

Using Natural Disturbance and Portfolio Concepts to Guide Aquatic–Riparian Ecosystem Management

Brooke E. Penaluna | U.S. Forest Service, Pacific Northwest Research Station, 3200 Southwest Jefferson Way, Corvallis, OR 97331.
E-mail: bepenaluna@fs.fed.us

Gordon H. Reeves | U.S. Forest Service, Pacific Northwest Research Station, Corvallis, OR

Zanethia C. Barnett | U.S. Forest Service, Southern Research Station, Oxford, MS

Peter A. Bisson | U.S. Forest Service, Pacific Northwest Research Station, Corvallis, OR; and U.S. Forest Service, Pacific Northwest Research Station, Olympia, WA

John M. Buffington | U.S. Forest Service, Rocky Mountain Research Station, Boise, ID

C. Andrew Dolloff | U.S. Forest Service, Southern Research Station, Blacksburg, VA

Rebecca L. Flitcroft | U.S. Forest Service, Pacific Northwest Research Station, Corvallis, OR

Charles H. Luce | U.S. Forest Service, Rocky Mountain Research Station, Boise, ID

Keith H. Nislow | U.S. Forest Service, Northern Research Station, Amherst, MA

John D. Rothlisberger | U.S. Forest Service, Washington, D.C.

Melvin L. Warren Jr. | U.S. Forest Service, Southern Research Station, Oxford, MS

Steelhead landslide, North Fork Stillaguamish River, Oso, Washington, March 2014. Photo credit: Air Support Unit, King County Sheriff's Office

The U.S. Forest Service and other federal land managers are responsible for maintaining the productivity of aquatic-riparian ecosystems, the associated native biota, and the ecosystem services they provide. These public lands are important sources of water, recreation opportunities, and habitat for a suite of animals and plants, including many that are protected under the Endangered Species Act. To meet these challenges and responsibilities, recent science suggests modifying practices to provide a broader array of habitat, biological conditions, and ecosystem functions than are associated with traditional management approaches. We suggest that by linking approaches based on natural disturbance and portfolio concepts, managers can achieve a robust strategy and desired outcomes more reliably and cost effectively. Locally complex habitat conditions created by natural disturbances provide the template for biological diversity to play out if provided enough time. Accordingly, natural disturbance regimes play an important role in creating and sustaining habitat and biological complexities on the landscape, suggesting that, to the extent possible, management actions should emulate natural disturbance processes at appropriate spatial and temporal scales. In concert with this approach, the portfolio effect (i.e., diversity that mitigates risk) provides justification for promoting connected heterogeneous habitats that reduce the risk of synchronous large-scale population and ecosystem collapse. In this article, we describe how disturbance and portfolio concepts fit into a broader strategy of conserving ecosystem integrity and dynamism and provide examples of how these concepts can be used to address a wide range of management concerns. Ultimately, the outcome for populations, habitats, and landscapes depends on how well environmental change is understood, the degree to which change is appropriately addressed by natural resource managers, and solutions that allow populations and ecosystems to persist in the presence of and be resilient to a growing scope of human influences.

INTRODUCTION

Aquatic ecosystems, including rivers, streams, lakes, and their adjacent riparian zones, provide water (Brown et al. 2008), recreation opportunities (Gillespie et al. 2018, this issue), and habitat for biota (Postel and Carpenter 1997), the provision of which is especially important on federal lands in the USA. However, growing human needs and demands have led to increased global consumption of natural resources and an overall decline in ecosystem services (MEA 2005), warranting a potential shift in management goals and action plans. The traditional management approach to meeting these responsibilities has been to create and maintain a standard set of conditions across a landscape, often targeted toward a subset of selected organisms. This perspective assumes that (1) once the desired outcomes are achieved, a well-managed landscape will remain relatively static; and (2) a static state best supports sustainable ecosystem services. However, a static ecosystem perspective does not capture the dynamic nature of natural systems that is necessary to support long-term habitat complexity and species diversity (Montgomery 1999; White and Jentsch 2001; Bisson et al. 2003; Hiers et al. 2016). Emerging views of aquatic-riparian ecosystems describe them as having a range of processes and attributes that are inherently complex, nonlinear, and dynamic (Reeves et al. 1995; Wallington et al. 2005; Penaluna et al. 2016). In particular, habitat conditions that are currently deemed unfavorable could become high-quality habitat in the future because natural processes promote habitat change over space and time. From this perspective, concepts of disturbance and portfolio effects are central ecological tenets, where “disturbance” refers to natural processes initiating renewal or change (Box 1), and “portfolio” refers to diversified population characteristics (diversity in life-history strategies, life-history patterns, age structure, forms, genetics, and behaviors) that result from maintaining a mosaic of habitat conditions through natural disturbances (Box 2). We posit that guiding habitat management using natural disturbance and portfolio concepts provides a broader array of biophysical complexities and ecosystem functions than would occur under a static ecosystem perspective. In addition, these concepts are foundational ideas used to create the *Rise to the Future: National Fish and Aquatic Strategy for the U.S. Forest Service* (Shively et al. 2018, this issue).

Land and resource management based on natural disturbance and portfolio concepts promotes and uses the inherent variability in populations, habitats, and landscapes to ensure their long-term productivity. Natural disturbance regimes locally stimulate ecological processes that sustain heterogeneity of habitats and biological responses across the landscape (Box 1). To the extent possible, if managers emulate and/or allow natural disturbance processes at naturally occurring frequencies and magnitudes across the landscape, a mosaic of biophysical conditions will develop over time (e.g., Schmidt et al. 2001). In this regard, the temporal and spatial scales of disturbance are fundamental metrics for understanding—and consequently managing—dynamic ecosystems (Miller et al. 2003; Hessburg et al. 2015). In general, a landscape that is variable in space and time offers opportunities for the expression of a broad spectrum of life-history strategies and individual-level responses (McCabe and Gotelli 2000).

In ecology, the portfolio effect also plays out at the landscape scale and reflects the diversity of behavioral and life-history variability within populations that safeguards the metapopulation against temporally variable conditions (Box 2; Hilborn et al. 2003; Figge 2004; Stein et al. 2014). Phenotypic plasticity and diversity within a population may reflect past genetic adaptation to variable environmental conditions. This type of biological diversity may only be expressed in a population when a diversity of habitat types is available (e.g., estuary habitat use by juvenile Coho Salmon *Oncorhynchus kisutch*; Jones et al. 2014). Accordingly, portfolio concepts provide justification for maintaining connected heterogeneous habitats with different disturbance regimes that have experienced different types of disturbance (e.g., flood, fire, and wind storms) across as broad a spatial extent as possible to minimize the risk of population failure that might otherwise occur for homogeneous conditions or spatially limited populations. When local population extirpation occurs, habitat heterogeneity decouples local conditions from broader spatial and temporal scales, thereby softening its effects on the rest of the population (Schindler et al. 2015). As some individuals or local populations disappear across a landscape due to natural disturbances, others do not (progressive species turnover; Gutiérrez-Cánovas et al. 2013), thereby allowing the overall population complex to persist over time (Figure 1). For example, over time in different

BOX 1

THE ROLE OF NATURAL DISTURBANCE AND RENEWAL IN AQUATIC-RIPARIAN ECOSYSTEMS

Natural disturbance regimes are inherently variable, containing both disturbance events and a period of renewal (Reeves et al. 1995; White and Jentsch 2001). Disturbance initiates change that sustains heterogeneity of habitats and biological patterns, which is immediately followed by a period of renewal and, in some cases, transition toward a novel state. A disturbance event is characterized by its frequency, magnitude, and severity (White and Pickett 1985; Resh et al. 1988; Poff 1992). Disturbance events interact with riparian (Gregory et al. 1991), floodplain (Junk et al. 1989; Benke et al. 2000), upslope (Montgomery 1999), and surface and groundwater (Stanford and Ward 1993; Buffington and Tonina 2009) zones to form multi-scale habitats over space and time. Disturbances include low-frequency, high-magnitude events, which can reshape the present-day course of rivers, alter channel morphology, and have substantial effects on habitat (e.g., glaciation, megafloods, megadroughts, volcanic eruptions, earthquakes, and severe wildfire; Resh et al. 1988; Swanson et al. 1988; Reeves et al. 1995). In contrast, high-frequency, low-magnitude disturbances typically have smaller habitat effects (e.g., small landslides, rilling of bare hillslopes, annual floods, seasonal low flow, wind events, disease, and variations in marine and freshwater productivity; Waples et al. 2008). All of these disturbance events are important for the long-term productivity of aquatic-riparian ecosystems (Bisson et al. 2009).

Following natural disturbance is a period of renewal, in which physical and biological processes reorganize as inputs of wood, sediment and nutrients from the disturbance are sorted by the river network, with consequent changes in habitat type and configuration occurring over time. These processes of change and organization vary on time scales of a season to millennia before the next disturbance occurs and resets the system. Renewal begins at a point encompassing the collection of legacies of all past and current natural disturbances and human actions. Short-term disturbance effects can result in habitat loss and eradication of local populations. However, over the long term, natural disturbance

events will rejuvenate habitat by providing critical inputs of wood and sediment—the building blocks of complex aquatic habitat (Reeves et al. 1995). Disturbance followed by renewal is a process that ecosystems require for maintaining their long-term productivity and integrity. In addition, some systems may exhibit nonstationary disturbance regimes (e.g., in response to climate change) that can cause emergence of novel habitat states over time. Moreover, disturbance regimes and ecosystem function may need to be rescaled in systems that are limited by human use (e.g., where the natural disturbance regime has been altered to protect infrastructure or to extract water for human consumption). In such cases, it may be possible to develop dynamic ecosystems if sufficient levels and patterns of disturbance can be achieved within the limits of human use (e.g., USFWS and HVT 1999), even though it may not be feasible to restore the natural disturbance regime *sensu stricto*.

Natural disturbance processes in river corridors vary according to location within the network (Figure 2), creating habitats within habitats (Frissell et al. 1986). The composition and structure of rivers and riparian zones are shaped by disturbances at patch, reach, subbasin, and catchment scales. Systematic downstream changes in disturbance regimes give rise to spatially covarying habitats (Figure 2), with downstream trends locally disrupted or reset by physical heterogeneity (e.g., tributary junctions, changes in lithology, geomorphic history, or land-use). Disturbance processes of channel migration, avulsion, and flooding dominate in unconfined floodplain rivers compared to flooding, debris-flow scour/deposition, and hillslope avalanches that occur in confined channels (Montgomery 1999). Lower portions of a river network are also more variable through time, leading to different biological patterns than stream segments in the upper and middle portion of the network, which can exhibit substantial, but infrequent, habitat changes (Naiman et al. 1993; Benda and Dunne 1997a, 1997b; Buffington 2012). Similar patterns of heterogeneity are seen within riparian areas of forest stands (Lindenmayer and Franklin 2002).

geologic regions in Bristol Bay, Alaska, various life-history strategies of Sockeye Salmon *O. nerka* have been the major producers of these fish in the basin (Hilborn et al. 2003). As noted by Hilborn et al. (2003:6567), the implication is that “If managers in earlier times had decided to focus management on the most productive runs at the time and had neglected the less productive runs, the biocomplexity that later proved important could have been lost.” Similarly, variation in Brook Trout *Salvelinus fontinalis* life histories due to differences in flow and temperature in headwater tributaries versus mainstem habitats in the Connecticut River basin of New England has contributed to the long-term persistence of this metapopulation (Kanno et al. 2014; Letcher et al. 2015; Bassar et al. 2016). However, individuals or populations can also disappear across a landscape due to human actions, with the resulting communities differing from those formed by natural disturbances. For example, macroinvertebrate communities in rivers can lose specialist taxa in response to human actions whereas there is progressive species turnover resulting in different taxa diversity and communities from natural disturbances (Gutiérrez-Cánovas et al. 2013).

Although portfolio (DuFour et al. 2015; Schindler et al. 2015) and natural disturbance concepts (Reeves et al. 1995; Lindenmayer and Franklin 2002; Sibley et al. 2012) have been proposed separately as foundations for management, we suggest that the two can be combined to provide a robust framework for guiding management actions. The portfolio concept places aquatic biota at the center of management goals emphasizing the importance of diversified populations. Both natural disturbance and portfolio concepts provide perspective on management of habitats, landscapes, and aquatic-riparian ecosystems by (1) emulating or allowing natural disturbance in management to encourage habitat heterogeneity and (2) promoting connected heterogeneous habitats across broad spatial extents.

EMULATING NATURAL DISTURBANCE IN MANAGEMENT TO ENCOURAGE HABITAT HETEROGENEITY

Managing for landscape heterogeneity requires emulating or restoring underlying disturbance processes to support and generate diversity across spatial extents and ecological levels

BOX 2
THE CONCEPT OF A PORTFOLIO EFFECT APPLIED
TO POPULATIONS, HABITATS, AND LANDSCAPES

Analogous to economic portfolios in which managers minimize risk by diversifying investments (e.g., currency, stocks, bonds, and real estate), thereby creating stability across an investment strategy, the ecological diversity that contributes to long-term resilience in variable environmental conditions is referred to as a “portfolio effect” (e.g., Tilman and Downing 1994; Luck et al. 2003; Schindler et al. 2010). Increased biocomplexity produces temporally stable systems because of complementary or independent dynamics among species, populations, individuals, or genes that perform similar ecosystem functions (Luck et al. 2003; Figge 2004). Populations that do not show portfolio effects may be more vulnerable than populations with higher biocomplexity in the face of habitat modification (e.g., road networks, fire, timber harvest, dams/diversions) or overfishing, leaving those populations susceptible to natural fluctuations, further human exploitation, and stressors (Hilborn et al. 2003; Carlson and Satterthwaite 2011; DuFour et al. 2015). However, when sufficient data are available to evaluate the portfolio effect of focal populations, managers can make better-informed decisions (DuFour et al. 2015) about populations, communities, habitats, landscapes, and ecosystems.

Under portfolio concepts, all natural habitat classes have value because it is understood that habitat quality changes over space and time, especially considering that ecosystems are constantly in flux (Figure 1). As is consistent with concepts from metapopulation dynamics, the “lights of individual patches wink on and off unpredictably, but the overall average level of illumination—the overall density of the... populations—may remain relatively stable” (May 1994). Populations that maintain a diverse portfolio of characteristics (diversity in life-history strategies, life-history patterns, age structure, forms, genetics, and behaviors) persist in highly variable conditions because their innate diversity of responses and conditions insures against variable outcomes (life-history strategies; Hilborn et al. 2003). Because the portfolio concept provides insights into how species interact and how evolutionary strategies develop, it can also be used to explain how ecosystems are organized (Schindler et al. 2015). Conservation plans that encourage a mosaic of habitat conditions, changing through time, support a portfolio concept of population, community, habitat, landscape, and ecosystem diversity.

of organization under the portfolio concept. This may involve mimicking the underlying process through novel disturbances (e.g., cutting trees to simulate wildfire loss that initiates stand dynamics but also leaving the forest to recover) or restoring natural disturbance regimes. Allowing natural disturbance processes to play out, however, may sometimes be unfeasible because of other societal demands on forests and water. For example, fire-related management activities may disrupt watershed processes and degrade habitat for sensitive fishes (Rieman et al. 2010). Human influences offer a means of promoting disturbance and biological response but frequently differ from natural disturbances in the timing, magnitude,

spatial extent, and nature of the disturbance (Lindenmayer and Franklin 2002; Hessburg et al. 2005), and may result in ecosystem structure and connectivity that differ from natural conditions (Stanford and Ward 1992). Human actions interrupt migratory life histories of aquatic organisms through road crossings and other barriers (Dunham et al. 2003; Rieman et al. 2003); alter sediment production and transport regimes (Istanbulluoglu et al. 2004; Goode et al. 2012; Maturana et al. 2014); change flow, bed scour, and temperature regimes (Marks et al. 1998; Lessard and Hayes 2003; Tonina et al. 2008); and alter wood loading and channel morphology (Montgomery et al. 1995; Wood-Smith and Buffington 1996; Benda et al. 2003; May and Gresswell 2003). Although many of these environmental conditions can be affected by both human actions and natural disturbances, human actions rarely mimic natural regimes and frequently introduce novel—and potentially detrimental—conditions. For example, chronic supplies of fine sediment from forest roads can have a greater and longer-lasting impact on salmonid spawning habitats than an equal volume of material introduced as a sediment pulse by a naturally occurring debris flow or landslide (Maturana et al. 2014). Road systems also affect aquatic habitats by increasing turbidity, which can affect fish feeding (Bilby 1985). Beyond creating potentially detrimental conditions, aquatic organisms are likely not adapted to human disturbances, which tend to be more intensive and frequently result in simplified habitats (e.g., Sedell and Froggatt 1984; Wood-Smith and Buffington 1996). Understanding how natural ecosystems maintain habitat complexity is critical for effectively mimicking natural dynamics, or at the very least not impeding them, and potentially managing human actions to produce patterns that are more similar to natural disturbances. Because natural disturbance initiates much of the ecosystem dynamism in aquatic-riparian ecosystems (Figure 2), emulating and (to the extent possible) allowing natural disturbance processes in management practices may lead to long-term productivity and resilience of ecosystem services (Koellner and Schmitz 2006; Penaluna et al. 2016).

There have been two signature approaches to the inclusion of disturbance processes in management: pragmatism and deliberate design. Each approach has value and provides options to managers interested in incorporating natural disturbance processes into their management plans. Both approaches use geospatial tools (e.g., LandTrendr: www.landtrendr.forestry.oregonstate.edu; Netmap: www.terrainworks.com) to evaluate natural variability of aquatic-riparian ecosystems and disturbance processes. A pragmatic approach uses this information to inform decisions in ad hoc applications. An example would be placement of large wood in streams after a timber sale, with the intent of improving aspects of aquatic habitat condition but not to reproduce the natural wood input regime per se. In contrast, deliberate designs attempt to mimic disturbance processes by using strategic planning. For example, a watershed-scale study in Augusta Creek, Oregon, compared two different management approaches and determined that the approach based on historical fire regimes offered the best outcomes over the long term for aquatic-riparian ecosystems (Cissel et al. 1998). However, emulating disturbance in management could also collapse an entire population or ecosystem if we act with hubris. Inclusion of decision support systems (where models can evaluate proposed management actions) and adaptive management programs (where we learn from prior mistakes and successes) can reduce such

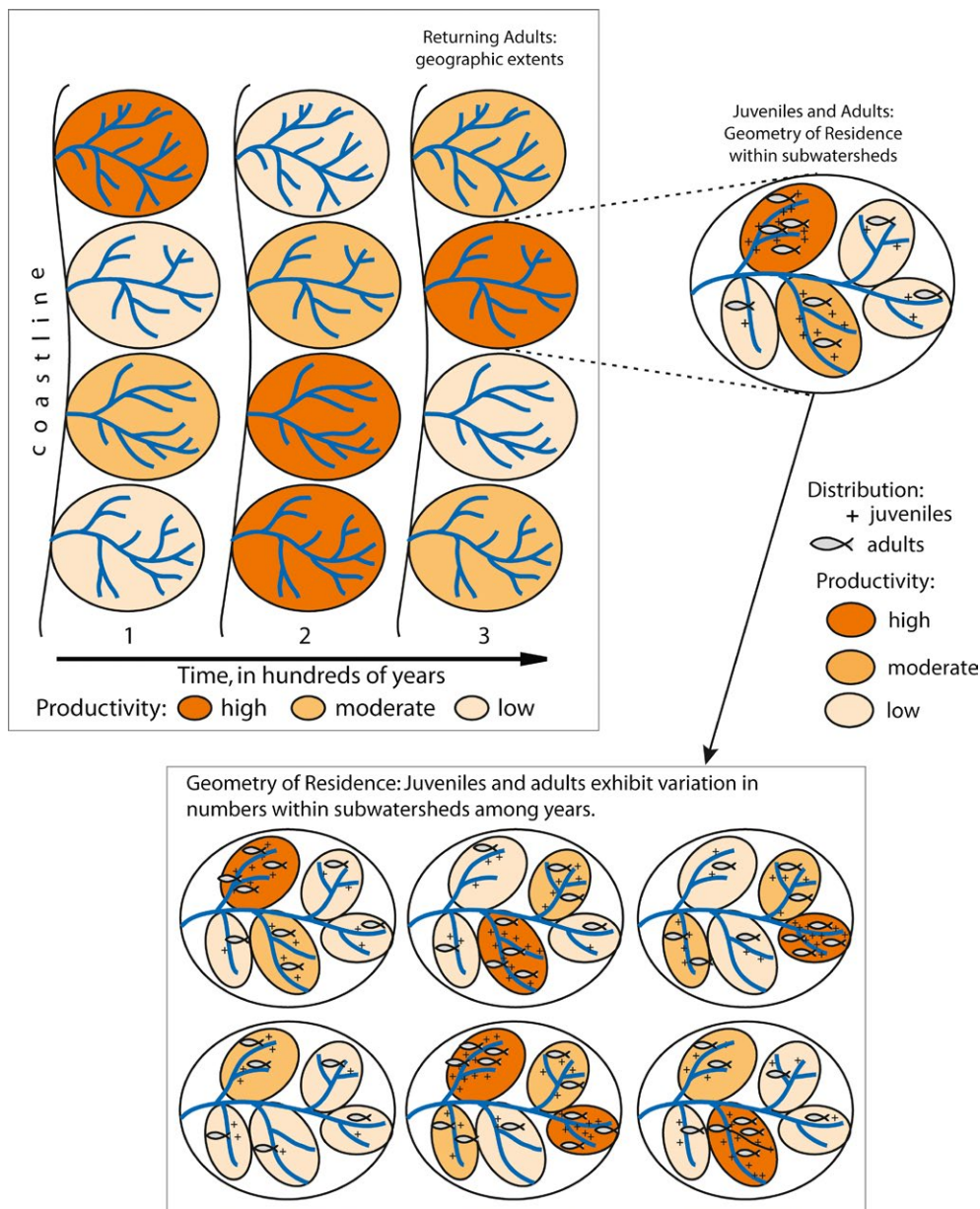


Figure 1. Conceptual scheme of the portfolio concept, showing how habitat quality changes over space and time. As habitat changes at varying scales of spatial organization, local populations of fishes will experience positive or negative effects over time. Resident fishes with limited mobility may be most limited in the short-term, postdisturbance time period as local habitat is compromised. Fishes that are more mobile or that display diverse behaviors or life-history strategies may be better able to cope with the varying habitat quality in a specific location over time because they can take advantage of higher-quality habitats located elsewhere in the matrix of stream habitats.

risk. If human activities are designed to support ecological processes that mimic disturbance processes in time and space, then native aquatic species whose populations are adapted to those conditions may be better equipped to cope with change (Waples et al. 2008).

Aquatic-riparian ecosystems typically maintain high levels of structural complexity after natural disturbances due to biological legacies reflecting underlying processes and previous conditions (Lindenmayer and Franklin 2002). Consequently, managers may ensure a broad range of variability across the landscape by emulating underlying processes associated with disturbance in their region to offer populations the best opportunity for resilience. Across the USA, natural

disturbances vary regionally in terms of the frequency, spatial extent, magnitude, and potential ecological effects for both present and future conditions. To illustrate how managers can think about disturbance in their region, we used professional judgement as a starting point for conversations about emulating or restoring natural disturbances in the context of human stressors (Figures 3–6). For example, wildfire and drought are frequent disturbances affecting the whole region in the northern Rocky Mountains, leading to extreme ecological effects (Figure 5). Within a given region, natural disturbances and their effects on the ecosystem vary by position in a river network, the associated local conditions, and the legacy of past natural and human disturbances in the watershed (Figure 2).

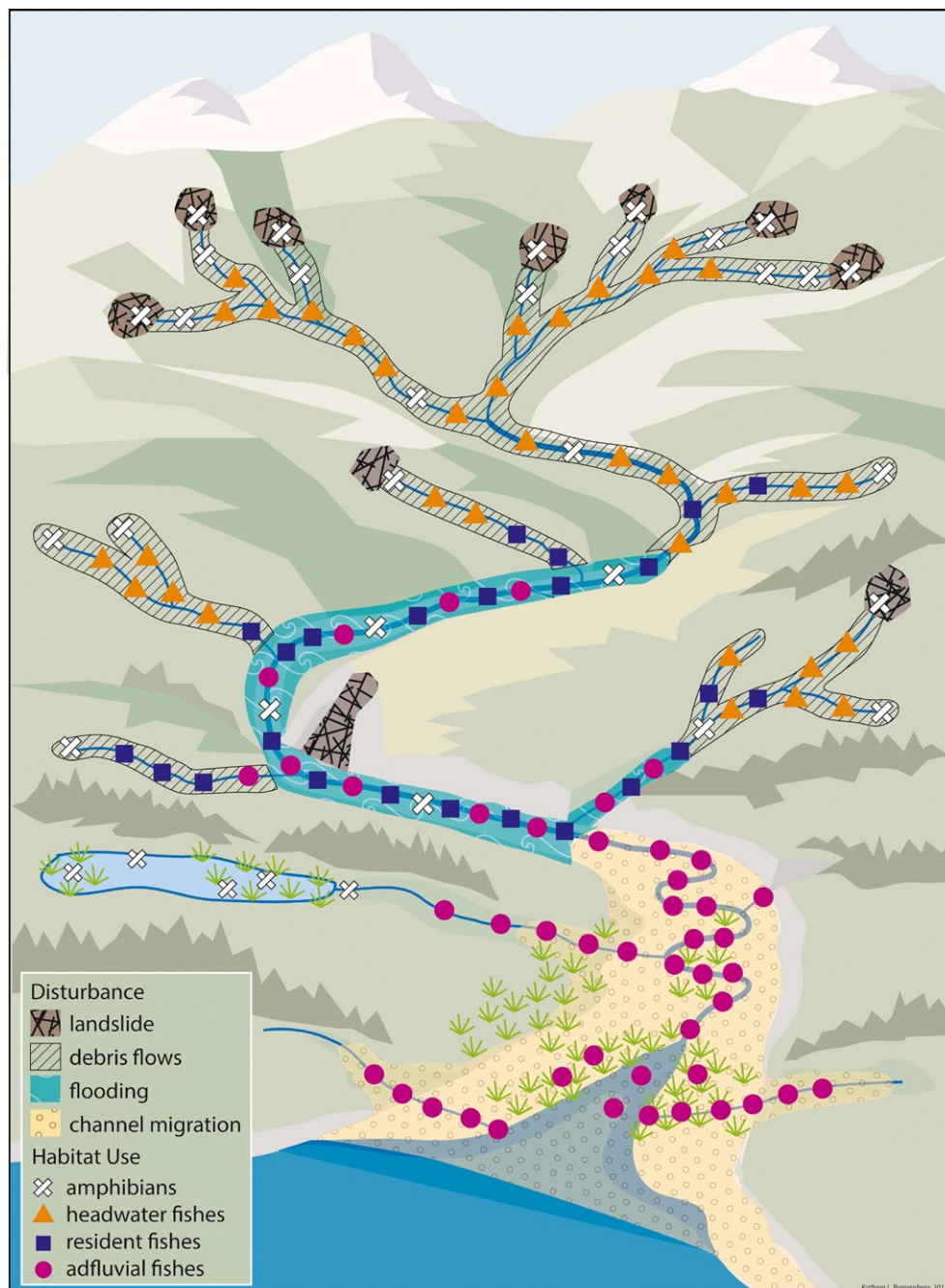
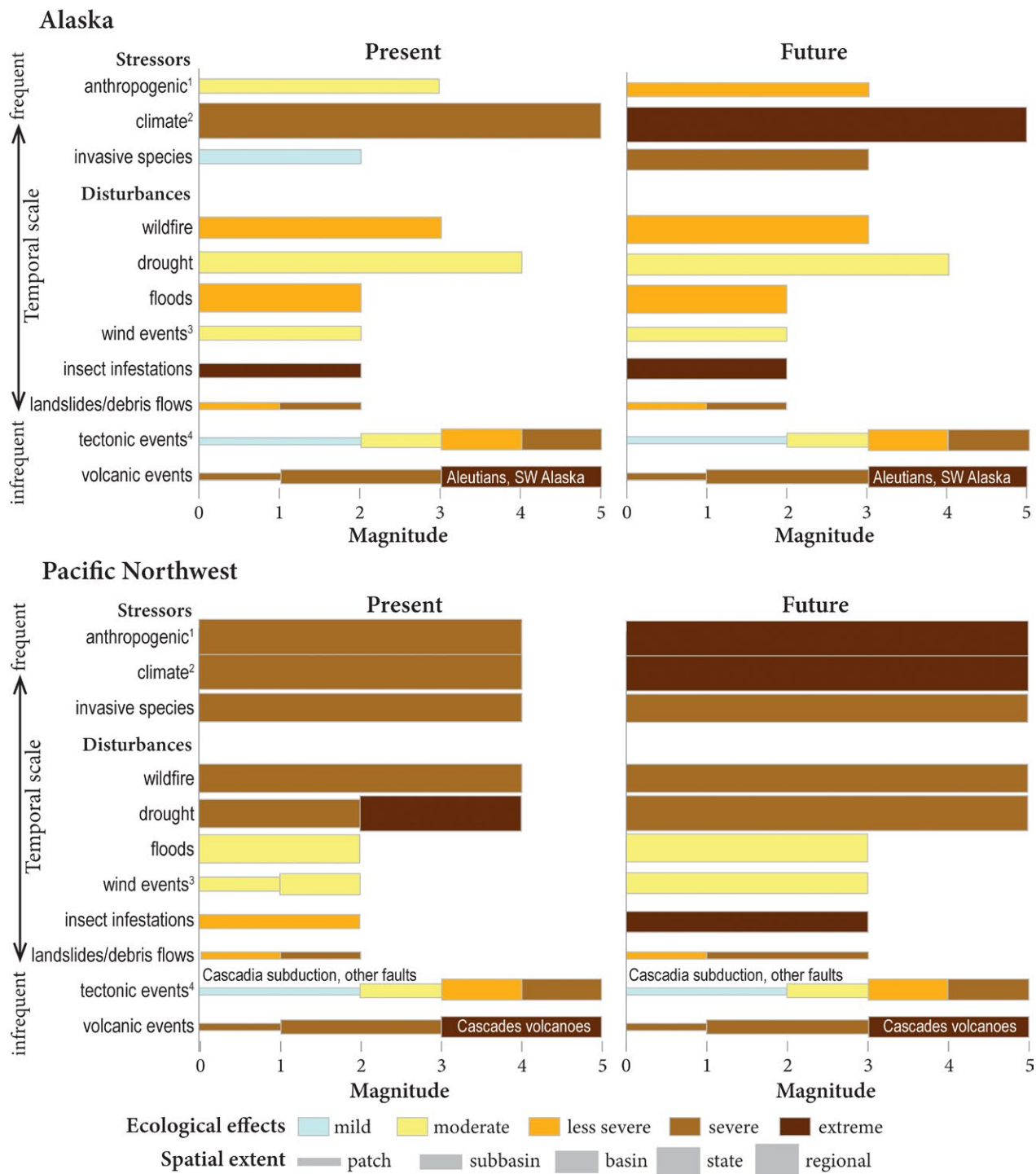


Figure 2. Generalized natural disturbances in a river network (modified from Montgomery 1999). Overlaid are types of aquatic species that are generally adapted to each area. The actual occurrence of a disturbance event depends on local conditions, including topography and soil type, and the legacy of past natural and human disturbances, such as the extent to which best management practices have been implemented regarding riparian buffers, conservation tillage, and culvert upgrades.

In places where emulating natural disturbances is no longer possible (e.g., due to development), managers may have to use active restoration to return key system structures and functions to a desired level so that future natural disturbances and human actions may operate without undesired consequences (Rieman et al. 2010; Penaluna et al. 2016). Natural disturbances that are neither too infrequent nor too recurrent maximize species diversity (intermediate disturbance hypothesis; Connell 1978). Consequently, it will be important for researchers and managers to identify processes that underlie regionally relevant natural disturbances to guide management decisions.

Aquatic-riparian management actions merit designs that maintain biological legacies that result from natural disturbances by emulating underlying processes of the natural disturbances (Lindenmayer and Franklin 2002). Biological legacies often persist in streams through multiple natural disturbance events; for example, wood persists in streams through various floods for seasons to years (Wohl and Goode 2008). Large wood creates physical complexity and habitat diversity in streams and rivers. However, stream simplification through wood removal can result in the loss of habitat-forming processes and associated biological legacies



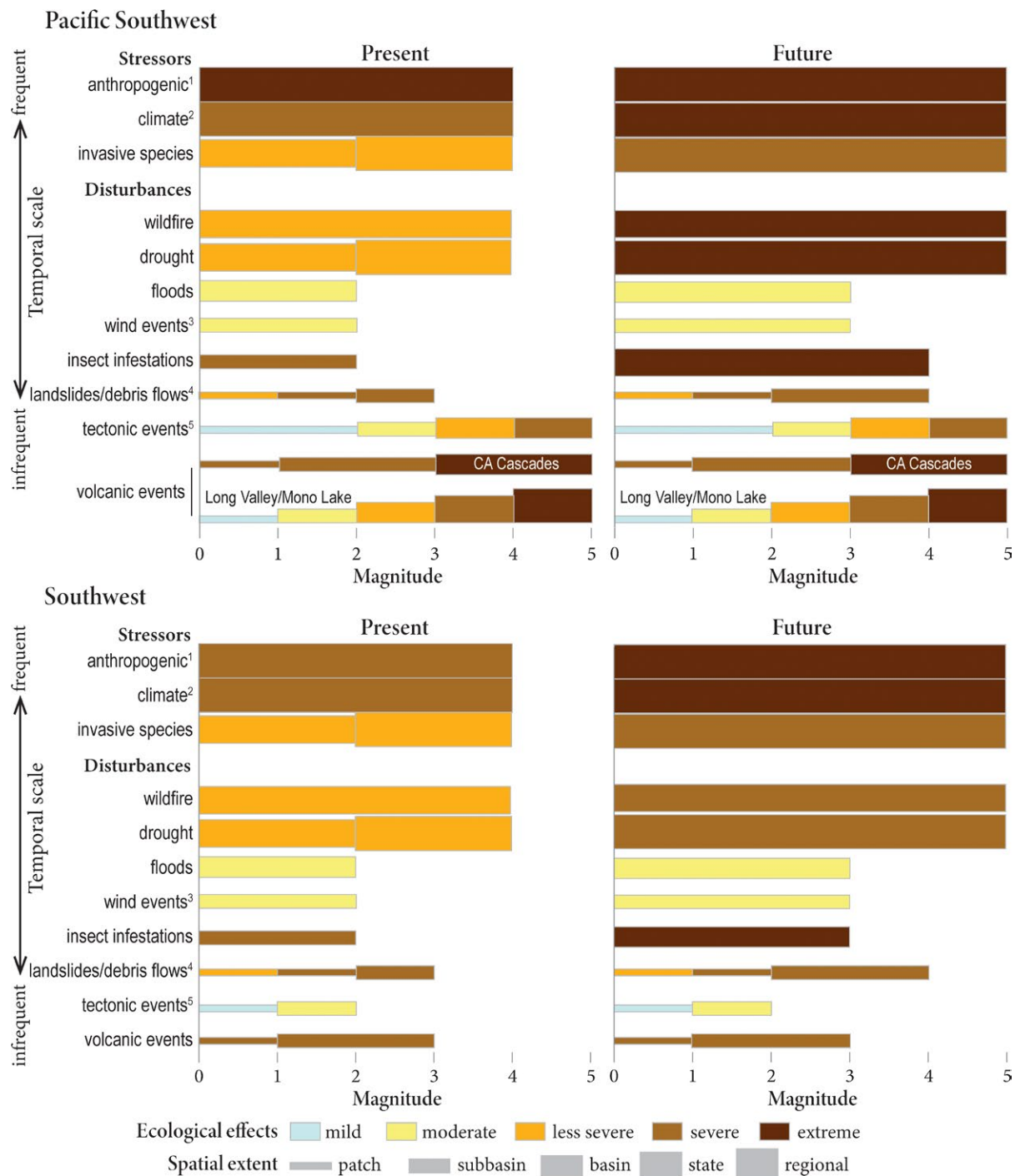
¹Resource extraction, urbanization, rural development, hydropower, channel modification, water withdrawals, agriculture (crop, pasture, rangelands), pollution

²Climate change affects physical, biological, and human-made systems by increasing air and water temperatures, sea-level rise and coastal erosion, melting permafrost, glaciers, snow and ice, and increasing variability in extreme events

³Hurricanes, tornadoes, windstorms

⁴Earthquakes and associated tsunamis in coastal areas

Figure 3. Hypothesized disturbances of Alaska and the U.S. Pacific Northwest based on professional judgment, illustrating the details of how managers can think about disturbance in these regions. Disturbances incorporate temporal frequency (return timing), spatial extent, magnitude, and potential ecological effects at present and projections for the near future (2100 AD). Comparisons of the relative magnitude of each disturbance metric can be made across all regions in the USA (see also Figures 4–6). Disturbance followed by recovery is of central importance to sustaining heterogeneity of habitats and resetting biological patterns in aquatic-riparian ecosystems. Modification to the natural disturbance regime for each region has cascading effects on the ecological structure and function of aquatic-riparian ecosystems.



¹Resource extraction, urbanization, rural development, hydropower, channel modification, water withdrawals, agriculture (crop, pasture, rangelands), pollution

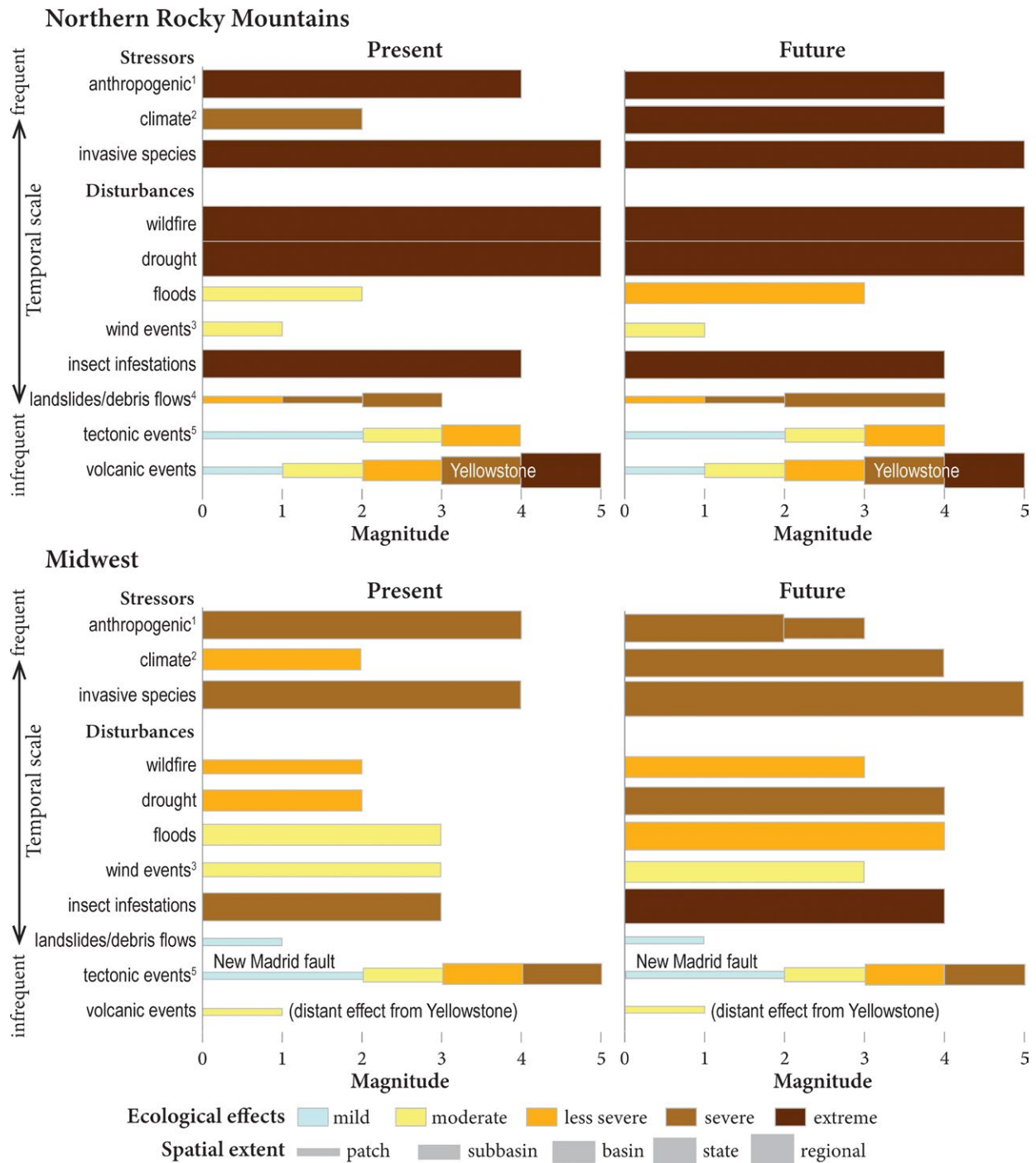
²Climate change affects physical, biological, and human-made systems by increasing air and water temperatures, sea-level rise and coastal erosion, melting permafrost, glaciers, snow and ice, and increasing variability in extreme events

³Hurricanes, tornadoes, windstorms

⁴Includes bulking debris flows in semi-arid basins

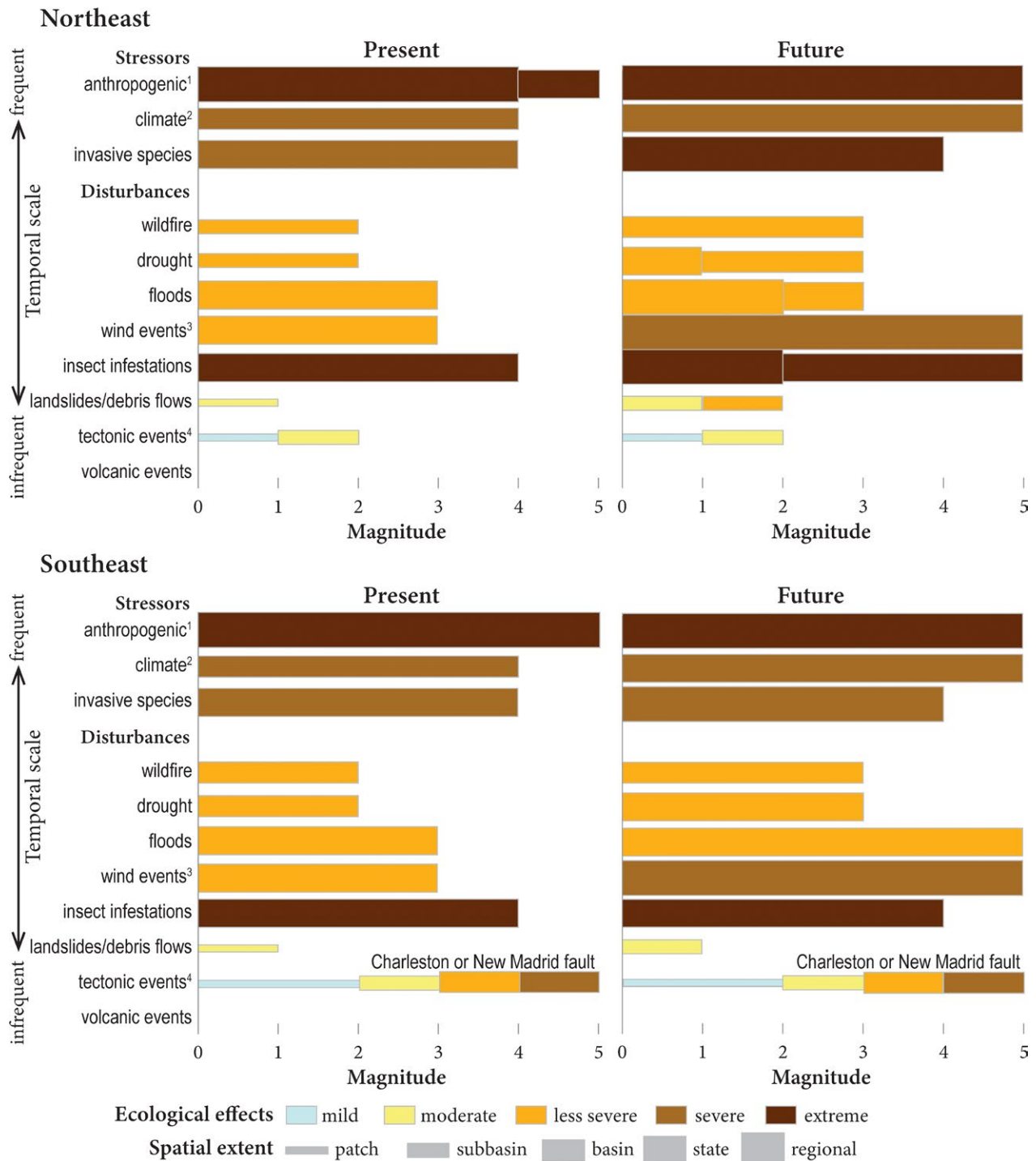
⁵Earthquakes and associated tsunamis in coastal areas

Figure 4. Hypothesized disturbances for the U.S. Pacific Southwest (excluding Hawaii) and Southwest based on professional judgement, illustrating the details of how managers can think about disturbance. See the Figure 3 caption for further explanation.



- ¹Resource extraction, urbanization, rural development, hydropower, channel modification, water withdrawals, agriculture (crop, pasture, rangelands), pollution
- ²Climate change affects physical, biological, and human-made systems by increasing air and water temperatures, sea-level rise and coastal erosion, melting permafrost, glaciers, snow and ice, and increasing variability in extreme events
- ³Hurricanes, tornadoes, windstorms
- ⁴Includes bulking debris flows in semi-arid basins
- ⁵Earthquakes and associated tsunamis in coastal areas

Figure 5. Hypothesized disturbances for the U.S. northern Rocky Mountains and Midwest based on professional judgment, illustrating the details of how managers can think about disturbance. See the Figure 3 caption for further explanation.



¹Resource extraction, urbanization, rural development, hydropower, channel modification, water withdrawals, agriculture (crop, pasture, rangelands), pollution

²Climate change affects physical, biological, and human-made systems by increasing air and water temperatures, sea-level rise and coastal erosion, melting permafrost, glaciers, snow and ice, and increasing variability in extreme events

³Hurricanes, tornadoes, windstorms

⁴Earthquakes and associated tsunamis in coastal areas

Figure 6. Hypothesized disturbances for the northeastern and southeastern USA based on professional judgment, illustrating the details of how managers can think about disturbance. See the Figure 3 caption for further explanation.

(Sedell and Froggatt 1984; Wood-Smith and Buffington 1996). Another natural disturbance that leaves biological legacies is wildfire, which generally consumes less than 10% of the wood in a forest, leaving large quantities of dead and down wood (Fosters and Reiners 1983; Payette et al. 1990). Clearcutting has been advocated as a human disturbance that mimics natural disturbances, such as wildfire; however, up to 95% of the above-ground wood volume is removed in clearcutting (Angelstam 1996), resulting in potentially novel biological legacies that may disrupt natural ecosystem function and resilience. A key challenge is designing management programs that better mimic natural disturbances and the associated variation and complexity of habitat conditions for populations through time and under changing land-use conditions.

If the terrestrial component of a landscape becomes homogenized, large synchronous disturbances become more likely (Hessburg et al. 2015), which can encourage homogenization of aquatic habitats. As the complexity of the aquatic component of a landscape decreases, its ability to support diverse populations declines (Southwood 1977; McCabe and Gotelli 2000), thus affecting other components of the food web that depend on them (Ruff et al. 2011). Homogenization of aquatic ecosystems occurs from habitat degradation, suppressing natural disturbances, overexploitation of populations, and the introduction of nonnative species. For example, a lack of habitat availability and diversity due to dams and other human influences was credited as causing a reduction in the expression of life-history diversity in Chinook Salmon *O. tshawytscha* populations, leading to their collapse in the Central Valley of California (Carlson and Satterthwaite 2011) and the lower Columbia River (Fullerton et al. 2011). Similarly, loss of habitats promoting anadromous and migratory strategies in the eastern and upper midwestern USA has resulted in isolated headwater populations with limited recreational fisheries value and high vulnerability to local extinction (Whiteley et al. 2015). In addition, degradation and homogenization of natural fish habitat by dams in the southeastern USA led to substantial losses; in one case, 11 major dams on the upper Tennessee River system permanently eliminated more than one-third of the river habitat for resident native fishes and other aquatic organisms (Neves and Angermeier 1990).

PROMOTING CONNECTED HETEROGENEOUS HABITATS ACROSS BROAD SPATIAL EXTENTS

Under the portfolio approach, managers would promote diversity of habitats and connectivity of heterogeneous habitats across broad spatial extents to allow for the expression of biocomplexity (e.g., Dunham and Rieman 1999). Habitat connectivity is the degree to which habitat facilitates movement of organisms through the river network over time, which varies by life stage (juvenile versus adult), species, and biological level of organization (genes, individual, and population). Within a population, movement facilitates diversity (diversity in life-history strategies, life-history patterns, age structure, forms, genetics, and behaviors) and provides the foundation for long-term persistence. For species with long-distance migrations, habitat connectivity is required across broad spatial and temporal extents that may include routes between freshwater and saltwater (Waldman et al. 2016). The long-term productivity of fishes, such as Pacific salmonids *Oncorhynchus* spp., Atlantic Salmon *Salmo salar*, Pacific Lampreys *Entosphenus tridentatus*, Alewives *Alosa pseudoharengus* and shads *Alosa*

spp., Striped Bass *Morone saxatilis*, sturgeons, and American Eels *Anguilla rostrata*, requires this inherent variability and diversity of connected heterogeneous habitats across a broad extent (Waldman et al. 2016). For resident species with shorter migrations, long-term maintenance of connectivity among suitable habitats and populations is important for maintaining various migratory life histories critical for postdisturbance, population-scale survival.

Connectivity requirements vary depending on movement ranges, with mid- to long-range migrators (diadromous, fluvial, and adfluvial) needing access to habitats across broader spatial extents compared to resident populations that need access to local mainstem river corridors and tributaries during specific time frames. Resident individuals track the heterogeneity in their environment by actively navigating the riverscape in search of suitable habitats at the local scale, leading to changes in population and community-level dynamics. For example, minnows (e.g., Highback Chub *Hybopsis hypsinotus* and Bandfin Shiner *Luxilus zonistius*) aggregate by the thousands to spawn over the active rock-mound nests of river chubs, such as the Bluehead Chub *Nocomis leptoccephalus* (McClennan 2014). At a broader spatial scale, animals track ephemeral but predictable food sources as resource waves across a landscape. For example, Kodiak brown bears *Ursus arctos* visit multiple Pacific salmon (*Oncorhynchus* spp.) sites in synchrony with the order of spawning phenology (Deacy et al. 2016). Another example is the daily migration of juvenile Coho Salmon to consume the eggs of Sockeye Salmon (Armstrong and Schindler 2011).

As individuals move across connected patches and habitats within the landscape, they use interpatches or corridors (Southwood 1977) and experience barriers and discontinuities (Ward and Stanford 1983, 1995) of varying spatial or temporal extents. Barriers, such as dams and perched culverts, can cause physical habitat fragmentation that affects dispersal and local movements (Fagan 2002). However, barriers are also created by shifting thermal and discharge regimes from dams, diversions, or pumping, which create impassable conditions for some aquatic species (Clarkson and Childs 2000; Lessard and Hayes 2003; Light 2003). Stream communities can drastically change due to the reduction or extirpation of locally adapted organisms, both upstream and downstream of barriers (Adams 2013). For example, a severe loss of freshwater habitat due to fragmentation, predominately from dams, is underacknowledged and is likely contributing to the decline of American Eels (Haro 2014; Secor 2015), sturgeons (Kuhajda 2014), suckers (Harris et al. 2014), and other migratory fishes. Changes in water quality and quantity (Haag and Williams 2014), along with loss and degradation of habitat due to dams, have also contributed to the decline of mussels (Layzer et al. 1993; Watters 1999; McGregor and Garner 2003).

Discontinuities are areas in space or time that may be unfavorable, may become barriers to movement, or may be lethal to aquatic species. Discontinuities can be caused by either human actions or natural disturbances, but responses from human actions often deserve attention and mitigation by managers. Because desert fishes are isolated in patches of habitat that may be disconnected for long periods of the year after stream desiccation, they are particularly vulnerable to local extirpation from human stressors (Fagan 2002). For coldwater-obligate species, thermal refugia are particularly important when migrating through areas with elevated thermal conditions, such as those caused by dams. For instance, steelhead *O. mykiss* use

thermal refugia in the lower Columbia River when water temperature is 19–21°C, and they use tributaries when main-stem water temperature exceeds 21°C (Keefer et al. 2009). Coldwater species may become isolated in headwater areas, effectively limiting opportunities for metapopulation dynamics and increasing the risk of local extinction due to wildfire or climate change (Falke et al. 2016). On the Cumberland River, Kentucky, a 128-km section remains unpounded, but more than 50 freshwater mussel species (as well as most native fishes) were eliminated due to chronically depressed water temperatures and dramatic nonseasonal fluctuation in the tailwater release from a large upstream dam (Haag 2012). Consequently, all tributary populations of warmwater fishes and mussels in this river reach are disconnected from one another.

ROLE OF FEDERAL LANDS IN A BROADER MATRIX OF OWNERSHIP AND LAND USES

A riverscape is commonly composed of a patchwork of different land ownerships, allocations, and management, which disrupts landscape and ecosystem patterns (Spies 2002; Hessburg et al. 2015). Federal lands represent large areas of protected land encompassing long-term stability of the land's integrity under relatively unified management plans, which present unique opportunities to apply disturbance and portfolio concepts in their jurisdictions. This is clearly possible in the western USA, including Alaska, but also in the eastern USA, where there are fewer contiguous acres of federal lands. Federal lands across the country lie in the headwaters for many river systems and supply the great majority of water for them (e.g., Brown et al. 2008; Luce et al. 2017; Roper et al. 2018, this issue). Federal lands deliver high-quality water to downstream habitats, which is important considering that cold, clean water is essential for high survival rates of eggs and young fish. In addition, protection and careful management of riparian canopy for shade and inputs of organic matter that fuel aquatic food webs (e.g., Dwire and Kauffman 2003; Wipfli and Baxter 2010), along with careful management of roads in upstream forests, can improve habitat in downstream ownerships (Luce et al. 2001; Spies 2002). Accordingly, the contribution of federal lands to the recovery and persistence of aquatic–riparian species continues to be important, with specific contributions depending on species-specific habitat needs and the location of federal lands in given basins and regions of the country.

In the southeastern USA, federal holdings, particularly the National Forest System, are more limited compared to those in the western USA, but they represent the largest tracts of contiguous forests in their states or region. Federal lands are paramount for the continued existence of some species and play a more limited role for the survival of others. For example, federal lands in both the southeastern and northeastern USA and their immediate downstream waters provide a substantial proportion of the total suitable remaining habitat for native species, such as Brook Trout (Flebbe et al. 2006; Hudy et al. 2008), Blackside Dace *Chrosomus cumberlandensis* (Black et al. 2013; Detar and Mattingly 2013), Grandfather Mountain crayfish *Cambarus eeseehensis* (Ewing et al. 2016), and numerous other aquatic species, many of which are range-restricted endemics that occupy small, upland streams in densely forested catchments. In contrast, the entire life history of species such as the Alabama Sturgeon *Scaphirhynchus suttkusi* is limited to the largest rivers in the Mobile River basin, which have relatively small headwater catchments on federal lands (Kuhajda 2014). However, federal lands generally

produce high-quality water, which can mitigate some of the downstream impacts caused by more intensive management on private lands.

In the Pacific Northwest, the direct role of federal lands in the recovery of Pacific salmon and steelhead is limited because these lands either have a restricted capacity to provide high-quality habitat (e.g., Burnett et al. 2007; Reeves et al. 2016) or are upstream of major dam complexes, where habitats are extensive and high quality (Thurrow 2000). In Oregon and Washington, federally managed lands are generally located in the middle to upper portions of catchments, which tend to have steeper gradients and confined valleys and floodplains, making them inherently less productive for some fishes (Burnett et al. 2007). In this context, the location of the federal lands in the basin precludes them from offering habitats, such as floodplain wetlands and oxbow lakes, that are critical for some fishes. In this same region, however, some amphibian species, including the Oregon slender salamander *Batrachoseps wrighti*, have a strong association with older forest conditions, which are most frequently found on federal lands (Blaustein et al. 1995). Across the Rocky Mountains, coldwater refugia that would support Bull Trout *Salvelinus confluentus* and subspecies of Cutthroat Trout *O. clarkii* generally occur in large headwater networks of federal ownership, highlighting the importance of federal lands for trout and char in this region (>90% of refugia are on federal land; Isaak et al. 2015).

We also emphasize that it is important for disturbance and portfolio concepts to extend beyond federal lands because in some regions, there may be critical or unique habitat types found only on tribal, state, or private lands, and such habitats could be lost if only habitats associated with federal lands are retained. This broader perspective should enhance habitat diversity, thereby strengthening the ecological portfolio of a region. Consequently, it is important for federal land managers to coordinate with tribes, state agencies, private landowners, and other stakeholders to develop comprehensive management efforts for the persistence and recovery of aquatic–riparian species. For example, through the Joint Chief's Landscape Restoration Partnership, the U.S. Forest Service and the Natural Resource Conservation Service (U.S. Department of Agriculture) are working together to improve the health of forests where public forests and grasslands connect to privately owned land. An example project through this initiative is the Salmon Superhighway, which, along with other partners, aims to reconnect historic habitat in the Nestucca and Tillamook river catchments of the northern Oregon coast to restore and improve habitat and ultimately improve the resilience of Coho Salmon and other aquatic species by improving their portfolio effect (www.salmonsuperhwy.org). The Salmon Superhighway project has identified a combination of habitats that warrant reconnection to benefit salmon and steelhead during 93 projects over 10 years. In another example, state and federal agencies along with other partners are coordinating to protect, restore, and enhance Brook Trout populations and habitats across the species' U.S. range through the Eastern Brook Trout Joint Venture (www.easternbrooktrout.org). The Venture is a comprehensive, nonregulatory Brook Trout conservation strategy that is geographically focused, locally driven, and scientifically based. Reeves et al. (2016) presented a method for conducting these types of coordinated assessments across a mixed-ownership landscape.

MOUNTING PRESSURES

Climate change is occurring simultaneously with other stressors, including habitat degradation from forest harvest, agriculture, cattle grazing, mining, migration barriers, and urbanization as well as the extensive introduction of non-native species. Current pressures on land use are driving the conversion of forests to human uses, primarily for housing, especially in the eastern USA, where more than 44 million acres of private forest are projected to experience housing density increases through 2030 (Alig et al. 2010). Nonnative species are increasingly introduced into aquatic-riparian ecosystems, changing the behavior of native species and affecting their ability to optimize the full potential of their portfolio; for example, by limiting their movements to certain habitats or by increasing their risk of predation (Strayer 1999, 2010; Solomon et al. 2016). Given the suite of interactions among these stressors, management approaches that maintain a portfolio of connected habitat types and complexity offer the greatest potential for species and ecosystem resistance and persistence.

Historic patterns of disturbance and recovery elucidate how aquatic habitats and fishes relate to the landscape, but they may no longer predict what to expect in terms of future patterns due to the combined effects of human disturbance and climate change. The legacy of past and current human actions has led to current conditions that strongly depart, in many cases, from conditions and dynamics that naturally existed across aquatic-riparian ecosystems (Luce et al. 2012). Similarly, climate-driven changes in disturbance patterns can cause departure from historic conditions (e.g., Scheffer et al. 2001; Aplet and McKinley 2017). Climate change impacts on aquatic ecosystems are largely mediated by hydrology and riparian conditions (e.g., Furniss et al. 2010; Arismendi et al. 2012), and many aspects of aquatic habitat are undergoing climate-related changes, although effects may vary across locations in terms of the rate of change (e.g., stream temperature; Luce et al. 2014). In the western USA, stream temperatures are warming (Arismendi et al. 2012; Isaak et al. 2012); low flows are becoming lower (Kormos et al. 2016); wildfires are increasing (Westerling et al. 2006; Littell et al. 2016), leading to increases in sediment yields (Goode et al. 2012); and winter flooding is worsening, with consequences for redd scour (Goode et al. 2013). In the eastern USA, stream temperature is also warming, low flows and total annual flows are increasing, and the frequency and magnitude of extreme precipitation events have increased (Kaushal et al. 2010; Kelleher et al. 2011; van Vliet et al. 2013).

The observed effects of climate change and other stressors highlight the importance of disturbance and portfolio concepts in management. Adaptation to climate-forced changes in streams and riparian areas is closely tied to and parallel with adaptation in surrounding forests (e.g., Millar et al. 2007). For example, using management to intentionally break up continuity of fuels and fire-prone forest types may introduce temporary disturbance now (e.g., some types of salvage logging) but means that disturbances after such management may lessen the probability of megafires on the landscape (Jones et al. 2016). Identifying refugia where water temperatures are resilient to changing climates for various reasons, including riparian cover and groundwater influences (e.g., Kelleher et al. 2011; Arismendi et al. 2012; Mayer 2012; Luce et al. 2014; Isaak et al. 2016), will be important for setting priorities. Fortunately, the cold aquatic headwater habitats provided by

federal lands across the country are also some of the most resilient (Isaak et al. 2015), emphasizing their importance as part of the portfolio for long-term conservation. Their context in the larger forest disturbance mosaic likely will be important to the success of the overall portfolio. However, challenges with this approach may arise when trying to implement this type of management strategy on highly modified lands, such as urban, agricultural, or industrial forestlands, which may have a high potential to support certain species or life stages but have been so altered that natural disturbance processes are no longer possible or cannot support a portfolio of habitats. Consequently, a comprehensive management approach will need to include a process for incorporating highly modified lands that works toward transitioning them to encompass a range of variable conditions.

Carrying forward a financial analogy for the portfolio concept (Box 2), there is a need to systematically guide selection and management of portfolio components to hedge the growing risks associated with climate change and other stressors (Aplet and McKinley 2017). A deeply underappreciated component of such a strategy is the role of information gathering in making intelligent decisions based on inventory and monitoring of habitats that can be used to inform climate-related decisions (e.g., Luce et al. 2012). Prioritizing watersheds or populations based solely on resilience but without considering disturbance and portfolio concepts can lead to portfolios that are insufficiently diversified, potentially increasing their vulnerability. Specifically, the genetic diversity and life-history diversity of populations living in dynamic, highly variable habitats may differ from those of populations of the same species living in more stable habitats. If only resilient or stable habitats are retained, important aspects of species diversity may be lost. Furthermore, conservation efforts are usually focused on perennial systems to the detriment of intermittent and ephemeral ones, which occupy more than 50% of drainage networks globally (Datry et al. 2014). Given that intermittent and ephemeral systems have different natural disturbance regimes and support different species than perennial systems (Meyer et al. 2007), the management and evaluation of the ecological status of intermittent and ephemeral systems may require different ecological indices and thresholds (e.g., Bruno et al. 2016). Intermittent and ephemeral systems host a diversity of taxa that are usually adapted to high natural dynamism, potentially making them more resilient to climate change than taxa from perennial systems.

CONCLUSIONS

Disturbance and portfolio concepts are unifying themes for managers and can serve as a guide so that populations, habitats, and landscapes will be better equipped to deal with change, especially considering the growing scope of human influences. Because aquatic ecosystems are mosaics of habitats linked by diverse processes, when habitats are managed for processes that allow for or emulate natural disturbances that give rise to a diverse portfolio of habitat conditions, long-term productivity is maintained. By considering and managing for disturbance and portfolio concepts, managers can also bring about integrity and dynamism of ecosystems because the management goals of populations, habitats, and landscapes are based on optimizing natural variability or at least achieving the best attainable conditions (Stoddard et al. 2006) for landscapes that are limited by human use. As large, integrated landscapes, federal lands play an important role in

achieving these goals. We highlight the urgent need to understand uncertainties related to relationships within and across scales (Isaak et al. 2018, this issue), sources of variation that drive population productivity and persistence, and the capacity of catchments to provide favorable conditions for populations through time and under changing land-use conditions. Societies may have to undergo a fundamental change in attitude to reverse the current trend of increasing habitat degradation and fragmentation in aquatic-riparian ecosystems to support populations, landscapes, and, ultimately, ourselves (Rosenzweig and Barnes 2003; Couvet and Ducarme 2014; Rieman et al. 2015). Meeting the challenges of managing the novel aquatic-riparian ecosystem of the future will take an integrated effort by resource economists and physical, biological, and social scientists.

ACKNOWLEDGMENTS

Kathryn Ronnenberg prepared figures. Susan Salafsky discussed portfolio ideas. The manuscript benefited from reviews by Sue Eggert, Scott Spaulding, Michael Donaldson, and two anonymous reviewers. There is no conflict of interest declared in this article.

REFERENCES

- Adams, S. B. 2013. Effects of small impoundments on downstream crayfish assemblages. *Freshwater Science* 32:1318–1332.
- Alig, R., S. Stewart, D. Wear, S. Stein, and D. Nowak. 2010. Conversion of forest land: trends, determinants, projections, and policy considerations. Pages 1–26 in J. M. Pye, H. M. Rauscher, Y. Sands, D. C. Lee, and J. S. Beatty, editors. *Advances in threat assessment and their application to forest and rangeland management*. U.S. Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-802, Portland, Oregon.
- Angelstam, P. 1996. The ghost of forest past—natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. Pages 287–337 in R. M. DeGraf and R. I. Miller, editors. *Conservation of faunal diversity in forested landscapes*. Chapman and Hall, London.
- Aplet, G. H., and P. S. McKinley. 2017. A portfolio approach to managing ecological risks of global change. *Ecosystem Health and Sustainability* 3(2):1–15.
- Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert. 2012. The paradox of cooling streams in a warming world: regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* [online serial] 39:L10401.
- Armstrong, J. B., and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. *Nature* 476:84–87.
- Bassar, R. D., B. H. Letcher, K. H. Nislow, and A. R. Whiteley. 2016. Changes in seasonal climate output compensatory density-dependence in eastern Brook Trout. *Global Change Biology* 22:577–593.
- Benda, L., and T. Dunne. 1997a. Stochastic forcing of sediment supply to channel networks from landsliding and debris flow. *Water Resources Research* 33:2849–2864.
- Benda, L., and T. Dunne. 1997b. Stochastic forcing of sediment routing and storage in channel networks. *Water Resources Research* 33:2865–2880.
- Benda, L., D. Miller, P. Bigelow, and K. Andras. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. *Forest Ecology and Management* 178:105–119.
- Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. *Ecology* 81:2730–2741.
- Bilby, R. E. 1985. Contributions of road surface sediment to a western Washington stream. *Forest Science* 31:827–838.
- Bisson, P. A., J. B. Dunham, and G. H. Reeves. 2009. Freshwater ecosystems and resilience of Pacific salmon: habitat management based on natural variability. *Ecology and Society* [online serial] 14(1):45.
- Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessburg, D. C. Lee, J. L. Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management* 178:213–229.
- Black, T. R., J. E. Detar, and H. T. Mattingly. 2013. Population densities of the threatened Blackside Dace, *Chrosomus cumberlandensis*, in Kentucky and Tennessee. *Southeastern Naturalist* 12(4):6–26.
- Blaustein, A. R., J. J. Beatty, D. H. Olson, and R. M. Storm. 1995. The biology of amphibians and reptiles in old-growth forests in the Pacific Northwest. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-337, Portland, Oregon.
- Brown, T. C., M. T. Hobbins, and J. A. Ramirez. 2008. Spatial distribution of water supply in the coterminous United States. *Journal of the American Water Resources Association* 44:1474–1487.
- Bruno, D., C. Gutierrez-Canovas, J. Velasco, and D. Sanchez-Fernandez. 2016. Functional redundancy as a tool for bioassessment: A test using riparian vegetation. *Science of the Total Environment* 566-567:1268–1276.
- Buffington, J. M. 2012. Changes in channel morphology over human time scales. Pages 435–463 in M. Church, P. M. Biron, and A. G. Roy, editors. *Gravel-bed rivers: processes, tools, environments*. Wiley, Chichester, UK.
- Buffington, J. M., and D. Tonina. 2009. Hyporheic exchange in mountain rivers II: effects of channel morphology on mechanics, scales and rates of exchange. *Geography Compass* 3:1038–1062.
- Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecological Applications* 17(1):66–80.
- Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1579–1589.
- Cissel, J. H., F. J. Swanson, G. E. Grant, D. H. Olson, S. V. Gregory, S. L. Garman, L. R. Ashkenas, M. G. Hunter, J. A. Kertis, M. H. Mayo, M. D. McSwain, S. G. Swetland, K. A. Swindle, and D. O. Wallin. 1998. A landscape plan based on historical fire regimes for a managed forest ecosystem: the Augusta Creek study. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-422, Portland, Oregon.
- Clarkson, R. W., and M. R. Childs. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River basin big river fishes. *Copeia* 2000:402–412.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Couvet, D., and F. Ducarme. 2014. Reconciliation ecology, from biological to social challenges. *Revue d'ethnoécologie* 6.
- Datry, T., S. T. Larned, and K. Tockner. 2014. Intermittent rivers: a challenge for freshwater ecology. *BioScience* 64:229–235.
- Deacy, W., W. Leacock, J. B. Armstrong, and J. A. Stanford. 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. *Ecology* 97:1091–1098.
- Detar, J. E., and H. T. Mattingly. 2013. Movement patterns of the threatened Blackside Dace, *Chrosomus cumberlandensis*, in two southeastern Kentucky watersheds. *Southeastern Naturalist* 12(4):64–81.
- DuFour, M. R., C. J. May, E. F. Roseman, S. A. Ludsins, C. S. Vandergoot, J. J. Pritt, M. E. Fraker, J. J. Davis, J. T. Tyson, J. G. Miner, E. A. Marschall, and C. M. Mayer. 2015. Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. *Ecosphere* 6(12):1–21.
- Dunham, J., and B. Rieman. 1999. Metapopulation structure of Bull Trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642–655.
- Dunham, J. B., M. K. Young, R. E. Gresswell, and B. E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management* 178:183–196.
- Dwire, K. A., and J. B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management* 178:61–74.
- Ewing, T. D., R. F. Thoma, S. J. Fraley, W. T. Russ, and J. Pope. 2016. Distribution and conservation status of the Grandfather Mountain crayfish. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 3:64–70.
- Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249.
- Falke, J. A., J. B. Dunham, D. Hockman-Wert, and R. Pahl. 2016. A simple prioritization tool to diagnose impairment of stream temperature for coldwater fishes in the Great Basin. *North American Journal of Fisheries Management* 36:147–160.

- Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. *Biodiversity and Conservation* 13:827–849.
- Flebbe, P. A., L. D. Roghair, and J. L. Bruggink. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. *Transactions of the American Fisheries Society* 135:1371–1382.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–214.
- Fullerton, A. H., S. T. Lindley, G. R. Pess, B. E. Feist, E. A. Steel, and P. McElhany. 2011. Human influence on the spatial structure of threatened Pacific salmon metapopulations. *Conservation Biology* 25:932–944.
- Furniss, M. J., B. P. Staab, S. Hazalhurst, C. Clifton, K. B. Roby, B. L. Ilhardt, and P. J. Edwards. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-812, Portland, Oregon.
- Gillespie, N. G., J. Epstein, S. Alexander, M. Bowker, R. Medel, M. Leonard, and A. Thoms. 2018. Socioeconomic benefits of recreational, commercial and subsistence fishing associated with national forests. *Fisheries* 43:432–439.
- Goode, J. R., J. M. Buffington, D. Tonina, D. J. Isaak, R. F. Thurow, S. Wenger, D. Nagel, C. Luce, D. Tetzlaff, and C. Soulsby. 2013. Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrological Processes* 27:750–765.
- Goode, J. R., C. H. Luce, and J. M. Buffington. 2012. Enhanced sediment delivery in a changing climate in semi-arid mountain basins: implications for water resource management and aquatic habitat in the Northern Rocky Mountains. *Geomorphology* 139:1–15.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540–551.
- Gutiérrez-Cánovas, C., A. Millán, J. Velasco, I. P. Vaughan, and S. J. Ormerod. 2013. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography* 22:796–805.
- Haag, W. R. 2012. North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, New York.
- Haag, W. R., and J. D. Williams. 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. *Hydrobiologia* 735:45–60.
- Haro, A. 2014. Anguillidae: freshwater eels. Pages 313–331 in M. L. Warren, Jr. and B. M. Burr, editors. *Freshwater fishes of North America*, volume 1. Johns Hopkins University Press, Baltimore, Maryland.
- Harris, P. M., G. Hubbard, and M. Sandel. 2014. Catostomidae: suckers. Pages 451–501 in M. L. Warren, Jr. and B. M. Burr, editors. *Freshwater fishes of North America*, volume 1. Johns Hopkins University Press, Baltimore, Maryland.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Hessburg, P. F., D. J. Churchill, A. J. Larson, R. D. Haugo, C. Miller, T. A. Spies, M. P. North, N. A. Povak, R. T. Belote, P. H. Singleton, W. L. Gaines, R. E. Keane, G. H. Aplet, S. L. Stephens, P. Morgan, P. A. Bisson, B. E. Rieman, R. B. Salter, and G. H. Reeves. 2015. Restoring fire-prone inland Pacific landscapes: seven core principles. *Landscape Ecology* 30:1805–1835.
- Hiers, J. K., S. T. Jackson, R. J. Hobbs, E. S. Bernhardt, and L. E. Valentine. 2016. The precision problem in conservation and restoration. *Trends in Ecology and Evolution* 31:820–830.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* 100:6564–6568.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the eastern United States. *North American Journal of Fisheries Management* 28:1069–1085.
- Isaak, D., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Climatic Change* 113:499–524.
- Isaak, D. J., M. K. Young, C. H. Luce, S. W. Hostetler, S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, M. C. Groce, D. L. Horan, and D. E. Nagel. 2016. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 113:4374–4379.
- Isaak, D. J., M. Young, C. McConnell, B. Roper, E. Archer, B. Staab, C. Hirsch, D. Nagel, M. Schwartz, and G. Chandler. 2018. Crowd-sourced databases as essential elements for Forest Service partnerships and aquatic resource conservation. *Fisheries* 43:423–430.
- Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology* 21:2540–2553.
- Istanbulluoglu, E., D. G. Tarboton, R. T. Pack, and C. H. Luce. 2004. Modeling of the interactions between forest vegetation, disturbances, and sediment yields. *Journal of Geophysical Research: Earth Surface* [online serial] 109(F1):F09001.
- Jones, G. M., R. J. Gutierrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016. Megafires: an emerging threat to old-forest species. *Frontiers in Ecology and the Environment* 14:300–306.
- Jones, K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology* 85:52–80.
- Junk, W., P. Bayley, R. Sparks, and D. Dodge. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 in D. P. Dodge, editor. *Proceedings of the international large river symposium*. Canadian Special Publication of Fisheries and Aquatic Sciences 106.
- Kanno, Y., B. H. Letcher, J. A. Coombs, K. H. Nislow, and A. R. Whiteley. 2014. Linking movement and reproductive history of Brook Trout to assess habitat connectivity in a heterogeneous stream network. *Freshwater Biology* 59:142–154.
- Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* 8:461–466.
- Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1734–1747.
- Kelleher, C., T. Wagener, M. Gooseff, B. McGlynn, K. McGuire, and L. Marshall. 2011. Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes* 2:771–785.
- Koellner, T., and O. J. Schmitz. 2006. Biodiversity, ecosystem function, and investment risk. *BioScience* 56:977–985.
- Kormos, P. R., C. H. Luce, S. J. Wenger, and W. R. Berghuijs. 2016. Trends and sensitivities of low streamflow extremes to discharge timing and magnitude in Pacific Northwest mountain streams. *Water Resources Research* 52:4990–5007.
- Kuhajda, B. A. 2014. Acipenseridae: sturgeons. Pages 160–206 in M. L. Warren, Jr. and B. M. Burr, editors. *Freshwater fishes of North America*, volume 1. Johns Hopkins University Press, Baltimore, Maryland.
- Layzer, J. B., M. E. Gordon, and R. M. Anderson. 1993. Mussels: the forgotten fauna of regulated rivers: a case study of the Caney Fork River. *River Research and Application* 8(1–2):63–71.
- Lessard, J. L., and D. B. Hayes. 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications* 19:721–732.
- Letcher, B. H., P. Schueller, R. D. Bassar, K. H. Nislow, J. A. Coombs, K. Sakrejsa, M. Morrissey, D. B. Sigourney, A. R. Whiteley, M. J. O'Donnell, and T. L. Dubreuil. 2015. Robust estimates of environmental effects on population vital rates: an integrated capture-recapture model of seasonal Brook Trout growth, survival and movement in a stream network. *Journal of Animal Ecology* 84:337–352.
- Light, T. 2003. Success and failure in a lotic crayfish invasion: the roles of hydrologic variability and habitat alteration. *Freshwater Biology* 48:1886–1897.
- Lindenmayer, D. B., and J. F. Franklin. 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island Press, Washington, D.C.
- Littell, J. S., D. L. Peterson, K. L. Riley, Y. Liu, and C. H. Luce. 2016. A review of the relationships between drought and forest fire in the United States. *Global Change Biology* 22:2353–2369.
- Luce, C., P. Morgan, K. Dwire, D. Isaak, Z. Holden, and B. Rieman. 2012. Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. U.S. Forest Service, Rocky Mountain

- Research Station, General Technical Report RMRS-GTR-290, Fort Collins, Colorado.
- Luce, C., B. Staab, M. Kramer, S. Wenger, D. Isaak, and C. McConnell. 2014. Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. *Water Resources Research* 50:3428–3443.
- Luce, C. H., A. Lute, P. Kormos, and B. Livneh. 2017. Modeled historical streamflow metrics for the contiguous United States and national forest lands. Research Data Archive, U.S. Forest Service, Fort Collins, Colorado.
- Luce, C. H., B. E. Rieman, J. B. Dunham, J. L. Clayton, J. G. King, and T. A. Black. 2001. Incorporating aquatic ecology into decisions on prioritization of road decommissioning. *Water Resources Impact* 3(3):8–14.
- Luck, G. W., G. C. Daily, and P. R. Ehrlich. 2003. Population diversity and ecosystem services. *Trends in Ecology and Evolution* 18:331–336.
- Marks, D., J. Kimball, D. Tingey, and T. Link. 1998. The sensitivity of snow-melt processes to climate conditions and forest cover during rain-on-snow: a case study of the 1996 Pacific Northwest flood. *Hydrological Processes* 12:1569–1587.
- Maturana, O., D. Tonina, J. A. McKean, J. M. Buffington, C. H. Luce, and D. Caamaño. 2014. Modeling the effects of pulsed versus chronic sand inputs on salmonid spawning habitat in a low-gradient gravel-bed river. *Earth Surface Processes and Landforms* 39:877–889.
- May, C. L., and R. E. Gresswell. 2003. Processes and rates of sediment and wood accumulation in headwater streams of the Oregon Coast Range, USA. *Earth Surface Processes and Landforms* 28:409–424.
- May, R. M. 1994. The effects of spatial scale on questions and answers. Pages 1–17 in R. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, London.
- Mayer, T. 2012. Controls of summer stream temperature in the Pacific Northwest. *Journal of Hydrology* 475:323–335.
- McCabe, D., and N. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124:270–279.
- McClennan, D. A. 2014. Mating behavior of North American freshwater fishes. Pages 50–104 in M. L. Warren, Jr. and B. M. Burr, editors. *Freshwater fishes of North America*. Johns Hopkins University Press, Baltimore, Maryland.
- McGregor, S. W., and J. T. Garner. 2003. Changes in the freshwater mussel (*Bivalvia*: Unionidae) fauna of the Bear Creek system of northwest Alabama and northeast Mississippi. *American Malacological Bulletin* 18(1–2):61–70.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association* 43(1):86–103.
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and human well-being: synthesis*. World Resources Institute, Island Press, Washington, D.C. Available: <http://www.millenniumassessment.org/documents/document.356.aspx.pdf>. (September 2017).
- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17:2145–2151.
- Miller, D., C. Luce, and L. Benda. 2003. Time, space, and episodicity of physical disturbance in streams. *Forest Ecology and Management* 178:121–140.
- Montgomery, D. R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association* 35:397–410.
- Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. *Water Resources Research* 31:1097–1105.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.
- Neves, R. J., and P. L. Angermeier. 1990. Habitat alteration and its effects on native fishes in the upper Tennessee River, east-central USA. *Journal of Fish Biology* 37(Supplement A):45–52.
- Payette, S., L. Filion, and A. Delwaide. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20:1228–1241.
- Penaluna, B., D. H. Olson, R. L. Flitcroft, M. A. Weber, J. R. Bellmore, S. M. Wondzell, J. B. Dunham, S. L. Johnson, and G. H. Reeves. 2016. Aquatic biodiversity in forests: a weak link in ecological and ecosystem service resilience. *Biodiversity and Conservation* 26:3125–3155.
- Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* 11(1):86–92.
- Postel, S., and S. Carpenter. 1997. Freshwater ecosystem services. Pages 215–236 in G. C. Daily, editor. *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington, D.C.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 in J. L. Nielsen, editor. *Evolution and the aquatic ecosystem: defining unique units in population conservation*. American Fisheries Society, Symposium 17, Bethesda, Maryland.
- Reeves, G. H., B. R. Pickard, and K. N. Johnson. 2016. An initial evaluation of potential options for managing riparian reserves of the Aquatic Conservation Strategy of the Northwest Forest Plan. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-937, Portland, Oregon.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Rieman, B. E., P. F. Hessburg, C. Luce, and M. R. Dare. 2010. Wildfire and management of forests and native fishes: conflict or opportunity for convergent solutions? *BioScience* 60:460–468.
- Rieman, B. E., D. C. Lee, D. Burns, R. Gresswell, M. Young, R. Stowell, J. Rinne, and P. Howell. 2003. Status of native fishes in the western United States and issues for fire and fuels management. *Forest Ecology and Management* 178:197–211.
- Rieman, B. E., C. L. Smith, R. J. Naiman, G. T. Ruggerson, C. C. Wood, N. Huntly, E. N. Merrill, J. R. Alldredge, P. A. Bisson, J. Congleton, C. Levings, W. Pearcy, K. Fausch, D. Scarnecchia, and P. Smouse. 2015. A comprehensive approach for habitat restoration in the Columbia basin. *Fisheries* 40:124–135.
- Roper, B. B., J. M. Capurso, Y. Peroz, and M. K. Young. 2018. Aquatic biodiversity conservation in the context of multiple use management of National Forest System lands. *Fisheries* 43:396–405.
- Rosenzweig, E. S., and C. A. Barnes. 2003. Impact of aging on hippocampal function: plasticity, network dynamics, and cognition. *Progress in Neurobiology* 69:143–179.
- Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlaurin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. *Ecology* 92:2073–2084.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13:257–263.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schmidt, J. C., R. A. Parnell, P. E. Grams, J. E. Hazel, M. A. Kaplinski, L. E. Stevens, and T. L. Hoffnagle. 2001. The 1996 controlled flood in Grand Canyon: flow, sediment transport, and geomorphic change. *Ecological Applications* 11:657–671.
- Secor, D. H. 2015. American Eel: when does diversity matter? *Fisheries* 40:462–463.
- Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal: With 2 figures and 1 table in the text. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 22(3):1828–1834.
- Shively, D., J. Rothlisberger, N. Gillespie, M. Dombeck, V. Moore, C. Roghair, D. Demario, F. McCormick, and L. Weldon. 2018. Historical perspectives and an updated U.S. Forest Service strategy for fish and aquatic stewardship. *Fisheries* 43:386–395.
- Sibley, P. K., D. P. Kreutzweiser, B. J. Naylor, J. S. Richardson, and A. M. Gordon. 2012. Emulation of natural disturbance (END) for riparian

- forest management: synthesis and recommendations. *Freshwater Science* 31:258–264.
- Solomon, L. E., R. M. Pendleton, J. H. Chick, and A. F. Casper. 2016. Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. *Biological Invasions* 18:2283–2895.
- Southwood, T. R. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337–365.
- Spies, T. A., G. H. Reeves, K. M. Burnett, W. C. McComb, K. N. Johnson, G. Grant, J. L. Ohmann, S. L. Garman, and P. Bettinger. 2002. Assessing the ecological consequences of forest policies in a multi-ownership province in Oregon. Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge, UK.
- Stanford, J. A., and J. V. Ward. 1992. Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. Pages 91–124 in R. J. Naiman, editor. *Watershed management*. Springer, New York.
- Stanford, J. A., and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society* 12(1):48–60.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17:866–880.
- Stoddard, J. L., D. P. Larsen, C. P. Hawkins, R. K. Johnson, and R. H. Norris. 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications* 16:1267–1276.
- Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society* 18(1):74–98.
- Strayer, D. L. 2010. Alien species in freshwaters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55(s1):152–174.
- Swanson, F., T. Kratz, N. Caine, and R. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38(2):92–98.
- Thurow, R. F. 2000. Dynamics of Chinook Salmon populations within Idaho's Frank Church Wilderness: implications for persistence. Pages 143–151 in S. F. McCool, D. N. Cole, W. T. Borrie, and J. O'Loughlin, editors. *Wilderness science in a time of change conference, volume 3: wilderness as a place for scientific inquiry*. U.S. Forest Service, Rocky Mountain Research Station, RMRS-P15-VOL-3, Ogden, Utah.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.
- Tonina, D., C. H. Luce, B. Rieman, J. M. Buffington, P. Goodwin, S. R. Clayton, S. M. Ali, J. J. Barry, and C. Berenbrock. 2008. Hydrological response to timber harvest in northern Idaho: implications for channel scour and persistence of salmonids. *Hydrological Processes* 22:3223–3235.
- USFWS (U.S. Fish and Wildlife Service) and HVT (Hoopa Valley Tribe). 1999. Trinity River flow evaluation. Final Report prepared for the U.S. Department of the Interior, Washington, D.C. Available: <http://www.trrp.net/library/document/?id=226>. (October 2017).
- van Vliet, M. T. H., W. H. P. Franssen, J. R. Yearsley, F. Ludwig, I. Haddeland, D. P. Lettenmaier, and P. Kabat. 2013. Global river discharge and water temperature under climate change. *Global Environmental Change* 23:450–464.
- Waldman, J., K. A. Wilson, M. Mather, and N. P. Snyder. 2016. A resilience approach can improve anadromous fish restoration. *Fisheries* 41:116–126.
- Wallington, T. J., R. J. Hobbs, and S. A. Moore. 2005. Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecology and Society* [online serial] 10(1):15.
- Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. *Evolutionary Applications* 1:189–206.
- Ward, J. V., and J. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. *Dynamics of Lotic Ecosystems* 10:29–42.
- Ward, J. V., and J. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *River Research and Applications* 11:105–119.
- Watters, G. T. 1999. Freshwater mussels and water quality: a review of the effects of hydrologic and instream habitat alterations. Pages 261–274 in R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson, and R. S. Butler, editors. *Proceeding of the first freshwater mollusk conservation society symposium*. Ohio Biological Survey, Columbus, Ohio.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450.
- White, P. S., and S. T. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Elsevier, New York.
- Whiteley, A. R., J. A. Coombs, M. Cembrola, M. J. O'Donnell, M. Hudy, K. H. Nislow, and B. H. Letcher. 2015. Effective number of breeders provides a link between interannual variation in stream flow and individual reproductive contribution in a stream salmonid. *Molecular Ecology* 24:3585–3602.
- Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* 35:373–387.
- Wohl, E., and J. R. Goode. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research* [online serial] 44:W09429.
- Wood-Smith, R. D., and J. M. Buffington. 1996. Multivariate geomorphic analysis of forest streams: implications for assessment of land use impact on channel condition. *Earth Surface Processes and Landforms* 21:377–393. **AFS**