with examples of aquatic biodiversity and ecosystem services in forests of northwestern North America, also known as Northeast Pacific Rim. Encouraging management planning at broad as well as local spatial scales to recognize multi-state ecosystem

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management goals has promise for maintaining valuable ecosystem services. Ultimately, integration of information from socio-ecological ecosystems will be needed to maintain ecosystem services derived directly and indirectly from forest aquatic biota.

Keywords Freshwater biota · Forested streams and lakes · Salmonids · Amphibians · Ecological integrity · Native species · Final ecosystem services

Introduction

Globally, as the world enters a new era of species extinctions (Alroy 2015; Hoffmann et al. 2010; Wake and Vredenburg 2008; Stuart et al. 2004) accompanied by an unprecedented level of non-native species invasions and biotic homogenization (Kareiva et al. 1993; McKinney and Lockwood 1999; Olden et al. 2004; but see Murcia et al. 2014), there is an urgency to understand the scope of these changes and how they may influence both ecological integrity and the variety of ecosystem services it supports (Millennium Ecosystem Assessment 2005; Cardinale et al. 2012; Dirzo et al. 2014; Costanza et al. 1997; Daily 1997; Febria et al. 2015; Kremen 2005). Overall, species losses are projected to accelerate change in ecosystem processes rivaling effects of elevated CO_2, ozone, acidification, or nutrient pollution (Hooper et al. 2012). Because evolutionary biodiversity is not a renewable resource, upon extinction (of a particular gene, trait, life-form, species) it is gone. Identifying aspects of biodiversity that influence ecological integrity and, in turn, ecosystem services is thus of paramount importance (Kremen 2005).

Global defaunation and deforestation (Dirzo et al. 2014) are occurring with increasing magnitude and these two phenomena are intertwined, because forests are one of the most complex environments on the planet, hosting extremely high numbers and biomass of species (e.g., forests retain ~80 % of terrestrial biodiversity: http://www.iucn.org/about/work/programmes/forest/about_forest_conserv/; accessed 26 Mar 2015). An additional important subset of all biodiversity on Earth that has been overlooked is aquatic biodiversity in forests.

Forest and aquatic biodiversity are intimately connected, where the ecological integrity of forests relies at least in part on underlying processes and functions of aquatic-dependent elements. In forests, freshwater habitats include non-flowing and flowing water bodies, as well as moist microhabitats that may include stream- or pond-side riparian zones, water locked inside various pockets of vegetation and decaying wood or litter, or moisture-laden rocky substrates. The relationship between forests and water has long been recognized—as evidenced by debates in the Roman Senate in the first century BC (see Perlin 1989, p. 107). More recently it has been reported that forests intrinsically influence freshwater resources. For example, in the United States (US), over half of the freshwater used by humans comes from forests (Brown et al. 2008), affecting not only the US water supply, but nutrients and a diversity of organisms that depend on those waters (Pringle 2003; Freeman et al. 2007).

Although freshwater ecosystems are considered among the most biologically diverse of all ecosystems, supporting up to one-third of all vertebrates on the planet (Strayer and Dudgeon 2010), their biodiversity is less well understood than for other ecosystems, likely due to the relatively high level of endemism and cryptic species (Reid et al. 2013). However, aquatic biodiversity and ecosystems are recognized as among the most imperiled systems (Strayer and Dudgeon 2010), with freshwater vertebrates declining at a faster rate

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than terrestrial vertebrates and topping global lists of threatened and declining species (Ricciardi and Rasmussen 1999; Strayer and Dudgeon 2010; Vörösmarty et al. 2010; Reid et al. 2013; McLellen 2014; Alroy 2015). Freshwater turtles top the list, with >50 % of species vulnerable to losses (e.g., Kiester and Olson 2011), followed by freshwater fishes, with >40 % of assessed species vulnerable to losses (Reid et al. 2013), and amphibians, with 30–40 % (Stuart et al. 2004; Hoffmann et al. 2010). How these reported losses translate to forested aquatic ecosystems is not known because overall aquatic species richness has not been estimated in forests. One taxon has been assessed in this manner: over 80 % of amphibians (~6000 of 7530 species known to date; http://www.amphibiaweb.org; accessed 19 Apr 2016) rely on forests (http://www.iucnredlist.org/initiatives/amphibians/; accessed 27 Mar 2015). The decline in overall freshwater biodiversity from contemporary environmental changes provides additional rationale for determining aspects of aquatic biodiversity in forests that influence the integrity of ecological structures, functions, and processes, and in turn affect ecosystem services.

Biodiversity is a broadly used term measuring the variety of life on Earth at various levels of organization, including genes, traits, populations, species, communities, and ecosystems, and their numbers, abundance, and composition (Brooks et al. 2006), which have resulted from evolution over millennia. Biodiversity is not just the sum of all biotic forms, rather it includes biological subsets such as the variety of traits within a single taxon, or the community assemblage on a landscape. Although the number of native species is considered a key indicator of the biological integrity of an ecosystem (Angermeier and Karr 1994; Febria et al. 2015), a combination of structural complexity (based on species abundance), and taxonomic (a surrogate for genetic) and functional diversity (based on ecological roles and traits) may be considered essential components of biodiversity influencing ecosystems (Lyashevska and Farnsworth 2012). For example, across the Northeast Pacific Rim forests, vertebrate species richness of streams may be considered relatively low, but the within-taxon diversity of genetic, phenotypic, and life-history forms is relatively high among species, especially of Pacific salmon and trout (*Oncorhynchus* spp.) (Rieman et al. 2015). Pacific salmon and trout have flexible spawning-run timing that varies by stream, resulting in life-history diversity that supports persistence in a heterogeneous landscape prone to broad-scale natural disturbance events. The diversity of traits over space and time, rather than species diversity, provides the resilience necessary for salmonid populations to persist (Hilborn et al. 2003). In a broad sense, aquatic biodiversity is multi-tiered from genes to communities, inclusive of a rich array of compositions and their ecological processes, among which ecosystem services are adding new perspectives to their significance in forest ecosystems.

Here, we adapt and expand a conceptual framework for forested aquatic ecosystems that provides the basis for understanding links between biodiversity and ecosystem processes, functions, and services. We describe key threats to biodiversity and its services, and consequent management implications. We apply this framework to several examples of aquatic biodiversity and ecosystem services in forests of the United States (US) portion of the Northeast Pacific Rim (US Pacific Northwest), where considerable research has been conducted; our examples may reflect of other forest systems globally. More generally, the integration of ecosystem services into an ecological framework has been generally overlooked (Fisher et al. 2009; Martin-Ortega et al. 2015) and numerous knowledge gaps exist (e.g., relative to aquatic biodiversity: Febria et al. 2015; freshwater: Griebler and Avramov 2015; forests: Lawler et al. 2014). Managing for resilience in forested aquatic ecosystems using multi-scale and multi-state management planning that incorporates both broad and

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local scales and the complex nature of these ecosystems within a flexible and adaptive planning system has promise for maintaining these invaluable services.

Framework for considering aquatic biodiversity in forests

The framework we apply here (Fig. 1) is adapted and expanded from ideas developed by others (e.g., Warren et al. 1979; Ebersole et al. 1997; Gunderson 2000). Aquatic ecosystems in forests are multi-faceted and complex, and hence are best conceptualized as a set of spatially and temporally explicit ecological states within a domain (cup, Fig. 1a, b), which encompasses the range of ecosystem states or conditions. The number and variety of ecological states in a domain is in constant flux in response to changes in local conditions, stochastic processes, and mild disturbances (moving cup, Fig. 1b). Each domain, and consequently state, comprises a variety of components (balls in cup), including explicit abiotic and biotic conditions, functions, and processes at a place in a time-period. These conditions vary (schematically represented by different sizes and colors of balls) over time and space within and among forested watersheds.

Resilience is the capacity of an ecosystem to absorb change and remain within the dynamics of a domain in the face of natural disturbances and human stressors (Desjardins 2015). As ecosystems undergo larger shifts from natural disturbances and human stressors, the ecosystem can be redefined: ecosystem components, functions, and processes change, moving it from its current domain to an alternative domain (Fig. 1a, moving past a 'tipping point'). Some ecosystem components may remain through this transition, while others may be new, leading to a different set of states in a novel domain. For example, when taxa cannot absorb change over time, biodiversity may be lost, potentially leading to a change in system components and a new state within its domain (ecosystem), or even to a completely new domain, corresponding to different biodiversity structural components, and consequential differences in ecological functions and processes (e.g., Walker and Salt 2006). For aquatic biodiversity, with its apparent heightened vulnerability to losses, there is a growing concern about a general lack of resilience to contemporary stressors (described below). Due to the integral roles of aquatic biota for ecological functions and processes, aquatic biodiversity loss could emerge as a potential 'weak link' for ecosystem resilience. In addition, as ecosystems pass tipping points to new domains, their capacity to deliver ecosystem services important to people may change. Below we further frame these issues for forest aquatic ecosystems. First, we examine aquatic biodiversity in forests relative to ecosystem services and ecological functions. Second, we categorize primary contemporary threats to aquatic biodiversity in forests, which may singly or in concert contribute to ecosystem tipping points.

Drivers of aquatic biodiversity in forests

To understand the functional role of aquatic biodiversity in forests, more details are needed regarding the multi-state ecosystems that support aquatic biodiversity (Fig. 1a, balls), and how biodiversity responds to the diversity of habitats provided by variable aquatic and riparian conditions (Naiman et al. 2005). Many aquatic taxa are highly specialized to physical microhabitat conditions of the aquatic-forest interface. Aquatic species assemblages vary with water type and flow patterns (riparian/lentic/lotic habitats, ephemeral/perennial water availability, high/low gradient or current), structural heterogeneity (substrate/cover type), and temperature. In particular, streams in forests are heterogeneous mosaics of connected, patchy habitats that fluctuate across various spatio-temporal

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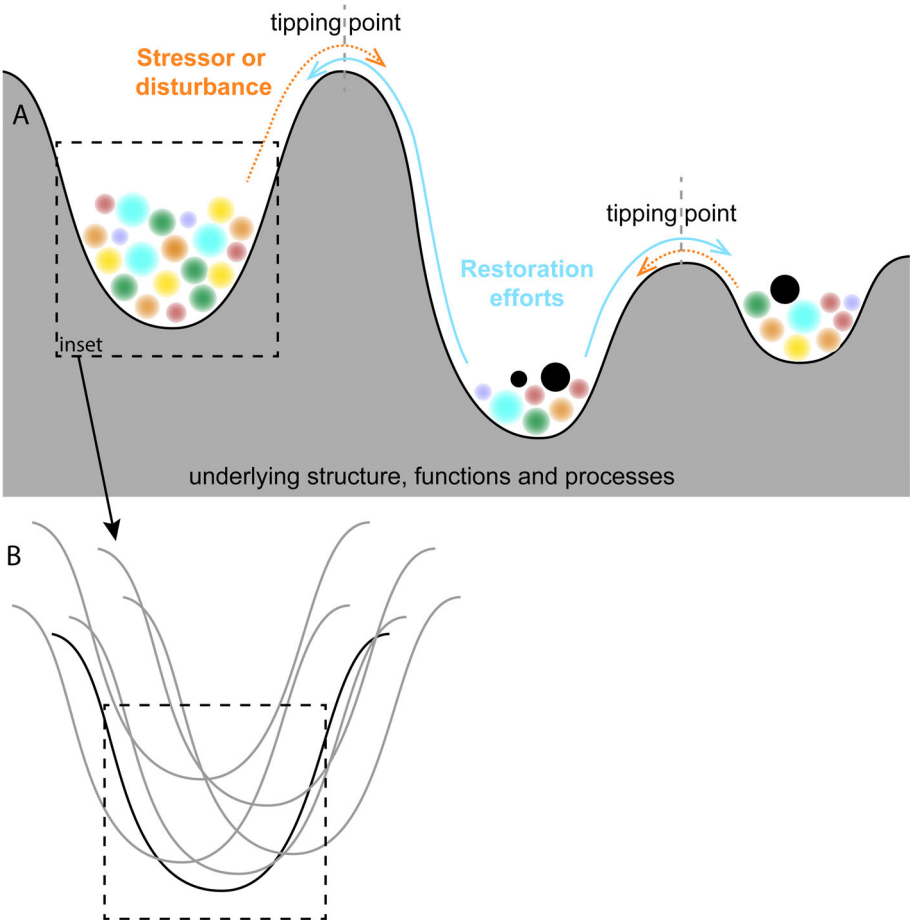

Fig. 1 Multi-state concept for changes in forested aquatic ecosystems over time (**a**). *Balls* represent diversity of focal level or components (genes, individuals, populations, species, communities, or ecosystems), *arrows* represent disturbances, stressors, or restoration efforts, *cups* represent domains, and *valleys* represent conditions or states. These states are dynamic and ever-changing (**b**) with the balls also constantly changing position. Resilience is the capacity of an ecosystem to absorb change and remain within the dynamics of a domain in the face of natural disturbances and human stressors. When an aquatic ecosystem exceeds its capacity to be resilient over time, diversity may be lost, leading to a more limited repertoire of components and a new domain corresponding to alternative structures, functions, or processes. For aquatic ecosystems and their biodiversity, there is a growing body of literature supporting their lack of resilience to contemporary stressors. In this context, restoration efforts may successfully help restore diversity if the lost components are available elsewhere on the landscape and if the ecological tipping point can be reversed (modified from Gunderson 2000; Desjardins 2015)

dimensions (Fausch et al. 2002; Poole 2002; Wiens 2002; Humphries et al. 2014). The interactions between forests and streams are multi-directional, and relative to streamflow, both latitudinal (toward and away from riparian zones) and longitudinal (up and down streams) processes significantly influence forest aquatic biota and associated ecological functions, particularly nutrient and trophic energy transport (Fausch et al. 2002; Poole 2002).

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Lateral (latitudinal) processes capture, modify, or reposition inputs from adjacent forests, have hydraulic and biogeochemical feedbacks, and periodically return materials to streamside forests (Gregory et al. 1991; Montgomery 1999). The vegetation composition of forested riparian zones greatly influences riparian and instream processes, habitat structure, and biodiversity, controlling the stream's energy budget and water temperature, and influencing inputs of large wood, leaf litter, and fine organic matter. The amount and size of wood in streams has major impacts on water and sediment routing that structure instream habitats (Gregory et al. 1991). Wood and leaf litter serve as both physical substrates and food resources for many organisms (Anderson and Cummins 1979; Cummins et al. 1984). Nutrients are transferred between forests and streams through direct inputs and decomposition of organic matter, as well as lateral delivery of water from hillslopes. The nutrient composition of hillslope water can be modified by riparian vegetation uptake and processing as the water moves toward the stream (Wondzell and Swanson 1996). Changes in forest cover due to forest harvest alter the quality and quantity of water for varying periods of time (Bryson and Murray 1977; Harr 1986; Harr and Fredriksen 1988; Jones and Post 2004) and potentially shift aquatic ecosystems toward a new state.

Streamside vegetation can strongly influence stream and riparian energy budgets—primarily by controlling the amount of solar radiation reaching the stream surface and ground and regulating the exchange of long-wave radiation. Thus, streamside vegetation influences both stream and riparian-zone temperatures and primary production (Hawkins et al. 1982a, b; Johnson 2004; Moore et al. 2005). In turn, stream water temperature controls rates and processes from individuals to ecosystems, including growth, metabolism, and decomposition (Magnuson et al. 1979). Many species have optimal temperature ranges, and temperature can influence species habitat preferences, behavior, distribution, and survival. Furthermore, streamside shade provides visual refuge where some aquatic species have reduced predation risk (Penaluna et al. 2015a).

Reciprocal subsidies between forests and streams include movement of nutrients and trophic energy laterally from streams to uplands (Nakano and Murakami 2001; Davic and Welsh 2004; Baxter et al. 2005; Muehlbauer et al. 2014). Some aquatic biota move into the forest at specific life stages, such as emerging aquatic insects flying into the forests as adults (e.g., Muchow and Richardson 2000; Progar and Moldenke 2002) or metamorphosing amphibians moving into upland habitats. These represent nutrient and trophic energy pulses to uplands, providing prey to bats, birds, and ground-dwelling forest carnivores. Aquatic species are also transferred to land by other processes. For example, salmon carcasses can be transported from streams to terrestrial zones by their predators (Cederholm et al. 1999). Stream water filters into the subsurface hyporheic system, where it can be tapped by streamside vegetation. When water is taken up by those plants the nitrogen in stream water can actually "flow" up into the forest system, forming a recognizable component of forest-stream interactions (Ashkenas et al. 2004).

Longitudinal processes are a critical component of ecological functions in forested streams (Vannote et al. 1980), where biological subsidies and their composite functions related to nutrient and trophic energy flow move along river networks from headwaters to oceans. Many rivers of the world have their headwaters in forested highlands, and headwater streams can account for over two-thirds of the total length of streams in river networks. The interaction and influence of forests on streams vary with stream size along the length of streams. In headwater streams, 60–70 % of materials such as wood or litter entering streams has been shown to be retained more locally and used in-place by organisms for various life-history functions (Anderson and Sedell 1979), whereas wood and litter entering larger streams are less likely to be retained or used where they enter a

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stream and more likely to be transported downstream (Naiman and Sedell 1979). A variety of upstream subsidies influence downstream reaches, such as arthropods from headwater forests becoming prey for downstream fishes (Wipfli and Gregovich 2002), and upstream large wood, smaller particulate organic matter, or sediment providing structural inputs to downstream waters (e.g., Benda and Cundy 1990; Benda and Dunne 1997a, b; Reeves et al. 2003; Hassan et al. 2005; Rashin et al. 2006; Reeves 2006). Native aquatic species in forests follow longitudinal patterns related to stream size as well, with increasing fish diversity in downstream reaches (Roper and Scarnecchia 2001). Conversely, headwaters are recognized as hotspots for amphibian diversity in river networks of the Northeast Pacific Rim (Olson et al. 2007; Welsh 2011). Overall, aquatic ecosystems in forests can be envisioned as a mosaic of complex multi-states within an ecosystem (Fig. 1; Humphries et al. 2014).

Forests are important to aquatic food-web interactions. Flow of nutrients and energy follows predictable trophic pathways. Common autotrophic pathways include light and nutrients, first to primary producers (algae, diatoms, mosses growing on rock and wood substrates), then to the consumers and other predators (scraping invertebrates, amphibians, or fish) (Power and Dietrich 2002). Heterotrophic pathways start with leaf litter and other detrital material, passing upward to microbial communities, invertebrates, amphibians, fish, and sometimes into terrestrial or marine systems.

Relative to energy flow, forest amphibians, in particular, are notable due to their large cumulative community biomass, which may exceed that of birds, mammals, and fishes (Peterman et al. 2008; Semlitsch et al. 2014). In other regions, instream amphibians have been shown to play a role in water quality, by their trophic effects on invertebrates, algal biomass, nitrogen, and stream respiration (Whiles et al. 2013). Upland forest amphibians, and likely similar predators, also may have the capacity to enhance carbon sequestration via predation on invertebrates that process leaf litter (Best and Welsh 2014; Semlitsch et al. 2014). Importantly, key aquatic predators may structure trophic cascades that affect community composition (Power 1992; Estes et al. 2011). Amphibians and fishes are voracious predators in many forested streams, with a strong role in local assemblage composition (Schlosser 1991).

With a native range that spans the northern Pacific Rim, salmonids provide a good example of aquatic biodiversity in forests and ties to ecological functions, both as apex predators and high-energy prey (Fig. 2). Pacific salmonids have persisted under dynamic conditions spanning disturbances of major geotectonic events, volcanic eruptions, advances and retreats of glaciers, and periodic floods, fires, and landslides. In the Northeast Pacific, populations of *Oncorhynchus* and *Salvelinus* exhibit a broad genetic, phenotypic, and life-history diversity (Waples 1991; Crozier et al. 2008; Schindler et al. 2010) and can respond rapidly to changing conditions (Healey and Prince 1995). Specifically, their genetic, phenotypic, and life-history diversity has allowed for their persistence under climate shifts (Miller and Brannon 1982; Behnke 2002) and in highly dynamic environments in the past (Waples et al. 2009). These traits also are likely to be key to their persistence into the future (Mangel and Tier 1994). Such diversity can spread the risk in a challenging environment by providing resilience against environmental change (Den Boer 1968). Nevertheless, Gienapp et al. (2005) cautioned that knowledge about the role of genetic variation and the ability of populations to respond to contemporary and future environmental change is limited, and that assuming adaptation will or can happen is risky because of the uncertain rate and extent of climate change, effects of invasive species, and altered ecological processes.

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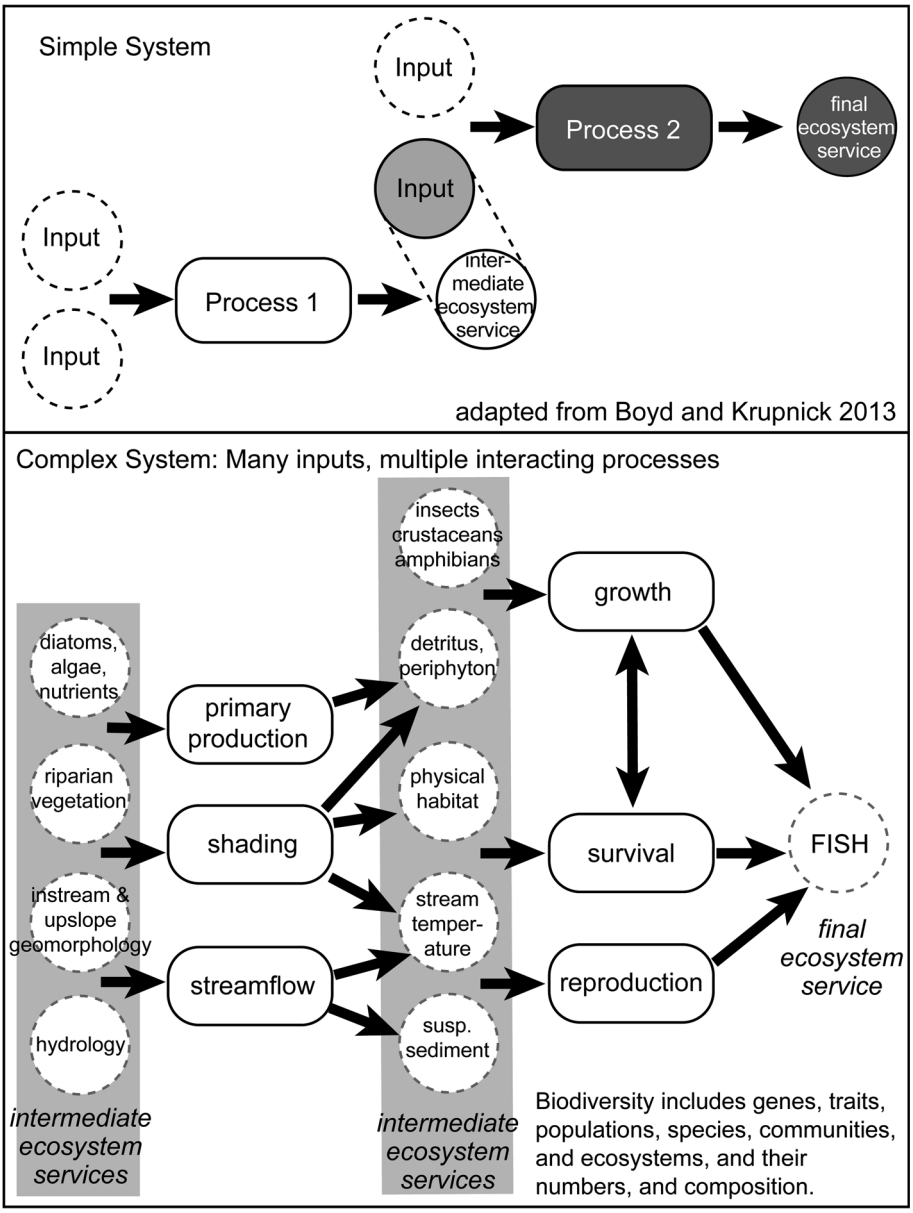

Fig. 2 Fish are a final ecosystem service that incorporate many processes and inputs as intermediate ecosystem services. This conceptual understanding is based on aquatic ecosystems in the Northeast Pacific Rim, and for simplicity not all relationships are shown. For example, suspended sediments affect reproduction, growth, and survival. Note that some intermediate services that support fish production, such as riparian vegetation, are also directly relevant to some stakeholders, thus acting as "dual" commodities being both intermediate and final ecosystem services

Pacific Rim salmonids have key ecological functions and are tied to final ecosystem services, supporting their role as an important component of forested aquatic ecosystems, being particularly important for both ecosystem functions and societal values (Fig. 2).

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Ecologically, they are dominant predators in forested streams, affecting assemblage composition of local habitats, but also serving as high-energy prey in the egg and juvenile stages (Quinn 2005). Further, sea-run salmonids bring terrestrial and freshwater subsidies to estuaries and oceans, linking nutrients and energy derived from the forest to the sea, and return ocean-derived nutrients to terrestrial systems via their spawning migrations (Quinn 2005). The persistence of salmonids in the face of natural disturbances and human stressors may provide an anchor for promoting broader ecosystem resilience due to their important role in the food web (Figs. 1, 2). Similar anchor roles may be filled by other aquatic taxa, such as sculpins (Cottidae) or salamanders (Dicamptodontidae, Rhyacotritonidae, Salamandridae) in some portions of watersheds, as these taxa are also centrally nested within food webs (being both prey and predators) and have consequent functional roles in energy transfer among system components. As native species, they have emergent societal values as well.

Disturbances to forested aquatic ecosystems provide a mosaic of dynamic and patchy conditions for aquatic freshwater species and facilitate the expression of genetic, phenotypic, and life-history diversity of native species (Fig. 3; Mantua and Francis 2004; Fausch et al. 2009). Contemporary natural disturbances that are critical to the structure of forested aquatic ecosystems include landslides and debris flows, floods, fires, ice storms, hurricanes,

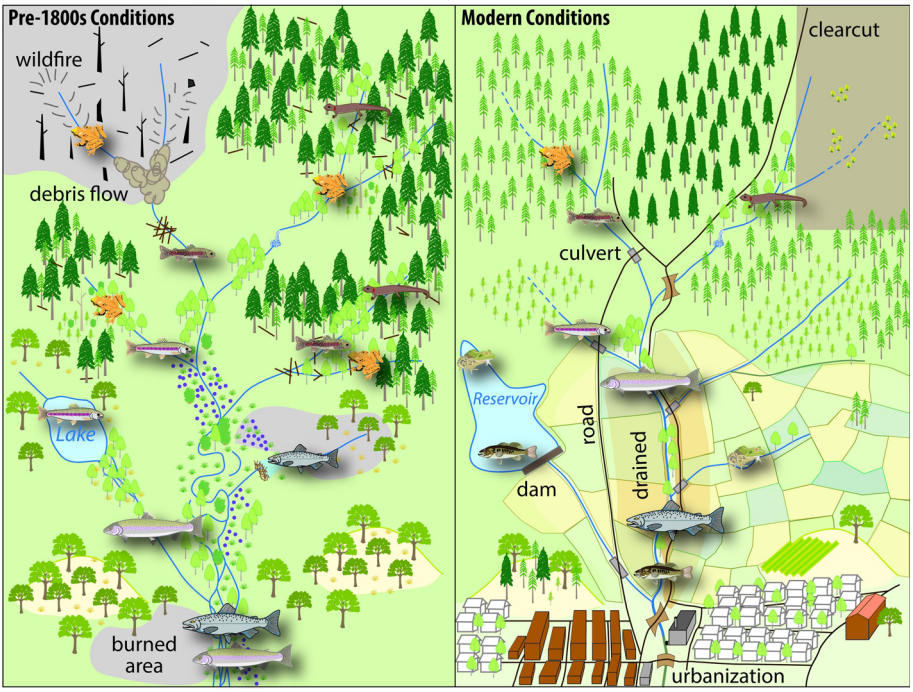

Fig. 3 A *snapshot* of past and present forested aquatic ecosystems of the Northeast Pacific Rim. The *left panel* represents pre-1800s conditions, with riparian habitat throughout the network, intact forests, and natural disturbances that shape these ecosystems, including wildfire, debris flows, and seasonal burning and resource harvest by Native Americans. The *right panel* illustrates modern conditions that add large-scale human stressors to previous conditions, including forest management, dams, culverts and roads, climate change (depicted by *dashed stream-line* denoting that some headwater streams become intermittent), and other land-use changes

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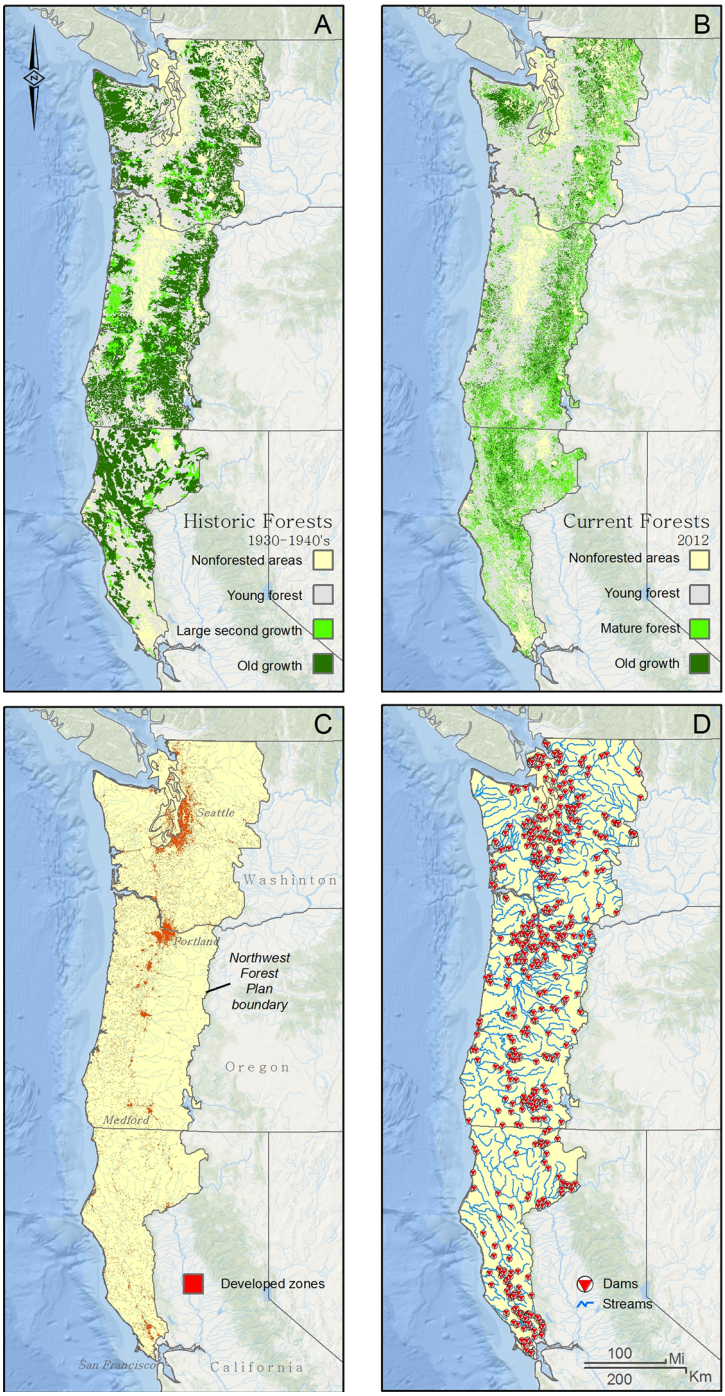

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◀**Fig. 4** A Northwest forest plan boundary map of **a** past and **b** present conditions. *Top panel* represents forest cover including historic (1930–1940s) and current (2012) conditions (from Davis et al. 2015). Under current conditions, *mature forest* (> = 80 yr old) represent a broad spectrum of forest conditions that include both mature stands and old growth, whereas *old growth* (>200 yr old) represents a narrower spectrum of old forest conditions that focuses more on old growth stands. **c** Current urbanized areas (NLCD 2006) and **d** shows locations of major dams (>7.6 m [>25 ft] high; NID 2013)

and wind-throw events. The natural disturbance regime is described by the frequency, magnitude, and spatial distribution of disturbances across a dynamic landscape covering the full extent of river networks (Benda et al. 2003; Reeves et al. 1995). Aquatic ecosystems are characterized by a mosaic of components and states that offer the capacity to absorb change (Fig. 1). However, alterations in disturbance regimes as a result of human management may simplify aquatic habitats, reduce system capacity to absorb change, and reduce biodiversity, such as in the form of life-history expression, particularly in salmonids (Fig. 1, moving past a 'tipping point'; Jones et al. 2014).

Disturbance processes often operate at broad spatial scales, making the watershed scale instructive in understanding how disturbances are linked to the ecology and aquatic biodiversity of forested aquatic systems. A natural disturbance regime describes both a set of disturbances and the spatio-temporal pattern of their occurrences, including time post-disturbance for the physical restructuring of materials that have been deposited by the event, such as wood and sediment from a landslide (Miller et al. 2003). Native aquatic species of the Northeast Pacific Rim are adapted to these processes through genetic, life-history, and behavioral diversity that enables recolonization and the use of newly formed and available habitats throughout the watershed (Reeves et al. 1995). At a watershed scale, the signature of habitat complexity and biological adaptation and life-history diversity can be observed.

Landscape ecology studies have demonstrated how aquatic habitats and their biodiversity in forests are inexorably tied to the upland landscape and its pattern-forming processes over spatial–temporal dimensions (Bisson et al. 2003). Instream conditions may be predicted by the geology, topography, vegetation, and disturbances inclusive of land-use conditions found in the upland forests (Burnett et al. 2007; Steel et al. 2012). For instance, intense wildfires occurring in summer may increase landslide potential as vegetation and trees are killed, resulting in reduced slope stability as rooting strength is compromised (Wondzell and King 2003). Debris flows and floods in winter can deliver wood and sediment to the stream channel (Johnson et al. 2000). The hydraulic action of the stream sorts these new inputs, changing aquatic habitat conditions over time (Minshall et al. 1985). Hence, responses to disturbances are rapid, and habitat quality changes from poor, immediately post-disturbance, to potentially high as habitats are rearranged. Without disturbances, hydraulic actions would eventually strip structural components from the stream, and reduce habitat heterogeneity (May and Gresswell 2003), thereby affecting the expression of biodiversity by aquatic species. By considering the diversity of habitats as they are found throughout a stream network, a broad range of biodiversity patterns can be seen through space and time as habitats change in response to environmental conditions.

Key threats and human stressors to aquatic biodiversity in forests

Several human stressors threaten aquatic biodiversity in forests by affecting taxa directly or by influencing their habitat. For example, if some biotic forms are not resilient to change over time, biodiversity may be lost, leading to a novel state with fewer or different

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components (Fig. 1a, b), or the ecosystem may shift toward a novel domain as the environment changes. Habitat loss and degradation, pollution, and invasive species are thought to be the most severe threats to freshwater species (Collen et al. 2014; IUCN: http://www.cmsdata.iucn.org/downloads/species_extinction_05_2007.pdf; accessed 26 Mar 2015). Reduced water availability and altered connectivity are dominant factors in habitat loss (Collen et al. 2014), and freshwater fishes are threatened by overexploitation, forestry practices that degrade habitat conditions, and climate change (http://www.iucnffsg.org/freshwater-fishes/major-threats/). Amphibians are threatened by diseases, which may be unrecognized for other aquatic taxa due to lack of knowledge. Here, we summarize several key threats relative to aquatic taxa in forests (Figs. 3, 4) and discuss implications for biodiversity-related ecosystem services.

Forest harvest

Aquatic ecosystems provide an example of the adaptive management of risk, with forest management practices changing through time to reduce risks to aquatic biodiversity and water quality. Forest management for the joint benefit of water quality and fisheries resources emerged significantly across the US in the mid-1900s with implementation of streamside protection zones and development of new road designs less prone to erosion and sedimentation to streams (e.g., Northcote and Hartman 2008; Stednick 2008). These forest management practices are now embodied in riparian management guidelines and best management practices, which vary by province, state, region and land ownership (e.g., Olson et al. 2007). The basic toolbox of actions to manage aquatic systems includes designation of riparian management zones, and a variety of prescriptions therein, and protected areas such as key watersheds for clean water or endangered species protections. Nevertheless, a legacy of forest practices from the past remains evident in many places, with some sensitive aquatic species and habitats not yet recovered from prior forest-harvest effects, including sedimentation from clearcut logging that restructured stream substrates, loss of shade that increased stream temperature for about 15 years, and direct habitat disturbances from splash dams and logging across streams (Sedell and Luchessa 1982). In some places, these harvest effects occurred coincidentally with other disturbances such as grazing, mining, damming, and overexploitation of fish, making cumulative effects on aquatic species much greater. Today, management of forests to minimize effects on fisheries and water quality are central tenets of forestry practices in the US and many other nations, and they continue to evolve as more information emerges about how critical fish habitats are altered by natural disturbances and human stressors.

Toward the end of the twentieth century, a broader perspective developed for retention and protection of aquatic biodiversity in forests. Elevation of a broad suite of native forest species for management consideration emerged with landscape-scale forest-management goals for maintaining forest ecosystem integrity, and consequent identification of species that were closely associated with late-successional forest conditions (e.g., Federal Northwest Forest Plan: FEMAT 1993; USDA and USDI 1994). Forest aquatic species were part of this evaluation of ecosystem integrity, and numerous assessments were initiated to address the specific associations of forest-occurring species with forest condition and their responses to forest management practices (Thomas et al. 1993). Today, riparian protection zones are not universal or consistent due to management priorities that vary with landownership. This results in wide variation in forest streamside management practices, even in the US portion of the Northeast Pacific Rim (e.g., Olson et al. 2007). Yet, the results of fragmentation from both human stressors and natural disturbances require

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iterative re-evaluation to continue to understand them as they change, across all lands, and it remains uncertain whether a semblance of historic aquatic biodiversity components are being sustained, or if those components are already on a new trajectory to a new ecosystem domain.

Sustainability is a core forest management goal. The fact that forests often remain as strongholds for at-risk aquatic species, that they provide widely valued ecosystem services, that they are critical sources of water, and that they are regionally extensive has led to the development of management rules and accompanying regulations designed to maintain or restore their ecological integrity, inclusive of aquatic forest biodiversity (Lindenmayer and Franklin 2002). Sustainable forest management is "the stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality, and potential to fulfill, now and in the future, relevant ecological, economic, and social functions at local, national, and global levels, and that does not cause damage to other ecosystems". Hence, management to promote resilient ecosystems and to maintain biota, especially fishes and other species with key ecological functions, are contemporary objectives. To ensure long-term sustainability of a multi-state forest aquatic ecosystem without degradation of critical elements, iterative reassessments of species and habitat status and trends are needed, with adaptive management to fine-tune management goals, for example to refine species and habitat protection and restoration approaches.

Fire

Wildfire is a dominant feature of many terrestrial landscapes, but can have profound influences on aquatic ecosystems, particularly streams (Fig. 3; Minshall et al. 1989; Gresswell 1999). The most commonly documented influences of fire on stream habitats include: (1) warming stream temperatures due to loss of shade from ripariantrees burned by wildfires (Dunham et al. 2007; Mahlum et al. 2011); (2) pulsed delivery of wood and sediment to stream channels, and increased probability of high-magnitude disturbances from debris flows and other erosional processes immediately following fire (Miller et al. 2003; Wondzell and King 2003); and (3) potential pulses of nutrients immediately post-fire (Minshall 2003; Spencer et al. 2003; Malison and Baxter 2010). Subsequent effects of fire on aquatic biota include a host of changes in species composition linked to the trophic status of streams (Minshall 2003; Malison and Baxter 2010), changes in species demography (Rosenberger et al. 2015), and in some cases losses of native species (Dunham et al. 2003). When viewed in the context of historical variability, these processes are part of the natural cycle of disturbance and recovery that drives the dynamics of healthy stream ecosystems (Gresswell 1999; Bisson et al. 2003).

Although fire is a natural process, especially in seasonally arid landscapes such as in western North America, historical fire suppression coupled with increasing air temperatures and drought have driven increases in the extent and severity of fires (e.g., Westerling et al. 2006; Dennison et al. 2014). If trends of increased fire continue, some aquatic species could be at much higher risk (e.g., Falke et al. 2015). More generally, threats posed to aquatic ecosystems by wildfires depend strongly on the context of other human influences that may constrain species' resilience in the face of disturbances generated by wildfire (Dunham et al. 2003; Pilliod et al. 2003). Although much of the literature on wildfire and streams has focused on relatively short-term (<20-year) threats posed by disturbances linked to wildfires, it is important to note that over longer time-frames, lack of fire-related disturbances may actually impair stream ecosystem function and lead to a loss of biological

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diversity (Bisson et al. 2003). For example, downstream productivity and biological diversity can depend on pulsed deliveries of sediment, wood, and nutrients from headwaters (Reeves et al. 1995; Benda et al. 2004).

Managing wildfire to address biodiversity in aquatic ecosystems is complex, and has been described in terms of pre-fire, during fire, and post-fire approaches (Dunham et al. 2003). Pre-fire management actions can be judiciously applied to reduce fuel loads in sensitive habitats for aquatic species, and are more likely to reduce threats to species at risk by wildfire (Dunham et al. 2003). Use of fire retardants has become a rapid-response tool, although potential adverse effects on aquatic biota remain poorly studied. Therefore, managers may need to consider the risk and benefit of such use near sensitive aquatic species' habitats. Post-fire, rapid assessments of fire effects and threats of other post-fire disturbances (e.g., landslides) are valuable for prioritizing subsequent management activities (Dunham et al. 2003).

Roads and culverts

Roads are a dominant feature of contemporary ecosystems, leading to a host of direct and indirect effects on ecosystem services and biodiversity (Fig. 3; Forman et al. 2002). In the US alone, for example, over 6 million km of roads cross streams more than 13 million times (Forman et al. 2002). With respect to aquatic biodiversity, one of the most-often cited influences of roads is the effects of road crossings or culverts on the movement of aquatic organisms (USDA 2008). Loss of individual movement or connectivity related to culverts has been linked to declines in overall species richness (Nislow et al. 2011), declines in the abundance and distribution of individual species (Chelgren and Dunham 2015), loss of phenotypic diversity (loss of migratory individuals), and loss of genetic variability within species (Wofford et al. 2005; Neville et al. 2009). Many forest roads were constructed for extraction of forest products, primarily timber. Alteration of forests through timber harvest and the effects of roads themselves have greatly altered the flux of water and sediment into aquatic ecosystems (Luce 2002), affecting species' habitats and life histories. The effects of roads on aquatic ecosystems can be highly variable and depend on how they are used by humans, and how they interact with larger controls imposed by climate, landform, geology, and vegetation (Trombulak and Frissell 2000; Luce et al. 2001).

The effects of stream-road crossings on aquatic biodiversity are well-documented, but identifying effective solutions for active restoration of stream network connectivity has proven challenging. The primary challenges include: (1) identifying biological trade-offs (e.g., benefits to native species, threats from invasion of non-native species; Fausch et al. 2006); (2) short- and long-term costs of restoration (King and O'Hanley 2014; Reagan 2015); (3) prioritizing restoration at local versus regional extents (Neeson et al. 2015); and (4) considering biodiversity in the context of other societal benefits associated with transportation infrastructure (Reagan 2015). The cost of local stream-crossing restoration projects typically ranges from approximately $50,000 to over $500,000 USD per crossing (Reagan 2015), and across the landscape can total to billions of dollars (US GAO 2001; Neeson et al. 2015). Accordingly, one of the major challenges for managers is economic: estimating the short- and long-term costs of restoration and scaling priorities appropriately to efficiently target limited available funding to address multiple objectives (King and O'Hanley 2014; Neeson et al. 2015; Reagan 2015). Recent work on the biological effectiveness of passage restoration has strongly emphasized the importance of scaling.

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Local restoration efforts may prove effective, but fail to significantly influence biological diversity across broader landscapes (Chelgren and Dunham 2015).

Dams and diversions

One of the most significant and intentional changes to aquatic ecosystems is the diversion and storage of water by dams (Fig. 4; Poff et al. 2007). In the US alone, there are over 75,000 dams over 1 m in height (US Army Corps of Engineers 2013); making dams an almost ubiquitous feature of watersheds, including those draining forests. Although dams are often viewed through a negative lens from an environmental perspective, most dams are constructed to provide important provisioning and regulating services for society, such as electricity, irrigation, drinking water, flood control, and recreation. However, dams can undermine the ability of these ecosystems to sustain some ecosystem services and biodiversity.

Dams and diversions impede the migration and movement of organisms, such as stream fishes, by severing the colonization dynamics that maintain genetic, life-history, and species diversity (Fausch et al. 2009). Across large swaths of the US portion of the Northeast Pacific Rim, for example, many large dams (e.g., Grande Coolee) have entirely blocked migration by anadromous salmon and steelhead and reduced fish diversity in the forested headwater streams where these fishes historically spawned and reared (Lichatowich 1999; Gustafson et al. 2007). In addition, reservoirs behind dams are generally low-energy environments relative to un-impounded stream sections; these "longitudinal discontinuities" in the river network can greatly modify the downstream transport of sediment, nutrients, and organic matter (Ward and Stanford 1983). The effects of these "discontinuities" are particularly evident downstream of dams. Severing sediment dynamics, for example, can coarsen bed sediments to such an extent that they can no longer be mobilized by spawning salmonids (Kondolf and Wolman 1993; Kondolf 1997), whereas similar reductions in the upstream supply of organic matter and nutrients can reduce the production and availability of the basal food resources that support healthy and diverse fish populations (e.g., Snyder et al. 2002; Cross et al. 2013). Many large dams also modify the natural flow and temperature regimes (Poff et al. 1997) to such an extent that native species can no longer be successful (Wheeler et al. 2014). For instance, the status of native trout populations was negatively correlated with changes in hydrology in the greater Yellowstone ecosystem (Van Kirk and Benjamin 2001). Together, these changes undermine the natural processes that maintain biodiversity, and generally make conditions more favorable for potential invaders. This is amplified by the fact that reservoirs and associated boat-ramps provide a vector for the passive and active introduction of potentially harmful invasive species by humans (Johnson et al. 2008).

Managing for resilient, sustainable, and biodiverse communities in this context is difficult (Fig. 1). At some dams, the installation of fish-passage facilities has alleviated, to varying degrees, the effects of dams on movement and associated upstream biodiversity of stream salmonids (Pess et al. 2014). However, passage facilities do not address the effect of dams on flow, temperature, and the downstream transport of sediment and organic matter. In some cases, modification in dam operation (when water is stored and released), may alleviate some of these concerns (Olden and Naiman 2010), particularly when dam operations are at odds with the phenology of stream biota (spawn and migration timing). High-flow experiments also are being used as means of reinstating the natural disturbance dynamics that structure physical habitat and ecological processes (Konrad et al. 2011). Temperature-control devices, which selectively draw water from different depths of

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reservoirs, also show promise for creating water temperatures more suitable for native salmonids (e.g., Hanna et al. 1999). Finally, where possibilities for river restoration or improved safety exceed the benefits of retaining a dam, removal is more often being considered a viable option (e.g., Null et al. 2014). To date, there have been close to 1200 dam removals in the US (American Rivers 2014). Although the science of measuring responses and assessing effectiveness is still in its infancy, initial evidence suggests that rivers and associated stream fishes can recover quickly following removal (O'Connor et al. 2015). In systems that retain much of their historic character, such as the Elwha River in Washington state, hopes are high that dam removal will restore biological communities and associated biodiversity (Hart et al. 2002; Duda et al. 2008).

Climate change

Climate change is rapidly altering aquatic ecosystems in forests around the globe (Fig. 3); it will test the resilience of aquatic biodiversity in forests, and the capacity for adaptation by species. In addition, aquatic ecosystems are greatly influenced by the synergistic effects of climate change and other stressors. Increasing air tempteratures and climate model projections suggest that aquatic habitats in forests could become warmer, have more variable thermal and hydrologic regimes, and have increased natural disturbances such as wildfires, floods, and droughts (Jentsch et al. 2007). Specific effects of climate change on aquatic biota in forests will largely depend on the ability of species to withstand or adapt to more extreme climatic conditions. Although species have come and gone throughout Earth's history as climate has altered aquatic ecosystems in forests, recent rapid change in climate may affect the ability of species to cope, leading to a loss of biodiversity. More generally, many species have been unable to keep up with the pace and scale of projected climate change, and as a result are at an increased risk of extinction (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2010). Species and ecosystems that are already at, or close to, the extremes of temperature tolerances or moisture requirements may be at particularly high risk. For example, aquatic species associated with forested ephemeral streams and ponds and seasonally moist microhabitats are vulnerable fauna (Shoo et al. 2011). Although global temperatures are rising everywhere, microclimatic and microhabitat features such as riparian and topographic shading of streams, areas of groundwater upwelling, or even logs in forests can buffer climate extremes for aquatic-dependent species (Shoo et al. 2011; Arismendi et al. 2012). Aquatic-obligate cold- and cool-water species may be particularly vulnerable to the effects of climate change because they require cold, connected, and high-quality habitats. Under contemporary climate change, fish and amphibians are shifting, including range contractions (e.g., Araújo et al. 2006; Wenger et al. 2010), fluctuations in phenology (Parmesan and Yohe 2003), and reductions in body size (Penaluna et al. 2015b). As climate change continues into the future, extinctions of life-history forms and species can be anticipated, especially because high endemism is characteristic of aquatic organisms. Although freshwater biodiversity in forests has persisted under dynamic conditions over the past millennia, showing its adaptive potential, many life-history forms or species have not had to adapt to the influence of rapid climate change combined with other stressors.

Management plans that recognize that climate change and disturbances are integral components of ecosystems may facilitate continued diversity of aquatic ecosystems (Hobbs and Cramer 2008) and the ability to provide ecosystem services. The persistence of aquatic biodiversity in forests will depend on the capacity of populations or species to respond to change and whether effective tools for adaptation management can be designed.

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Aquatic invasive species

Novel ecosystems are developing due to a variety of human activities, including the introduction of new species with the potential to engineer habitat structures and functions, or become key players in food webs and trophic cascades. Invasive species scenarios can unfold rapidly in forest aquatic systems through a variety of transmission pathways, with ecosystem-altering effects. Although the addition of non-native species may temporarily increase the local richness, given enough time they have been shown to be detrimental to native freshwater species (e.g., due to predation, disease, competition, or changes in food supply) (Dudgeon et al. 2006). For example, the introductions of the European Brown Trout (*Salmo trutta*) into South America (Soto et al. 2006) and New Zealand (Townsend 1996) and the Eastern Mosquitofish (*Gambusia holbrooki*) into Australia (Hamer et al. 2002) have caused major reductions in native fauna, inclusive of fish, amphibians, and invertebrates. Similar adverse effects on native amphibians and other ecosystem components have been supported by fish-stocking practices (reviews: Kats and Ferrer 2003; Dunham et al. 2004). Live bait for fishing has been linked to introductions of both non-native species and diseases (e.g., Ranavirus on salamanders in the bait trade, Picco and Collins 2008). Similarly, with the increase in residential water gardens and exotic pets, a variety of aquatic invasive species can be inadvertently spread. Furthermore, concern has been raised for spread of invasive species during water transportation, such as draws from water bodies for wildfire management or other uses (Olson et al. 2013), or with human transportation (float planes, recreational boats).

Due to combined biodiversity conservation and economic concerns to commercial or agricultural interests, including forest integrity, some aquatic invasive species are considered nuisance or injurious species. The International Union for the Conservation of Nature has compiled the 100 worst invasive species for the world (Lowe et al. 2004), and among these are many aquatic species that can occur in forested areas, such as: Japanese Knotweed (*Polygonum cuspidatum*); Water Hyacinth (*Eichhornia crassipes*); amphibian chytrid fungus (*Batrachochytrium* spp.); Zebra Mussel (*Dreissena polymporpha*); and American Bullfrog (*Lithobates catesbeianus*). Ten fish diseases, seven mollusk diseases, eight crustacean diseases, and two amphibian diseases are listed as notifiable by the World Organization for Animal Health (OIE; http://www.oie.int/en/animal-health-in-the-world/oie-listed-diseases-2015/; accessed 29 Apr 2015), which provides recommendations to forestall their spread. The US Department of Agriculture highlights some aquatic nuisance species (http://www.invasivespeciesinfo.gov/aquatics/main.shtml; accessed 28 Apr 2015) and the US Fish and Wildlife Service names several aquatic species as injurious and covered under the US Lacey Act (50 CFR 16; http://www.fws.gov/fisheries/ANS/index.html; accessed 28 Apr 2015). In Canada, the federal government has proposed new regulations to control import, transport, possession, and release of 88 aquatic invasive species and an additional 14 species that may be native in some areas of Canada and invasive in other places (http://www.bcinvasives.ca/documents/Proposed_Federal_regulation_on_ais_2014.pdf; accessed 29 Apr 2015). The net result of numerous aquatic invasive species is a tide of change challenging ecosystem resilience, moving ecosystems to altered compositions and functions, the extent of which is likely not yet realized. Initial focal points for management are losses of native species and impediments to human uses of waters from fouling organisms, as novel ecosystems equilibrate.

In the forests of the Northeast Pacific Rim, the native aquatic biodiversity is encompassed in a multi-state ecosystem, and the addition of aquatic invasive species potentially

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moves the ecosystem into a new domain (Fig. 1). Aquatic invasive species are in a very high rate of flux, with many taxa in apparent early stages of invasion, many being highly managed to forestall their gaining a foothold in regional waters, and others already more established and expanding their distribution. Warm-water aquatic invaders appear to have become more established in many ecosystems, with extensive populations of American Bullfrog, Smallmouth Bass (*Micropterus dolomieu*), Reed Canary Grass (*Phalaris arundinacea*), and other species with warmer habitat requirements (Sanderson et al. 2009). Forested lakes at higher elevations that were naturally fishless have been intentionally stocked with game fishes such as the Brook Trout (*Salvelinus fontinalis*), native to eastern North America, or with hatchery-raised Rainbow Trout (*Oncorhynchus mykiss*) which have dispersed through many connecting streams and now populate entire drainages. As recreational fisheries have been established, food-web alterations have been noted, such as reductions in zooplankton density, and disease issues have arisen (e.g., Whirling disease, *Myxobolus cerebralis*, a disease affecting salmonids, found in transported hatchery fish). Furthermore, as emerging infectious diseases are recognized globally, the potential effect of trade on their introduction to new areas has been elevated as a new biosecurity concern. For example, the recently described amphibian chytrid fungus *Batrachochytrium salamandrivorans* may be fatal to newts native to forests of the Northeast Pacific Rim (Martel et al. 2014). In addition, with some native salmonid species being farmed in local hatcheries to boost recreational fisheries opportunities, genetic and trait differences between wild and hatchery salmon are becoming a concern, where genetic integrity of native stocks is at risk (Pearsons 2008; Muhlfeld et al. 2014). This represents a trade-off of ecosystem services between sustainability of native biodiversity and recreational fisheries experiences and fish production.

There is consensus to expend significant resources to control some aquatic invasive species, especially in the Northeast Pacific Rim. Invasive species councils are well-established in British Columbia, Canada, and the US states of Alaska, Oregon, and Washington, each addressing both pathways of spread and controlling infestations. For example, in Washington state, the 2015 Report to the Legislature (http://www.wdfw.wa.gov/publications/01697/; accessed 29 Apr 2015) reported results from 2011–2013, including: (1) >27,000 boat inspections, with decontamination of 83 boats with aquatic invasive species, of which 19 boats had Zebra or Quagga mussels (*Dreissena bugensis*); and (2) 6 new infestations of New Zealand Mudsnails (*Potamopyrgus antipodarum*). Despite region-wide efforts, some species are recognized as requiring continuous management, whereas for other species, control effectiveness is low. As a result, some invasive species seem to be fully established, pushing affected aquatic ecosystems into new domains (Fig. 1). The future appears to include purposeful management of the multi-state system beyond that which has occurred naturally, to designate both wild and non-wild states, where in some places a semblance of pristine native ecosystems prevails and in other places, where different ecosystem services (e.g., for fishing experiences) can be fostered or diligence for controlling non-natives can be relaxed. Managing for multi-state ecosystems is part of a future New Normal regionally, if not globally (Marris 2010).

Ecosystem functions provided by aquatic biodiversity in forests

Recently, general principles have emerged for the role of biodiversity relative to ecosystem functioning (Hooper et al. 2005, 2012) and several hypotheses have been posed. The "diversity-stability" hypothesis has been the conventional view, that as species are lost, ecosystem function is proportionately affected (McCann 2000). The "rivet" hypothesis

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argues that a loss of species has minimal effect on function until an ecological tipping point is passed, beyond which ecosystem functioning substantially changes (Ehrlich and Ehrlich 1981; Lawton 1994). Extending from the rivet hypothesis is the "redundancy" hypothesis, stating that species are redundant, and the loss of one species leads to no loss to ecosystem function because many species perform the same role. Lastly, the idiosyncratic hypothesis states that there are no general rules and that functioning may be unaffected by the loss of certain species, but greatly affected by the loss of others (Naeem et al. 1994, 1995). Following the idiosyncratic hypothesis, some species may be more important than others, such as those with key ecological functions. Some ecosystem services are dependent on particular species (Hooper et al. 2012). At lower trophic levels, there is a high level of functional redundancy among species. Hence, species loss at lower trophic levels may not necessarily be as detrimental to ecosystem functioning as species loss at higher trophic levels, especially because many ecosystem functions are controlled by a few common species at high trophic levels (Petchey and Gaston 2002). Although trophic levels can overlap due to weak interactions, omnivory, and plasticity, predators at higher trophic levels are fewer and have little to no redundancy (Estes et al. 2011). Reduction of predator diversity and abundance can have cascading consequences in ecosystems, such as a loss in regulation of the assemblage structure, food web, and ultimately ecosystem function (Hairston et al. 1960; Power 1992; Estes et al. 2011). Although this is not well studied in Pacific Northwest streams, in perennial streams of western forests, Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) and Coastal Giant Salamanders (*Dicamptodon tenebrosus*) are top predators thought to exert strong trophic cascades through aquatic food webs. Where they coexist, giant salamanders appear subordinate to trout and rely on coarse substrates for habitat refugia and predator avoidance (Rundio and Olson 2003). Smaller torrent salamanders, *Rhyacotriton* spp., are predators in these same systems but occur upstream in intermittent or discontinuous headwater stream reaches; their spatial segregation is likely due in part to the effects of downstream predation (Rundio and Olson 2003). Such patterns of assemblage structure beg questions about consequent roles for food webs and ecosystem functions in different parts of the stream network. These functions remain to be examined. Although diet analyses show all these stream predators to be gape-limited, and hence prey are partioned by body size, ties to ecosystem processes are not well-grounded. However, insights from salamander studies in terrestrial contexts suggest their effects on arthropods breaking down forest litter and general energy transfer are significant, potentially having a signature on carbon sequestration (Best and Welsh 2014; Semlitsch et al. 2014).

Ecosystem services supported by aquatic biodiversity in forests

The term "*ecosystem services*" is commonly used to describe the goods and services enjoyed by people that are provided by functional ecosystems without substantial human input (Daily 1997; Millennium Ecosystem Assessment 2005). The advent of ecosystem services terminology led by these above efforts aligned with the work of a subset of economists who had already been accounting for the value of nature to people. Hence, these two disciplinary approaches produced different frameworks that are now being reconciled (Wallace 2007; Boyd and Banzhaf 2007; Fisher et al. 2009). Although there is no single standard definition of ecosystem services, we chose the "final" ecosystem services perspective to promote a focus on ecological outcomes with a clear connection to social value (Boyd and Banzhaf 2007; Johnston and Russell 2011; Ringold et al. 2013; Landers and Nahlik 2013; Boyd and Krupnick 2013; Weber and Ringold 2015; Boyd et al.

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in press). In forest aquatic systems, fish are an example of a final ecosystem service, providing market benefits such as a food and income source, as well as nonmarket benefits including recreation opportunities and species protection value (Table 1; Fig. 2).

In contrast to final ecosystem services, intermediate ecosystem services are those that support final services. However, many services offer "dual services" by contributing to both intermediate and final ecosystem services. Although biodiversity is a dual service, there are numerous aspects of ecosystems and biodiversity that are primarily intermediate services (Febria et al. 2015; Table 1; Fig. 2). Focusing on final services does not diminish the importance of intermediate services, but rather emphasizes them, because they are the foundation of complex ecological processes and functions producing outcomes that constitute final ecosystem services. For example, in valuing fish as a final ecosystem service, other aspects of biodiversity including the role of amphibians, crustaceans, and invertebrates are valued because they affect the production and diversity of fish, but again some of these taxa may be directly valued, making them dual services (Fig. 2). The focus on final ecosystem services avoids double-counting the ultimate impact of changes in ecosystem services on human well-being. A systematic way to account for ecosystem services values is important because numerous aquatic ecosystem services (clean water, fisheries, native species) are in decline, potentially leading to concerns for ecosystem transitions over tipping points in response to a variety of natural disturbances and human stressors (Fig. 1).

Costs of changes to ecosystem services

In light of contemporary disturbances, an appropriate question is 'what does this mean for human well-being?' Both intermediate and final ecosystem services are affected by the

Table 1 Intermediate and final ecosystem services potentially provided by aquatic biodiversity in forests

Ecosystem service	Explanation	Examples
Intermediate	Ecological structures, functions, and processes that are relevant for human well-being or sustaining ecosystem structure or processes	Erosion control; water quality; instream habitat; riparian habitat; forest water cycle; amphibian and invertebrate communities; biodiversity of fish; cross-ecosystem subsidies; thermal, hydrological, and chemical regimes; food webs; nutrient cycling; energy flux; decomposition; carbon sequestration; climate stability
Final	Valued based on direct relevance to the public	Water quantity sufficient for human use; water quality safe for human consumption; timber; food; pharmaceuticals; flood mitigation; fire prevention; riparian habitat; biodiversity of fish; individual fish species; recreation opportunities; ecotourism opportunities; education opportunities

These examples are hypothesized—the true test of a final ecosystem service (vs. intermediate) is whether it is valued in and of itself. Thus our categorization above is context-dependent. For example, some people appreciate invertebrates directly, not just as indicators for healthy fish conditions. Furthermore, note that many services are "dual", being both valued in and of themselves, but also intermediates involved in the production of other final services (Boyd and Krupnick 2013). Above, biodiversity of fish is thought to be such a dual commodity, and we place it in both the intermediate and final categories. Riparian habitat is another example of a dual service—people directly appreciate streamside vegetation, as well as the birds and other wildlife it attracts

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same threats, refocusing attention on valuation. Effects on human well-being are strongly context-specific. For example, increased access to clean water has an extraordinarily high value where such access is lacking; in locations where clean water is plentiful, the value of accessing an additional unit is not as high. Furthermore, value depends on the sheer scale of change for a particular final ecosystem service. All else being equal, smaller changes are not as important for human well-being as large changes. Hence, ecosystem tipping points are especially important, because they can herald threats to transcendent ecosystem services with heightened human value.

Despite the challenges to offering a full accounting of the value of ecosystem services associated with past and potential changes in aquatic biodiversity, some progress forests can be reported in the context of Northeast Pacific Rim. Although empirical investigation of the range of ecosystem services which resonate with people is still new for social scientists, a series of focus groups convened in Oregon on the topic of rivers and streams found recurrent interest in relatively few themes. A partial list of these services are water quality safe for swimming, flooding that causes property damage, native species, and gamefish (Weber and Ringold, unpublished data). Such results lend hope that a finite and operational list of final ecosystem services can be documented for a given group of persons for a given ecosystem, and thus serve as a way of focusing attention for both ecological investigation and collaborative valuation research. Valuation results for changes in Pacific Northwest regional salmonid populations are intriguing because so much of the total economic value appears to be due to 'nonuse' cultural values, thus extending well beyond anglers. In fact, available evidence shows that people from other places in the US highly value Pacific salmon (Pate and Loomis 1997). Several studies since 1990 have contributed to this body of knowledge (Olsen et al. 1991; Hanemann et al. 1991; Loomis 1996; Bell et al. 2003; and Mansfield et al. 2012) as summarized by Weber (2015). The monetized values for increases in wild Pacific salmon and steelhead (*Oncorhynchus* spp.) abundance (as published, not adjusted to reflect net present value in 2015 $USD) range from $10 (for 120,000 additional fish) to more than $400 per household per year (for 2,500,000 additional fish) (Mansfield et al. 2012; one negative estimate attributed to poor significance of model variables, p. 8–3 to 8–5). Some of these results reflect households in non-western states, however there was still significant support for western US salmon, emphasizing the importance of nonuse values. Both in the western US and elsewhere in the US, values between $10 and $68 per household per year were reported for improvements of 120,000 additional migrating wild Pacific salmon and steelhead in the Klamath River, and an additional 300,000 migrating wild Chinook Salmon (*O. tshawytscha*) in the Elwha River of the Olympic Peninsula, respectively, expected to be achieved by dam removal in both instances. Although such information does not provide a complete portrait of the value of all the changing ecosystem services related to aquatic biodiversity in forests, it demonstrates that the total economic value for just one high-profile final ecosystem service has been estimated to be quite large, particularly when aggregated across the number of years of payment and number of relevant households, locally and nationally.

Valuing the future—a view downstream

Given the emerging issues and complexities involved in protecting and enhancing aquatic biodiversity in forested ecosystems, is it possible to map out a specific path or to provide operational advice for practitioners? The sheer number of players, processes, values, and uncertainties associated with aquatic biodiversity dictate a carefully measured approach. We can offer a few specific suggestions based on our analyses of the issues herein. First, as

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we progress toward the future, it can be useful to look back in time to understand historical processes and events that shaped the current aquatic biodiversity present today. Yet, it is also clear that it will not be possible to return ecosystems to a state that perfectly replicates historical ecosystem goods and services. Critical information on historical processes always may be lacking, and it is clear that many historical processes are no longer operative, or have been supplanted by both new and difficult-to-reverse changes that will likely become magnified in coming decades. Peering into to the future, uncertainty reigns regarding an understanding of processes and projections. Accordingly, the call for a "measured" approach is literally a call for measurements: better quantification of ecosystem processes, development of alternative mechanistic models to understand process interactions, monitoring of ecosystem services, human values, and well-being, and development of approaches that integrate this information in the form of decision-support tools that practitioners can readily apply. By identifying final ecosystem services, managers can reverse-engineer—deconstruct natural systems to understand the underlying structure, functions, and processes that also may have extended management considerations. As pressures continue, and demand for ecosystem services associated with aquatic biodiversity increases, the need to better understand these resources will increase, hence tying final to intermediate services is likely to become more of a priority. We suggest that to achieve complex multi-state systems, management objectives may need to be more complex as well, and tied to local- and watershed-scale conditions. Management solutions that worked in the past may not continue to work now or in the future. It is equally important to recognize that choosing not to manage or to allow passive restoration is also a management action. By continually questioning, evaluating, and refining assumptions about the most useful and effective practices, managers may have greater success in managing aquatic biodiversity in forested ecosystems.

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