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Chapter 9

Forest-Stream Interactions in Eastern Old-Growth Forests

Dana R. Warren, William S. Keeton, Heather A. Bechtold, and Clifford E. Kraft

The largescale recovery of eastern forests from historic clearing is a remarkable example of forest ecosystem resilience (Foster and Aber 2004). More than 150 years after the peak of agricultural clearing in eastern North America, many forests across the region have reached maturity and some are progressing toward an old-growth condition (Brooks et al. 2012; figure 9-1). With this forest recovery and an increasing abundance of old-growth stands, we see the recovery of ecosystem functions and ecosystem services not only in the terrestrial environment but also in the streams and rivers that flow through this increasingly complex forested landscape (Warren et al. 2016; Urbano and Keeton 2017).

Since the emergence of stream ecology as a subfield of ecology in the late 1970s and early 1980s, scientists have studied forest-stream interactions. Early studies focused on how the simple presence or absence of forest cover within stream corridors (riparian zones) affected streams (e.g. Burton and Likens 1973; Bisson and Sedell 1984; Bilby and Bisson 1992). But as the field has developed further, we are learning that forest-stream interactions are governed by far more than just whether riparian forests are present. The age, developmental condition, and architecture (or "structure") of streamside forests strongly influence stream ecosystem processes and the resilience of stream corridors to disturbance (Gregory et al. 1991). From recent studies it is clear that streams bordered by old-growth forests, in particular, are profoundly different from those surrounded by younger forests in the eastern United States (Keeton et al. 2007; Valett et al. 2002; Warren et al. 2009; Bechtold et al. 2017). Therefore, as forests along stream corridors (riparian zones) continue to develop in the coming decades, we can expect to see increasing complexity

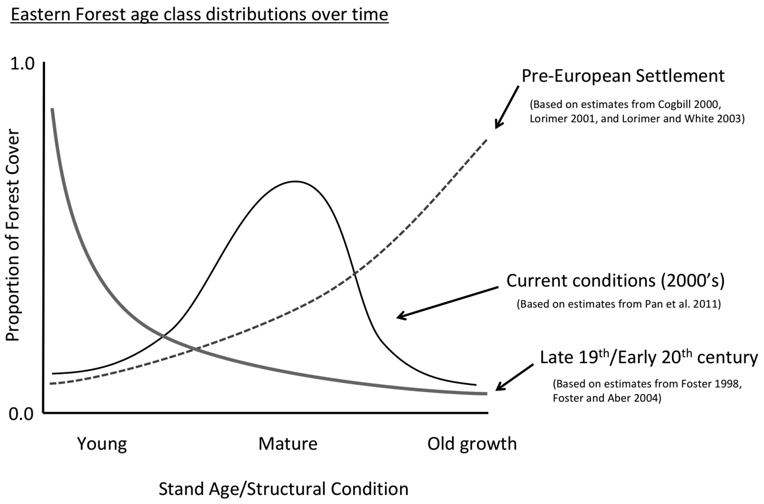

FIGURE 9-1. Stand age class distributions in the past over three periods—preEuro-American settlement, nineteenth- and early twentieth-century (period of greatest open, agricultural, or early successional land in the region), and current conditions. Curves are based on Foster et al. (1998); Cogbill (2000); Lorimer (2001); Lorimer and White (2003); Foster and Aber (2004); and Pan et al. (2011).

not only in riparian forest structural characteristics but also in the streams that flow through those forests.

Assessing how and why streams that flow through old-growth forests might differ from those that flow through younger forests begins with an understanding of the key links between forests and streams. Most research on aquatic-terrestrial linkages has focused on headwater ecosystems (streams generally less than 15 meters wide) where riparian forests have been found to influence many stream features and functions, including physical characteristics, the structure and complexity of food webs, and the cycling and retention of nutrients. For example, the input of wood from riparian forests can influence the width of a stream as well as the size and frequency of pool habitats (Gregory et al. 2003). Forests also influence stream food webs directly through the input of leaf litter and other smaller organic material that provide food for aquatic microbes and larger stream biota (Hall et al. 2000). Indirectly, the forests influence stream food webs by controlling stream light availability which, in turn, regulates in-stream primary productivity and temperature (Hill et al.1995; Wootton 2012; Bilby and Bisson 1992). Through controls on organic matter inputs, large wood structure, and light, riparian forests also strongly influence nutrient cycling in stream environments (Bernot et al. 2010). In addition, the complex structural characteristics that develop together in old-growth forests and the streams flowing through them enhance the resilience of these systems to flood disturbances (Keeton et al. 2017).

In this chapter, we explore key forest-stream interactions and explain how these may be influenced by riparian forest development, age, and structure with an emphasis on old-growth riparian forest conditions. In the final section, we present a conceptual framework to describe how stream function may change over time with the progression of riparian forests from structurally simple younger stands towards more complex old-growth stands.

Importance of Wood in Streams

In dominant forest types of the eastern United States, streams that flow through old-growth stands generally contain large amounts of dead wood (figure 9-2). Not only is dead wood usually more abundant in late-successional forest streams, the individual logs are, on average, larger than those in streams flowing through younger forests (Warren et al. 2009; Valett et al. 2002; Keeton et al. 2007). The size and abundance of wood in a stream is important because wood is a key structural element that can influence streams in multiple ways. For example, wood inputs can increase favorable habitat for stream fish by creating pools and by enhancing overall habitat complexity (Flebbe 1999; Montgomery et al. 2003). In addition, sediment and organic material retained by wood and debris jams comprise a large carbon sink (Beckman and Wohl 2014), and these structures strongly influence the processing and retention of nutrients like phosphorous and nitrogen (Steinhart et al. 2000; Warren et al. 2007; Valett et al. 2002; Beckman and Wohl 2014). In low gradient streams with soft or highly mobile substrates, wood also provides a critical substrate for many invertebrates (Smock et al. 1989; Lamberti and Berg 1995).

Certainly, there is an overall trend toward more and larger wood in old-growth streams. However, there are also notable exceptions in situations where disturbances kill trees and lead to pulse recruitment of logs into streams, particularly periodic partial or intermediate intensity disturbances (e.g., Meigs and Keeton 2018), such as microburst wind events, ice storms, and some insect outbreaks (see chapter 6). Indeed, periodic or episodic disturbances can lead to enormously high wood vol-

Figure 9-2. Large woody debris in two streams running through old-growth riparian forests in the Adirondacks, New York State. Some of the large logs are able to anchor on either side of the stream channel, around which debris dams form. This structure, in turn, creates pool habitats, armors banks, traps sediment, elevates nutrient uptake and spiraling (or processing) rates, and increases "roughness" or the surface area capable of dissipating kinetic energy. Photo credit: W. S. Keeton.

umes in eastern forest streams of all ages (Kraft et al. 2002), and wood recruitment after high intensity, stand-replacing disturbances follows a different dynamic. In these stand-replacing disturbance situations, wood volume and debris-dam frequency are typically high immediately after the disturbance, they decline as logs break down or decay, then they remain relatively low as a young forest regenerates (Valett et al. 2002). Density-dependent mortality (i.e., intertree competition) and density independent events (e.g., windthrow events or ice storms) during the early and middle phases of stand development recruit some logs into the stream channel, but loading rates are generally low and the trees that die tend to be from smaller diameter, less vigorous stems. Wood loading increases later in stand development when both further density-dependent mortality combined with density-independent events and individual tree deaths lead to the mortality of much larger trees (Franklin and Van Pelt 2004). These larger trees not only add more total wood volume, but the larger logs tend to persist longer and generally decay more slowly than smaller wood because, all else being equal, the surface area to volume ratio is lower on bigger trees. Collectively, in relation to forest use, wood volume in the stream takes on a U-shaped distribution when natural disturbances kill trees without removing them from the system (Valett et al. 2002). However, where riparian trees are cleared for timber or agriculture, linear or consistent increases in wood loading over time are likely to occur, with periodic pulses or elevated recruitment following disturbance events (Warren et al. 2009). We focus here on the overall tendency toward an increase in size and abundance of large wood in streams, which is useful in developing rules of thumb and broad hypotheses about ecosystem function. Nevertheless, disturbance history must always be considered when general patterns are applied to understanding a particular forest-stream location.

Benefits of Large Wood to Stream Fish

Prior to the 1970s, many fisheries managers thought large logs and debris dams were bad for fish, going so far even as to actively clear wood out of streams, thinking this would help fish passage. Fortunately, this practice has been discontinued, and we have learned that wood can be a critical structural feature in headwater streams (Nislow 2005). Large wood enhances stream habitat in a number of ways. Wood is itself an important source of cover for fish, and large stable wood can create or enlarge pool habitat (Riley and Fausch 1995: Flebbe 1999). Most work in eastern forests streams—and across North America—examining the role of wood in creating fish habitat has focused on trout and salmon. Although these salmonid fishes can use other stream habitat features (e.g., rocks and deep water in pools) as cover habitat to avoid predation (Sweka and Hartman 2006), researchers have found that fish use wood as a preferred cover type (Flebbe 1999). In systems with abundant wood and complex habitat architecture, visual isolation can reduce aggressive interactions among fish, allowing for higher densities in a given pool (Sundbaum and Naslund 1998). A number of studies in eastern North America have found increased fish abundance following experimental wood additions (Burgess and Bider 1980; Culp et al. 1996). Overall, increasing habitat complexity and pool size are expected to improve habitat for fish as more wood accumulates in streams bordered by old-growth riparian forests.

Not only do old-growth streams generally have more wood, the wood that enters often comes from larger trees and, therefore, is more stable (Braudrick and Grant 2000; Warren and Kraft 2008). Large, stable wood is also more likely to anchor wood jams, which are collections of multiple pieces of wood that often span the stream channel, sometimes nucleating around boulders (Keeton et al. 2007). Wood jams are a highly complex habitat structure that can increase fish abundance, particularly when they increase pool volume and habitat complexity along channels, resulting in braiding and backwater habitats (Warren and Kraft 2003; Burgess and Bider 1980).

Anglers have long recognized that larger pools generally have more and larger fish, an observation confirmed by many studies (Riley and Fausch 1995; Warren et al. 2010). Because wood is an important pool-forming feature (Montgomery et al. 1995), restoration efforts across eastern forest landscapes and throughout North America often focus on adding large logs to streams. Individual pieces of stable wood that span the wetted area of the stream functionally reduce the active channel dimensions of the stream, as does wood that projects into a channel. This decrease in channel size increases water velocity, thereby increasing local stream energy. Higher energy, in turn, allows for greater scour of stream substrates (Thompson and Hoffman 2001). Scour pools created by wood can be critical habitat for fish as they are often quite deep. Alternatively, many wood jams dissipate energy and create dammed pools upstream of the wood structures. In these cases the wood jams also tend to create plunge pools downstream of the structure (Montgomery et al. 1995). Experimental wood additions in Colorado streams created deep plunge pools where logs were added and then anchored to prevent movement during high flows. This increase in pool area resulted in more fish and, ultimately, greater overall trout production (Riley and Fausch 1995; White et al. 2011).

In eastern forest streams, Keeton et al. (2007) found that more large logs (defined in that study as wood greater than 30 centimeters in diameter) were present in streams flowing through old-growth riparian forests than streams flowing through mature forests. This difference in large-log frequency was notable because it was positively associated with pool habitat in the study reaches; by contrast, total wood abundance and total wood volume were *not* important in that analysis, indicating that the key factor was the presence of larger wood pieces. This highlights how and why streams in old-growth forests may differ from those in younger forests. However, increasing large wood in a stream does not necessarily benefit all fish species or all life stages, as noted in an experimental wood addition study by Langford et al. (2012). Other factors, such as stream temperature, macroinvertebrate abundance (i.e., food), and stream chemical conditions, also affect the number and size of fish in a stream, and wood will not always increase pool volume in a watershed with many boulders (Sweka and Hartman 2006). However, given high recruitment rates for large logs in old-growth streams, and given the role of this wood in creating high-quality trout habitat conditions, our working hypothesis in on-going research is that eastern old-growth riparian forests will foster stream habitats that are favorable to native brook trout (*Salvelinus fontinalis*) and other dominant stream fish.

Influence of Large Wood on Aquatic Macroinvertebrates

Macroinvertebates, such as mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera), spend most of their lives in their larval aquatic stage, living in a stream for months to years before emerging as adults to breed and then die. These insects play an important role in stream ecosystems, processing nutrients and linking the base of the food web with higher trophic levels. Despite a lack of research on macroinvertebrates in eastern old-growth forests, we expect that invertebrate communities will differ between systems with young, mature, and old-growth riparian forests. As with fish, increasing wood loads over time would be the most likely driver. In low gradient blackwater systems with soft streambeds, wood can provide critical substrate for many macroinvertebrates (Smock et al. 1989; Lamberti and Berg 1995). Similarly, in sand-bed streams and other systems with highly mobile substrates, stable wood offers refuge from scour (Borchardt 1993). Where large logs create jams, accumulated organic material supports macroinvertebrates in the shredder-feeding guild that consume leaves and other coarse organic material (Lemly and Hilderbrand 2000). As with fish habitat, the amount and stability of wood are key and are enhanced in old-growth riparian forests because of higher recruitment rates for large logs (Keeton et al. 2007). To date, there have been no studies of streams in the eastern United States that have explicitly investigated variation in macroinvertebrate communities across stand-development series extending into old growth. This contrasts with western Oregon, where researchers found higher stream macroinvertebrate biomass in old-growth forest reaches as compared to regenerating riparian forest sections of the same stream, with the difference attributed to greater light beneath frequent canopy gaps in old growth forest streams (Kaylor and Warren 2017).

Terrestrial Carbon Inputs to Streams

The amount, size, and energetic quality of organic matter are of interest to scientists across many ecological disciplines. The fixed carbon in organic matter is, in effect, the fundamental energetic medium of life on earth. Therefore, understanding carbon dynamics is important in understanding how food webs and ecosystems function. Further, sequestration and respiration of organic matter can influence the fate of carbon and whether it remains sequestered in a reduced state or is respired and returned to the atmosphere. Given its relatively slow decay, large wood may accumulate in streams for many years, and when left to accumulate, large wood can represent a sizable carbon pool in streams (Beckman and Wohl 2014). Greater wood volumes have also been found in late successional forest streams relative to streams with mature riparian forest in the eastern and upper Midwestern regions of the United States (Valett et al. 2002). In addition, a space-for-time study in the northeastern United States found a positive relationship between stand age and large-wood accumulation in streams, with little evidence of reduced accumulation rates even when the age of dominant riparian trees exceeded 300 years (Warren et al. 2009).

Slower decay rates for large logs, originating from the predisturbance stand but persisting through secondary succession (termed "biological legacies"), influence carbon accumulation rates in streams and disrupt the straightforward progression by which increasing stand age increases the amount of large wood. As noted above, older forest streams have more wood *on average* than younger forest streams, but slowly decaying logs that carry the legacy of past disturbances alter this relationship and increase carbon storage in streams. For example, one study in the central Appalachians found little evidence for a relationship between stream wood and riparian forest stand age (Hedman et al. 1996). However, this region was heavily impacted by the chestnut blight in the early 1900s. Therefore, many stream reaches retained large dead wood, originating from the slowly decaying old-growth American chestnut trees (*Castanea dentata*) that died almost a century before. When chestnut trees were removed from the assessments, an increase in wood volume over time was well in line with expectations. This highlights the importance of considering wood inputs from future disturbances and mortality agents. These include invasive insect pests such as the hemlock woolly adelgid (*Adelges tsugae*) and the emerald ash borer (*Agrilus planipennis*), as well as changes in physical export processes, such as increased flooding, but reduced ice flows in the northeastern United States as climate change proceeds (see Keeton et al. 2017). These drivers of future wood recruitment and loading dynamics will have important implications for predicting stream carbon dynamics over the coming decades.

Wood—particularly stable wood—dramatically influences annual and seasonal stream carbon dynamics through its effect on organic matter retention. In one of the first studies on this topic, conducted at the Hubbard Brook Experimental Forest in New Hampshire, Bilby (1981) found that wood removal caused up to a five-fold increase in fine particulate carbon export relative to reference conditions. A number of studies since then have highlighted the role of wood, boulders, and other channel roughness elements in the retention of leaves and other particulate organic matter throughout the autumn and winter seasons (Muotka and Laasonen 2002). In the headwater streams of old-growth forests, where large logs are more common and large wood jams occur regularly, more coarse and fine organic material will be retained that will increase carbon storage and whole ecosystem respiration (Bechtold et al. 2017).

Organic material from the riparian forest is particularly important in forested streams because this “allochthonous” (a term meaning “derived from outside the stream”) carbon is often the dominant basal resource supporting stream food webs (Wallace et al. 1997; Fisher and Likens 1972; Hall et al. 2000). Input of allochthonous material from the riparian forest affects not only the composition of the aquatic biotic community but also fundamental nutrient cycling along stream networks (Tank et al. 2010; Mulholland and Webster 2010). In a classic experiment conducted in the southern Appalachian Mountains, litter exclusion demonstrated that allochthonous carbon inputs can control stream insect communities and food web structure (Wallace et al. 1997; Hall et al. 2000). The type of litter that enters the stream is also important. Litter from deciduous trees is generally more labile (easy to break down) than that from conifers, but it also predominately enters the stream en masse in the autumn, whereas most conifers tend to distribute their litter input more evenly throughout the year. In riparian forests dominated by deciduous species, stream nutrient concentrations decline and ecosystem respiration spikes upward following leaf fall in autumn (Roberts and Mulholland 2007). Although leaf litter may persist for weeks to months in a stream, an increase in respiration and decline in stream nutrient concentrations are enhanced by the new litter and the highly accessible dissolved organic carbon that rapidly leaches from allochthonous leaves. Organic material from soils also washes into the stream, providing a consistent but low-level carbon source that can be substantial during seasonal or periodic flood events, especially in low gradients in floodplain forests.

Stream Light and In-Stream Primary Production

In forested headwater ecosystems, the structure of riparian forests directly influences the amount of light reaching a stream (Kaylor et al. 2017; Keeton et al. 2007; Bechtold et al. 2017). But canopy structure in riparian forests is not static or uniform. Instead, it changes dynamically as forests age, develop, and interact with natural disturbances, becoming spatially heterogeneous as canopy gaps develop (Van Pelt and Franklin 2000). The resulting complex light environment within riparian corridors and over stream channels is driven by canopy gap dynamics (Curzon and Keeton 2010). Light is a key limiting factor for primary production on stream substrates (Rosemond 1993; Bilby and Bisson 1992). Yet, only recently have scientists linked the temporal and spatial dynamics of in-stream primary production to the age and canopy architecture of adjoining riparian forests, particularly old-growth forest structure in eastern stream systems. (Curzon and Keeton 2010; Kaylor et al. 2017; Bechtold et al. 2017; Stovall et al. 2009).

While external plant material falling into channels is usually the dominant mass carbon source in forested streams, controls on primary production are important because stream algae provide a higher “quality” carbon source (Cross et al. 2005). Algae also generally have more nitrogen and phosphorous per unit carbon than leaves, branches, and other fine litter (Cross et al. 2005), and studies using isotope and gut analyses of fish and invertebrates have shown that the contributions of algae to stream food webs are disproportionately high relative to the availability of algae (McCutchan and Lewis 2002). Consequently, controls on stream light may affect not only algal production but also the productivity of secondary consumers in a system (Bilby and Bisson 1992; Rosemond 1993; Kaylor and Warren 2017).

From studies of headwater streams in both eastern deciduous forests and the coniferous forests of the Pacific Northwest, scientists have learned that old-growth riparian forests have, on average, more light reaching channels than do young and mature riparian forests (Keeton et al. 2007; Kaylor et al. 2017; Warren et al. 2013). However, this is not to say that streams within old-growth riparian forests receive greater light fluxes uniformly. As in terrestrial ecosystems, light availability is patchy in old-growth forest streams due to their complex canopies, characterized by continuous variation in both vertical (e.g., canopy layering) and horizontal (e.g., tree density, gaps) dimensions. Intense light patches in old forests are interspersed with areas of low light, leading to frequent transitions from light-controlled benthic algae production in the shaded reaches to nutrient regulated algae production in sections with greater light flux (Warren et al. 2017). In contrast, young and mature riparian forests are most often dominated by closed, more uniformly structured canopies, having fewer intense light patches and lower total light flux to the stream benthos. Bechtold et al. (2017) found that light flux to streams exhibited a U-shaped distribution over successional seres, with higher light soon after riparian clearing, lowest light in the middle stages of stand development and higher light later in stand evolution due to the development of canopy gaps. A similar pattern was observed by Kaylor et al. (2017) in a review of stream studies across the Pacific Northwest. Canopy "openness," a metric commonly used as a proxy for potential light exposure, was a dominant predictor of differences in stream vertebrate biomass in a comparison of paired reaches in old-growth and second-growth riparian forests (Kaylor and Warren 2017). In that study, the canopy openness proxy measure of stream light accounted for over 70 percent of the variability in the difference in vertebrate biomass between adjacent reaches with different riparian forest conditions. No comparable paired studies of the influence of riparian forest age class on stream vertebrate biomass have been conducted in eastern forests. However, given the distinct differences in canopy structure and stream light noted by Keeton et al. (2007) and Bechtold et al. (2017), and given the clear increases in algal standing stocks in light patches of eastern old-growth forests observed by Stovall et al. (2009), similar differences are likely in eastern stream systems.

Riparian forests and the shade they create are also important in regulating stream temperature, because solar radiation has the strongest thermal influence on streams (Johnson 2004; Garner et al. 2017). Removal of riparian forests, for instance by logging or natural disturbance, eliminates shade and can lead to substantial increases in stream temperature (Johnson 2004). Although light levels are generally higher in streams bordered by late successional and old-growth forests, a comparable increase in temperature has not been quantified in eastern forest ecosystems. This is likely due to the more moderate increases in light associated with patchy openings in the canopy of late successional forests relative to the larger changes induced by experiments in which forest cover was cleared (Klos and Link 2018; Janisch et al. 2012). Further, the presence of abundant logs and debris dams in old-growth streams may force water into subsurface flowpaths (the *hyporheic zone*) where it may remain cooler—at least in summer—and thereby insulate the stream from warming effects of solar radiation (Arrigoni et al. 2008).

Nutrient Dynamics in Old-Growth Streams

Medical doctors have shown that, as humans age, their dietary needs change in response to how the body absorbs, processes, and excretes nutrients; that is, the elderly eat less, are inefficient at absorption (due to decreased stomach acid), and, thus, excrete more vitamins and nutritive compounds than young humans. Similarly, a classic paradigm in ecosystem ecology suggests that as forests age, nutrients will be lost or leaked from the terrestrial system at higher rates than for younger forests (Likens et al. 1970; Vitousek and Reiners 1975). Viewing these processes with a holistic watershed-scale perspective requires that we consider the absorption, the processing, and the export of nutrients from both upland and in-stream components of the system. Thus, nutrient loss from terrestrial soils is accompanied by nutrient gain in downstream aquatic systems (Bechtold et al. 2017). We focus here on how streams that flow through aging forests retain, transform, and export nutrients, thereby regulating the interplay of nutrients between aquatic and terrestrial ecosystems (Bernhardt et al. 2003; Mulholland 2004). Most importantly, forest age and structure strongly influence these processes.

Streams have often been thought of as passive pipes flowing out of a watershed (Hotchkiss et al. 2015), where water and nutrients pass through rapidly and ultimately reach an end point. Nutrients are quickly assimilated by microbes and algae when they are available in aquatic systems. Then, after those microbes or algae die, the nutrients are again released back into the water and made available for uptake, thereby creating a cycle of nutrients between organic and inorganic forms. A similar cycle, called a "nutrient spiral," also occurs in terrestrial soils, but the longitudinal nature or downstream flow of water stretches this cycle into a springlike spiral. The spiral can be stretched out or contracted, depending on how quickly nutrients are absorbed from the water column and how long they are retained in stream biota (Mulholland et al. 1985). The average distance that a nutrient particle travels in a stream before being absorbed again can be measured and compared between systems. This value is referred to as the uptake length (S_w or the portion of the spiral in the water column). Thus, streams are not pipes. Instead, they cycle nutrients and are affected by many factors influenced by the structure and age of surrounding forests that, in turn, influence in-stream structural characteristics.

At the stream reach scale, there are many reasons to expect nutrient uptake to be greater in streams with old-growth riparian forests than in streams with young or mature riparian forest. As noted above, headwater streams in old-growth forests on average receive more sunlight than streams flowing through younger forests. This difference in light is important because increasing light in forested streams often leads to large increases in primary production and associated increases in stream nutrient demand. The role of light as a driver of stream nutrient dynamics has been most thoroughly explored in experimental studies in which all or nearly all of the riparian vegetation has been removed (Sabater et al. 2000). While differences in light availability between old-growth and second-growth forests are more subtle, they have been shown to alter nutrient uptake (Sobota et al. 2012). Old-growth forests have more frequent and larger light patches than younger forests, creating a patchwork of light and dark areas along the streambed. This light mosaic creates localized areas (hot spots) of nutrient demand due to greater algal standing stocks (Stovall et al. 2009) and produces in-stream fluctuations between light and nutrient limitation (Warren et al. 2017). Simultaneously, the downstream flowpaths of nutrient spirals elongate and shrink in response to the availability of leaky nutrients from forest soils and patches of sunlight from the old-growth canopy. As a result, we expect autotrophic nutrient demand to be greater in old-growth reaches based solely on differences in light dynamics between old-growth and mature forests.

In addition to greater light levels that can enhance autotrophic uptake, a higher frequency of large wood and wood jams in old-growth forest systems can also enhance nutrient uptake. This anticipated increase in uptake is attributed to heterotrophic fungi and microbes that process litter retained behind dams. These microbes have a high nutrient demand as they process dead wood, leaves, and other litter. Indeed, in a bioassay study comparing nitrogen losses among different stream substrates, Steinhardt (2000) found greater nitrogen loss potential in substrates behind wood jams relative to substrates in the open channel. Nutrient uptake was also found to decrease with the loss of a carbon subsidy in a litter removal study from a headwater stream in the southern Appalachian Mountains (Webster et al. 2000). As a result, we also expect increased nutrient demand in old-growth forest streams due to greater heterotrophic demand.

While the hypothesis that old-growth forest streams have greater nutrient demand than streams flowing through young forest is supported conceptually by the observational and manipulative studies noted above, research quantifying nutrient uptake in streams across a range of stand ages in the eastern United States has yielded surprisingly variable results. There was support for this hypothesis in a study comparing phosphate uptake between streams with late successional versus mature riparian forest stands in the central Appalachian Mountains, where uptake was distinctly higher in the old-growth reaches (Valett et al. 2002). In that study, the relationship between phosphate uptake and stand age was attributed to differences in carbon retention associated with wood and wood jams. The importance of wood jam frequency for stream phosphate uptake in eastern forests was further supported by a subsequent study in central New Hampshire (Warren et al. 2007), yet that study found no strong relationships between stream wood and nitrogen uptake. The absence of a relationship in that study was attributed to alternative factors affecting nitrogen uptake, such as autotrophic demand, use of nitrate in denitrification, or the influence of hydrologic retention times (Bernot and Dodds 2005). More recently, a study exploring nutrient uptake, primary production, and ecosystem respiration in streams across upstate New York and central New Hampshire, revealed inconsistent results when evaluating sites with riparian forests ranging from 10 to at least 360 years in age. Bechtold et al. (2017) did find greater primary production and greater respiration rates in old-growth forest streams. However, nutrient uptake did not follow this pattern. Some of the streams in old-growth reaches did indeed have greater uptake rates, but no consistent relationship was found between stand age and nutrient uptake.

In summary, available evidence provides some support for an increase in stream nutrient concentrations as riparian and upland forests age, but results are more equivocal in assessing stream nutrient cycling over time. Overall, empirical assessments are inconsistent despite credible reasons for expecting that stream nutrient uptake rates will increase as riparian forests progress toward old growth. As a result, we still have a long way to go in determining how, why, and to what degree nutrient cycling changes through the process of stand development in stream riparian zones.

Conclusion

The high degree of riparian functionality associated with old-growth forests is an ecosystem service that has received little attention, yet riparian influences will assume greater importance as eastern forest landscapes continue to recover and mature from historic land use. While forest development can follow multiple pathways (Lorimer and Halpin 2014; Urbano and Keeton 2017), current research suggests that development of complex late successional characteristics will lead to concurrent shifts in stream ecosystem function independent of the rate or pathway by which it occurs (Warren et al. 2016). Drivers of shifts in stream function as young and ma-

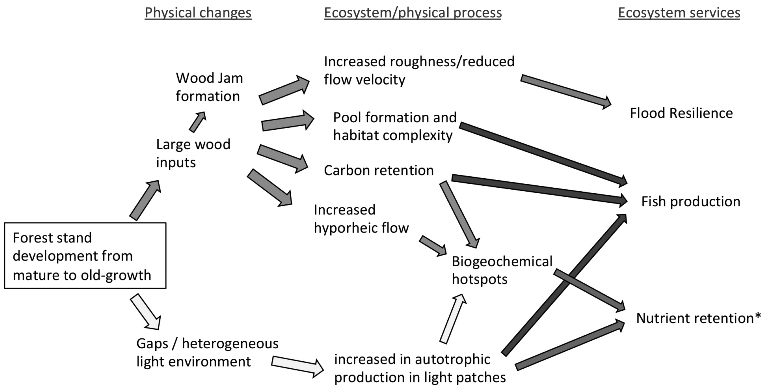

Figure 9-3. Pathways by which the transition from mature to old-growth riparian forests can affect physical and ecological processes in streams, with associated implications for stream ecosystem services. Empirical studies provide support for greater inorganic phosphorous uptake in older forest streams; results are equivocal for inorganic nitrogen uptake.

ture riparian forests progress toward old growth are directly and indirectly associated with increases in two key factors—large wood and stream light (figure 9-3), which influence stream ecosystem processes and stream biota. These, in turn, influence the ecosystem services provided by streams (figure 9-3). Streams with old-growth riparian forests have also been found to be more resilient to disturbance than those with younger riparian forests, resulting, in part, from the greater stand structural complexity of the forests and increased "roughness" and wood loading in the riparian zone (Keeton et al. 2017). Understanding that canopy structure and stream wood are key factors driving the differences in functionality between systems with old-growth versus younger riparian forests informs our projections of future change in eastern forest streams and the ecosystem service consequences of that change. This understanding also raises questions about how best to effectively manage or restore riparian forests to promote old-growth characteristics associated with desirable streams functions, such as flood resilience, nutrient processing, and high-quality fish habitat.

Further, understanding that stream ecosystem function is affected by wood loading, riparian forest canopy structure, and the species composition of riparian forest community allows us to consider how stream function may change in the future not only as a result of anticipated shifts in forest succession and age class distributions, but also as we see changes in forest structure due to increased species invasion, altered climate regimes, and changing land use. For example, the invasion of both the hemlock wooly adelgid and the emerald ash borer (see chapter 12) are both of particular importance to projections of stream ecosystem function in the future as these important riparian trees are lost, altering both wood loading and canopy structure in and along stream corridors. To date, land-use changes across eastern forests have been the driving factor affecting streamside forests and associated stream function. The removal of riparian forests for timber and agriculture in the nineteenth and early twentieth century fundamentally altered stream function, and the subsequent regeneration of riparian forests has led to a slow recovery toward historic function. But the remarkable redevelopment of secondary forest cover alone does not constitute a full recovery of riparian functionality. Important differences remain between streams that run through old-growth forests versus those that run through young and mature forests. And with few riparian forest stands currently in an old-growth condition, most forest headwaters have likely not fully returned to their historic level of functionality. With careful stewardship and adaptive management, we can hope that this will change in the future.

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