SYNTHESIS & INTEGRATION

Changing forests—changing streams: riparian forest stand development and ecosystem function in temperate headwaters

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Abstract. Light availability influences temperature, primary production, nutrient dynamics, and secondary production in aquatic ecosystems. In forested freshwater ecosystems, shading by streamside (riparian) vegetation is a dominant control on light flux and represents an important interaction at the aquatic–terrestrial interface. Changes in forest structure over time, particularly tree mortality processes that gradually increase light penetration through maturing forest canopies, are likely to influence stream light fluxes and associated ecosystem functions. We provide a set of conceptual models describing how stream light dynamics change with the development of complex canopy structure and how changes in light availability are likely to affect stream ecosystem processes. Shortly after a stand-replacing event, light flux to the stream is high, but light fluxes decline as canopies reestablish and close. Tree density, the degree of understory growth, patterns of tree mortality, and small-scale disturbances interact as drivers of multiple pathways of forest structural development. Changes in canopy structure will, in turn, influence stream light, which is expected to impact primary production and stream nutrient dynamics as well as the amount of autochthonous carbon supporting aquatic food webs. Ultimately, these conceptual models stress the importance of recovery from historic forest disturbances as well as future forest change as important factors influencing the long-term trajectories of ecosystem processes in headwaters.

Key words: aquatic–terrestrial linkages; benthic primary production; forest succession; land-use recovery; riparian forest; stand development; stream light.

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INTRODUCTION

Contemporary understanding of controls on forest ecosystem processes emphasizes the dynamic role of disturbance and its interaction with successional and stand development trajectories (North and Keeton 2008, Burton et al. 2009, Donato et al. 2012, Seidl et al. 2014). In temperate forested biomes, disturbance dynamics (and recovery from disturbance) that lead to changes

in growth, community composition, and overall structural characteristics of trees have important implications for terrestrial ecosystems and for adjacent aquatic environments. Changes in community composition and in the structure of riparian forests can alter the characteristics and function of forested freshwater ecosystems over time as a result of changes in the direct input of nutrients, organic matter, and large wood (Vitousek and Reiners 1975, Naiman and Decamps 1997, Valett et al. 2002, Warren et al. 2007). Changes in the structure of riparian forests also impact stream processes indirectly by changing the amount and spatial distribution of light fluxes to headwater streams (Keeton et al. 2007, Warren et al. 2013). In this synthesis, we integrate the concept of multiple trajectories of stand structural development with our understanding of how stand structure in the riparian forest influences light and stream ecosystem processes. From this, we present a series of conceptual models illustrating how alternate stand development pathways in the riparian forest could affect long-term trajectories of change in associated stream environments.

Light availability is a fundamental constraint on autotrophic production in terrestrial and aquatic environments. The influence of light is particularly important in forested headwater ecosystems where primary production rates and algal standing stocks can be regulated by the amount of photosynthetically active radiation (400–700 nm wavelength) reaching the streambed (Boston and Hill 1991, Hill et al. 1995, Julian et al. 2011). In these systems, light availability is controlled primarily by streamside vegetation; therefore, changes in the structure and composition of these streamside (riparian) plant communities can alter light flux, influencing stream primary production which, in turn, modifies stream nutrient dynamics and higher trophic level production (Noel et al. 1986, Boston and Hill 1991, McTammany et al. 2007, Sobota et al. 2012). Forested headwater streams run beneath the canopy, and we can therefore use research on understory light dynamics from terrestrial environments to develop hypotheses about how light flux to forested streams will change over time as stand structure changes (Emborg 1998, Parker et al. 2002, Bartemucci et al. 2006).

The greatest understory light levels occur after stand-replacing events such as forest harvest,

fires, or large windstorms that remove canopy shading. Following a high-intensity disturbance event, reestablishment of vegetation, particularly woody vegetation, leads to decreases in light availability as forest canopies develop and then ultimately close over the stream. However, as the riparian plant community recovers, forest structure may develop along a range of trajectories in response to plant successional dynamics, soil conditions, climate, and interactions with a range of disturbance types and intensities (Van Pelt et al. 2006, Burton et al. 2009, Romme et al. 2011, Reilly and Spies 2015). In widely used conceptual models of stream light dynamics over time that focus on forests in the Intermountain West and Pacific Northwest regions of North America, riparian shading is predicted to reach a maximum 40–80 yr after stand replacement (Gregory et al. 1987, Minshall et al. 1989). In this "stem-exclusion" or "self-thinning" phase in the riparian forest, competition among adjacent trees for light leads to individual tree mortality and a dense, closed canopy where gaps are filled quickly by adjacent tree growth (Sedell and Swanson 1984, Gregory et al. 1987, Oliver and Larson 1996). Eventually, light flux may increase late in stand development as complex canopy structure reestablishes. The density of residual trees (i.e., survivorship postdisturbance) during early stages of development can affect the degree of canopy coverage and how canopy coverage changes as these stands age. If trees regenerate at a high density and if high-intensity disturbances are infrequent, the canopy may remain closed until competition among adjacent trees for light and belowground resources thins the stand (Franklin et al. 2002). In cases where tree density is low in recovery from a stand-replacing event or if local disturbances occur frequently, the stem-exclusion phase may be short in duration or entirely absent. Regardless of initial density, stands will generally develop greater canopy complexity given adequate time. Increased understory growth and the development of multiple canopy layers are facilitated to a greater degree when canopy gaps cannot be filled by lateral growth of adjacent individuals (Franklin et al. 2002). The gaps created by tree senescence, pathogens, pests, or small-scale disturbance events ultimately lead to increases in localized understory light fluxes, and increased light to the understory promotes the growth of

previously suppressed vegetation (Van Pelt et al. 2006). Over time, the spatiotemporal nature of these gaps contributes to a complex forest structure consisting of multiple layers. Canopy gaps not only increase average light availability to the understory but they also increase light flux to associated streams (Stovall et al. 2009, Curzon and Keeton 2010, Gravel et al. 2010).

While the pathway described above is a useful benchmark for understanding stand development processes, especially in areas where there has been complete stand removal/replacement, recent evidence suggests that pathways of development can be considerably more complex depending on forest community, region, climate, and disturbance dynamics (Lorimer and Halpin 2014, Reilly and Spies 2015). Current models increasingly recognize the wide range of development trajectories and the importance of intermediate intensity or partial disturbances in creating complex canopy architecture and multiaged structures in which canopy closure and ground-level light varies dynamically over time and space, but not necessarily in accordance with the developmental pathway described above (Woods 2004, Hanson and Lorimer 2007). Forest clearing has been prevalent in the riparian zone of streams across North America and around the world over the past 100 yr, and we frame this study within the context of recovery from a complete stand removal event (e.g., few remnant trees, snags and dead wood following harvest). From the perspective of stream light, changes that influence the size and frequency of canopy gaps and other structural characteristics that affect light exposure on the forest floor (and in turn streams that run along the forest floor) are particularly important.

Changes in light associated with the development of greater structural complexity in riparian forests are an important consideration for ecological studies in the coming century. Currently, a majority of forest ecosystems across temperate North America are recovering from land clearing (stand removal) associated with historic forest management, agriculture, and development (Foster et al. 1998, Pan et al. 2011, Brooks et al. 2012, Richardson et al. 2012). While wholesale harvest continues to occur in forest uplands, removal of riparian vegetation due to logging or land-use conversion has declined substantially in many regions of North America (Lee et al. 2004).

For example, in the northeastern North America, riparian forests have been regenerating for almost a century; while in the Pacific Northwest changes implemented under the 1993 Northwest Forest Plan dramatically shifted riparian management on federal forests toward protection of riparian buffers and long-term restoration of late-successional characteristics (Gregory 1997, Richardson et al. 2012). The latter includes forest management of young to mature stands, such as variable density thinning and under planting of shade-tolerant conifers to enhance the development of complex canopy structure. Generally, contemporary management practices across North America emphasize some degree of protection for riparian buffers and corridors (Stuart and Edwards 2006, Naiman et al. 2010), although forestry practices vary considerably typically based on stream size, presence of fish, and potential for landslides (Blinn and Kilgore 2001, Lee et al. 2004, Richardson et al. 2012). The collective area of regenerating forest with stands between 40 and 80 yr of age encompasses millions of hectares across the continent (USDA Forest Service 2001, Pan et al. 2011), and within these forests, there are hundreds of thousands of kilometers of forested headwater streams. Regardless of the specific type of forest practice or disturbance, the coming century should bring a transition in many forests to increasingly complex stand structures with concurrent shifts in stream light availability (Franklin and Van Pelt 2004).

Most empirical work exploring the relationships between changing riparian forests and its influence on stream biota and stream ecosystem processes consider short-term (< 5 yr) responses. Studies on aquatic–terrestrial linkages have demonstrated the importance of riparian forests in regard to allochthonous carbon inputs that support stream food webs (Fisher and Likens 1972, Wallace et al. 1997, Hall et al. 2000) and in regard to large wood, which are key structural elements in streams (Bilby 1981, Montgomery et al. 1995, Gregory et al. 2003). Long-term stand development dynamics in the riparian zone have been incorporated into wood and litter input projections (Benda et al. 2002, Meleason et al. 2003, Warren et al. 2009), but stand development processes are rarely considered in exploring changes in stream light over longer time periods. The few existing papers presenting conceptual diagrams

of long-term changes in stand development and its influence on streams via changing light are derived from the western USA (Pacific Northwest and Intermountain west), and they tend to focus the response of biota along a single development trajectory (Sedell and Swanson 1984, Gregory et al. 1987, Minshall et al. 1989, Gresswell 1999, Mellina and Hinch 2009). The goal of this synthesis is to advance the broader framework for considering long-term changes in the riparian forests by more explicitly addressing development of late-successional forest structure and by explicitly presenting multiple stand development trajectories. While these processes have been considered in conceptual and empirical models focused on long-term trajectories in wood recruitment (Hedman et al. 1996, Benda et al. 2002, Meleason et al. 2003, Warren et al. 2009), they have not been included in our understanding of stream light dynamics. We focus here on light availability due to its importance in stream ecosystems, even when fluxes are relatively low (McCutchan and Lewis 2002, Lau et al. 2009*b*, Matheson et al. 2012). Further, by advancing the conceptual framework that relates riparian forest age and structure to stream food webs via bottom-up process and controls on stream light, this synthesis will help meet a demand in stream restoration to place riparian areas in a larger stream food web context (Naiman et al. 2012).

Importance of Light in Headwater Streams

Changes in canopy structure that create even small changes in stream light flux are likely to influence stream ecosystem function and structure in forested headwaters for two reasons. First, primary production can be limited by light availability in shaded forest streams (Boston and Hill 1991, Hill et al. 1995, Quinn et al. 1997, Hill and Dimick 2002). Light fluxes to the benthos of forested headwaters are often below the point of photosaturation for benthic primary producers; therefore, increasing light in these systems often leads to rapid and substantial increases in primary production (Boston and Hill 1991, Hill et al. 1995, 2009, Von Schiller et al. 2007). Even in systems where primary production may become light saturated fairly quickly (between 200 and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$), light can have a much stronger

influence on stream algal accrual than nutrient availability (Wellnitz et al. 1996, Ambrose et al. 2004, Bernhardt and Likens 2004, Greenwood and Rosemond 2005). Because primary production is closely associated with light, localized areas of elevated light that are created by canopy gaps are likely to have large influences on primary production both locally and in aggregate at the reach scale (Denicola et al. 1992, Hill et al. 1995, 2009, Stovall et al. 2009, Warren et al. 2016). Nutrient limitation is also important in forested headwaters, and the response to increasing light can be enhanced in systems with higher nutrients or inhibited in systems with lower nutrient availability (Kiffney 2008, Hill et al. 2009, Bernot et al. 2010, Sobota et al. 2012). Given the interaction of light, an nutrient demand by stream periphyton, increases in light that promote primary production, may also lead to greater nutrient demand—and therefore increases in reach-scale nutrient uptake (Johnson et al. 2009, Bernot et al. 2010, Finlay et al. 2011, Sobota et al. 2012, Warren et al. 2016). The second reason that small increases in stream light are likely to yield biologically meaningful responses in headwater streams is the potential for increases in the availability of "high-quality" food for invertebrates and fish that feed on benthic periphyton. Stream periphyton typically has a lower carbon-to-nitrogen ratio (C:N) than most allochthonous detritus (e.g., leaves and needles; Sterner and Elser 2002, Cross et al. 2005, Allen and Castillo 2007). With more N per unit biomass, the energetic benefits of assimilation increase for the same mass of material consumed, making periphyton a higher quality food source for consumers than leaf detritus (Pandian and Marian 1986, McCutchan and Lewis 2002, Cross et al. 2005, Hill et al. 2010). These increases in energy- and nutrient-rich food resources can in turn yield substantial bottom-up effects on stream food webs (Murphy et al. 1981, Kiffney and Roni 2007, McNeely et al. 2007, Kiffney et al. 2014). In addition, these changes likely result in changed benthic community composition, and this may further impact the food web and subsequent fish production (Steinman et al. 1997, Power and Dietrich 2002).

Conceptual Models

We present a set of conceptual models that represent five alternative development pathways for

forest structure. Although we focus on these pathways to illustrate the conceptual framework, there are many more ways in which stand development, community composition, and disturbance dynamics can interact to affect riparian forest structure and function (Naiman et al. 2010). In the conceptual figures, we hypothesize how riparian forest changes over time are likely to influence stream light and a set of associated ecosystem processes that are influenced directly and indirectly by light for each developmental pathway (Figs. 1–5). We focus on relationships with light, but the ecosystem processes evaluated here can be influenced by other factors that operate at different spatial and temporal scales. For example, algal growth rates in streams can be affected by nutrient additions in both high- and low-light conditions—although the magnitude of the response is often muted in low light (Greenwood and Rosemond 2005, Warren et al. 2016). Similarly, stream nutrient uptake can be influenced by stream habitat features such as wood dams that retain allochthonous carbon and thereby enhance local heterotrophic nutrient demand (Steinhart et al. 2000, Valett et al. 2002). Habitat features such as wood structure and stream pools can also affect nutrient uptake through controls on stream transient storage and flow path length (Hall et al. 2002, Ensign and Doyle 2005). We focus here on light dynamics because light is not as well understood or as well studied as a stream resource that changes over long time periods. In addition to average light flux, we discuss variability in light flux (blue dotted line in Figs. 1–5) defined by the spatial heterogeneity in light along a forested stream. While this has received relatively little attention, we expect that spatial variability in light along the stream has the potential to be important because localized areas of elevated or reduced light flux can create "hotspots" and "coolspots" of primary production (Stovall et al. 2009, Warren et al. 2016), and nutrient demand along the stream (Bernot et al. 2010, Sobota et al. 2012). In streams, hotspots of primary production and nutrient uptake affect not only local processes and local biota but also processes and biota downstream of the hotspot, and they may therefore have disproportionate influence on the system (McClain et al. 2003, Kiffney et al. 2006).

In all of the scenarios, we explore a stand-replacing disturbance to the riparian forest with the greatest light availability occurring immediately following the event. The response variables addressed in the models include the following: gross primary production (GPP), the relative contribution of autochthonous carbon to stream food webs, and stream nutrient demand/uptake/processing. In forested headwater streams, primary production is generally dominated by periphyton (a complex mixture of attached autotrophs, and heterotrophic bacteria and fungi embedded in a polysaccharide matrix) on rocks and wood substrates (Power and Dietrich 2002). We expect primary production at the reach scale (green line on Figs. 1–5) to largely match that of light dynamics (yellow line on Figs. 1–5) with high initial levels but steep declines early as canopies close. Subsequent changes in GPP are dependent upon riparian forest disturbance dynamics and canopy structural development that influence stream light. The tight relationship between light and GPP assumes minimal nutrient limitation of GPP, but stream autotrophs can have high nutrient demands, and therefore, high nutrient uptake (red-dashed line in Figs. 1–5) is expected to track GPP relatively closely early in stand development demand (Hill et al. 2001, Larned 2010, Mulholland and Webster 2010, Finlay et al. 2011). In the middle and later stages of stand development or after partial disturbance events when changes in light are accompanied by changes in stream wood, we see elevated nutrient demand above and beyond those associated with autotrophy alone. The presence of large wood in the stream can alter stream flow paths and can promote carbon retention, both of which can lead to additional heterotrophic nutrient demand (Benda et al. 2002, Valett et al. 2002, May and Gresswell 2003, Warren et al. 2007). While wood is not a focus of these models, we address its potential influence in regard to nutrient dynamics by applying a rate of increase in nutrient uptake late in stand development that exceeds that of stream light (and this assumes low initial wood volume following stand replacement). Light and nutrients can also interact. For example, the light levels at which periphyton become photosaturated can increase with increasing background nutrient levels (Hill and Fanta 2008, Kiffney 2008). Therefore, while photosaturation is depicted in these figures as occurring near the highest light levels soon after
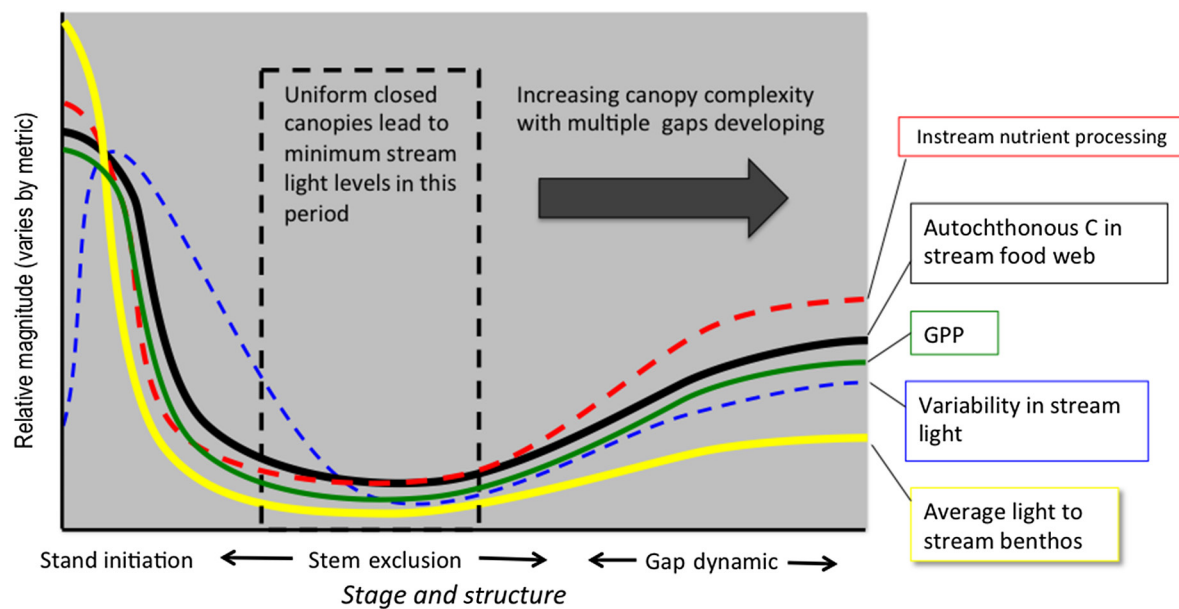
Fig. 1.   Conceptual diagram for how mean and variance of stream light, in-stream primary production, nutrient processing, and the amount of autochthonous carbon fueling the stream food web change through time following a high-density tree recruitment after stand-replacing disturbance. The dashed box encompasses the time period with lowest light. The arrow represents the start of the transition from the stem-exclusion phase of stand development progressing through to the gap-dynamic phase of stand development in a "classic" stand development framework with limited additional disturbance during regeneration. This model is the trajectory of stand development used in existing conceptual models that address long-term light dynamics in streams as a driver of gross primary production (GPP) and ultimately fish production in streams from the Pacific Northwest ecoregion: Sedell and Swanson (1984), Gregory et al. (1987), Mellina and Hinch (2009). **Scenario 1:** Hypothesized changes in stream ecosystems function with stand development under high-density riparian tree recruitment. Light reaches a minimum 20–60 yr after a stand-replacing event during the stem-exclusion phase of development. Stream GPP, light variability, and stream nutrient processing and the amount of autochthonous carbon incorporated into higher trophic levels in stream food web all reach a minimum at this time. Later in stand development, increasing canopy complexity creates patches of light beneath gaps that increase mean stream light and the spatial variability of stream light. This in turn leads to increases in GPP (assuming adequate nutrient availability), which increases autochthonous carbon in the food web. The proportion of autochthonous carbon increases more than GPP due to periphyton carbon quality. Increases in stream nutrient cycling in this scenario increase disproportionally due to additional contributions of stream wood later in stand development (data not shown) per Valett et al. (2002).

stand replacement (when GPP is flat while light levels increase), photosaturation could occur a lower light levels in low nutrient systems. As noted above, stream periphyton is a high-quality resource for stream biota and periphyton isotopic signals can be found in consumers at levels disproportionate to the availability of periphyton in the stream (McCutchan and Lewis 2002, Cross et al. 2005, Hill et al. 2010, Kelly et al. 2014). We, therefore, expect increases in the relative importance of autochthonous organic matter in

supporting higher trophic levels (black line in Figs. 1–5) to coincide largely with increases in stream light (but with higher rates of change). We keep the autochthonous carbon contribution line above the GPP line across all models.

Alternative stand development trajectories

1. In the first scenario, the riparian forest regenerates with high stem densities. The period of lowest light availability occurs during the
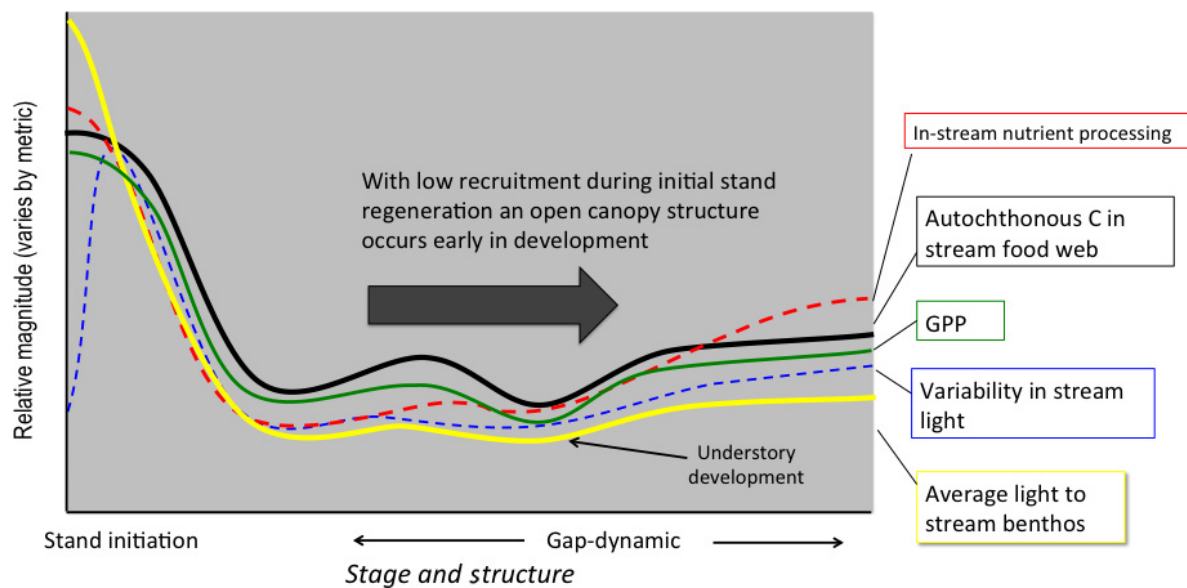
Fig. 2. Conceptual diagram for how mean and variance of stream light, in-stream primary production, nutrient processing, and the amount of autochthonous carbon fueling the stream food web change through time following a stand-replacing event in the riparian forest under low-density tree recruitment. Arrow represents the period when the system shifts toward gap-dynamic processes increasingly dominating stream light exposure. **Scenario 2:** Hypothesized changes in stream ecosystems function with stand development under low-density riparian tree recruitment. Light reaches a minimum 20–30 yr after a stand-replacing event, but due to low stem density, there is limited stem-exclusion mortality. Stream gross primary production (GPP), light variability, stream nutrient processing and the amount of autochthonous carbon incorporated into higher trophic levels in stream food web all reach a minimum after canopy closure, but the values are not as low as in a site with high-density tree regeneration due to greater diffuse light through a more sparse canopy and the capacity for individual mortality to create canopy gaps that in turn lead to associated increases in stream light. In the middle of stand development, light in the stream decreases slightly as the understory develops and then increases back to a mean level consistent with a late-successional system with complexity canopy structure. Stream GPP and autochthonous carbon contributions to the food web follow light with the proportion of autochthonous carbon increasing more than GPP due to high periphyton carbon quality. The larger increases in stream nutrient cycling later in stand development in this scenario are due to increases in larger log recruitment, which have greater probability of staying stable in the stream and therefore greater potential to modify stream habitat and carbon retention in wood jams.

stem-exclusion phase of development and after the stand has grown tall enough for the trees to shade the stream. The specific age at which canopy closure occurs will depend on stream size (sooner in smaller streams), plant community composition, and the climatic and localized conditions (e.g., soils) that influence stand growth rates. This first scenario reflects the stand development trajectory that is most commonly considered and reflects the trajectory used in the early and most commonly cited studies that focus on the temporal dynamics of stand development and its influences on stream light and ultimately fish populations (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009). In this scenario, following a period of low-light fluxes during stem exclusion, we expect a modest but biologically relevant increase in light availability late in stand development as canopy structure becomes increasingly complex and gaps that allow for patches of elevated light on the streambed become more common (Fig. 1, yellow line).
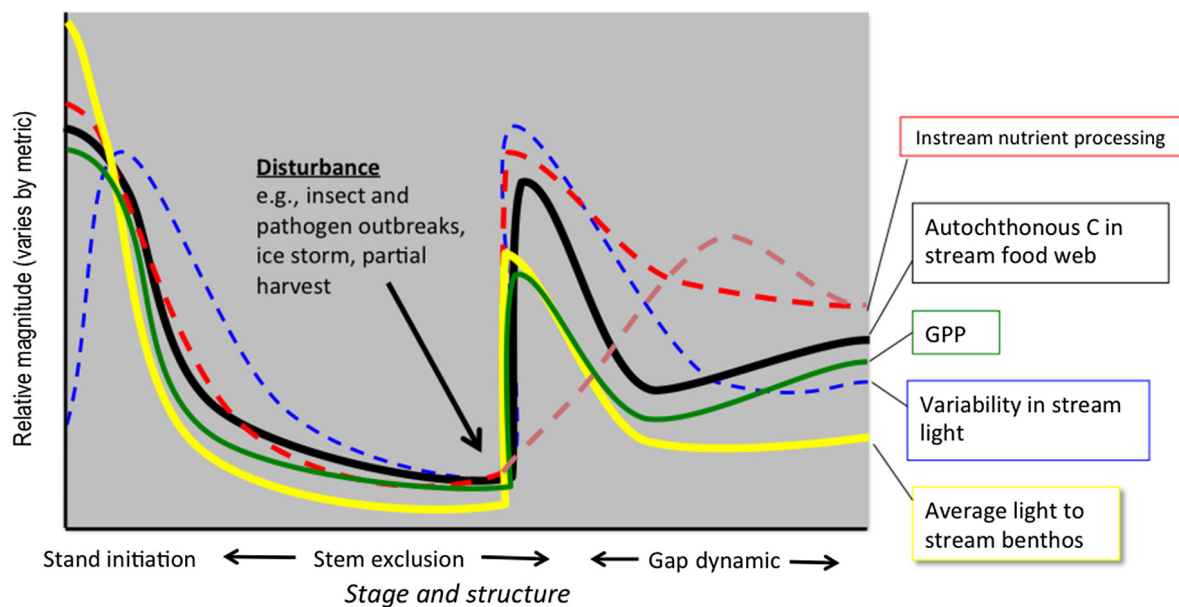
Fig. 3. Conceptual diagram for how mean and variance of stream light, in-stream primary production, nutrient processing, wood standing stocks, and the amount of autochthonous carbon fueling the stream food web change through time in a system that experience high-density riparian tree recruitment—and therefore goes through a stem-exclusion phase of stand development—but which then undergoes a non-stand-replacing disturbance event in the riparian zone that kill a subset of the dominant canopy trees (e.g., species-specific insect and pathogen outbreaks, ice storm). In this trajectory, the stream is wide and/or understory plant grow is limited following canopy opening, and therefore, the non-stand-replacing event increases stream light for a long period of time with the system eventually reverting to a gap-dynamic light condition. **Scenario 3:** Hypothesized changes in stream ecosystems function with stand development under high-density riparian tree recruitment and a non-stand-replacing disturbance event that occurs in mid-successional with limited understory growth over the stream. Light reaches a minimum 20–60 yr after a stand-replacing event, but a non-stand-replacing event in this period reduces canopy cover and increases mean stream light, which in turn leads to increases in stream gross primary production (GPP) (assuming adequate nutrient availability), light variability, stream nutrient processing, and the amount of autochthonous carbon incorporated into higher trophic levels. Canopies close within a few a few decades but with the reduction in tree density from the non-stand-replacing event the system shifts to a gap-dynamic (late successional) structure. The increase in GPP is not as large as the increase in light due to photosaturation effects in gaps. Later in stand development, increasing canopy complexity creates patches of light beneath gaps that increase mean stream light and the spatial variability of stream light. Increases in stream nutrient cycling in this scenario increase are due to increased autotrophic demand along with increased retention associated with large wood recruitment. For a wind-throw event, we would expect to see the dark red large dashed line response. For insect and pathogen outbreaks where wood recruitment will be delayed, we expect to see the light red, small dashed line response.

2. In our second scenario (Fig. 2), stand regeneration occurs at relatively low stem density. Consequently, stem exclusion will be limited and the system is likely to shift directly to a patch-dynamic landscape with localized gaps creating areas of elevated light from an early in the regeneration process. In these systems, we expect smaller changes in light later in stand development relative to early regeneration because, while age and community composition may change, canopy coverage over the stream is likely to remain irregular but more
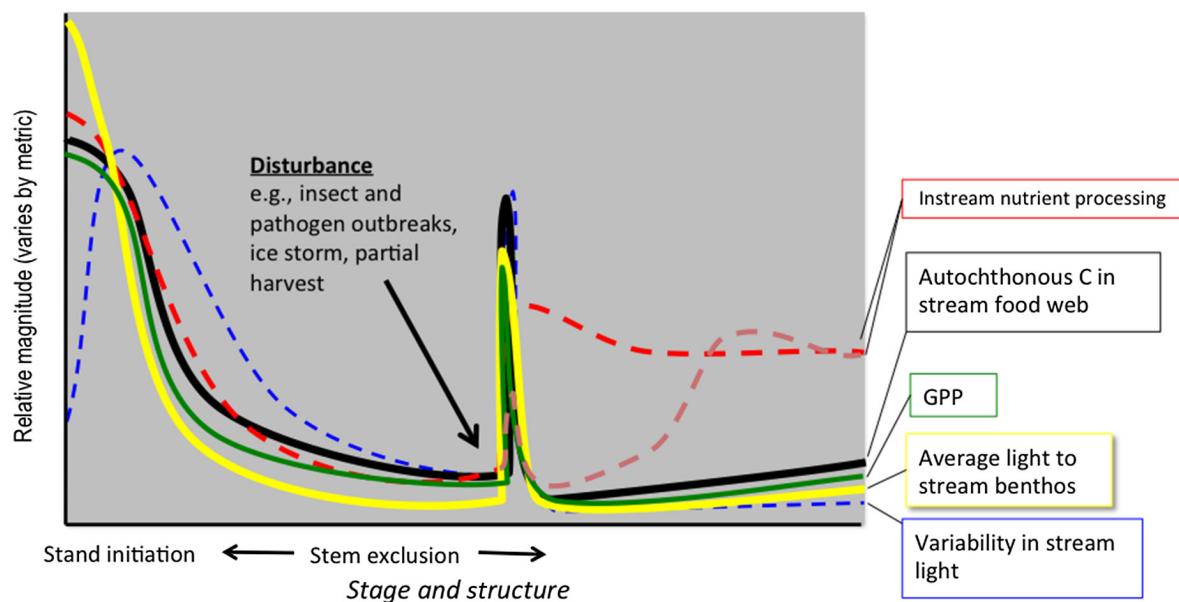
Fig. 4.   Conceptual diagram for how mean and variance of stream light, in-stream primary production, nutrient processing, wood standing stocks, and the amount of autochthonous carbon fueling the stream food web change through time in a system that experience high-density riparian tree recruitment—and therefore goes through a stem-exclusion phase of stand development—but which then undergoes a non-stand-replacing disturbance event in the riparian zone that kill a subset of the dominant canopy trees (e.g., species-specific insect and pathogen outbreaks, ice storm). In contrast to scenario 3 (Fig. 3), the stream in this case is narrow and/or understory plants are large and respond strongly to increases in understory light. Therefore, after a brief increase in primary production following the event, light fluxes to the stream are substantially reduced in the period following the disturbance with recovery to predisturbance levels occurring slowly. **Scenario 4:** Hypothesized changes in stream ecosystems function with stand development under high-density riparian tree recruitment and a non-stand-replacing disturbance event that occurs in mid-successional with a strong response in understory shrubs adjacent to the stream. Light reaches a minimum 20–60 yr after a stand-replacing event, but a non-stand-replacing event reduces canopy cover and increases mean stream light, which in turn leads to increases in stream gross primary production (assuming adequate nutrients), light variability, stream nutrient processing, and the amount of autochthonous carbon incorporated into higher trophic levels. The response in light is short, however, as understory canopies close within a few years. In this scenario, the strong response in understory shrubs persists, and dominates stream shading as the overstory canopy develops greater complexity. This scenario is broadly consistent with a trajectory discussed by Webster et al. (2012) and Northington et al. (2013) in which rhododendron (*Rhododendron maximum*) in the riparian zone responds strongly to the loss of overstory hemlock (*Tsuga canadensis*) and ultimately increases stream shading. Increases in stream nutrient cycling in this scenario are due to increased autotrophic demand along with increased retention associated with large wood recruitment. For a wind-throw event, we expect the dark red dashed line, and for insect and pathogen outbreaks where wood recruitment is delayed, we expect the light red, small dashed line.

consistent on average through time (Romme et al. 2011, Lorimer and Halpin 2014).

3. In the third and fourth scenarios (Figs. 3 and 4), we present a system that recovers with an initially high stem density but which goes through a non-stand-replacing disturbance event that alters the "classic" stand development trajectory portrayed in the first scenario. In scenario three, canopy trees dominate the light environment and the stream is wide enough that understory release does not affect stream light (Fig. 3). So the loss of canopy in the non-stand-replacing event leads to increases in stream light. In the fourth scenario, understory vegetation is
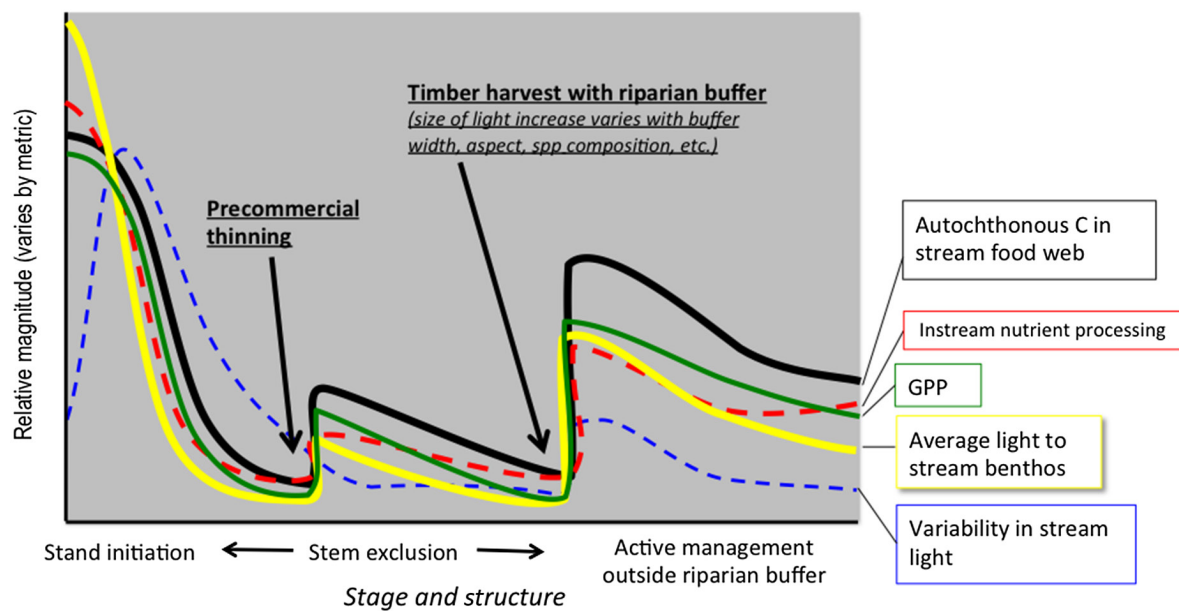
Fig. 5. Conceptual diagram for how mean and variance of stream light, in-stream primary production, nutrient processing, wood standing stocks, and the amount of autochthonous carbon fueling the stream food web change through time in a system that is actively managed. In this scenario, the riparian forest was cleared to the water's edge initially (reflecting historic land use) but a buffer is left in future management. There is a commercial thinning that is applied at about 30–40 yr and harvest outside the riparian forest at about 60 yr. Actual rotation rates and the size of the riparian buffer will affect the regularity of these cycles and the magnitude of the responses to upland clearing. **Scenario 5:** Hypothesized changes in stream ecosystems function with stand development under active current forest management (which leaves buffers on fish-bearing streams) following an historic forest clearing event when stands were removed to the water's edge. Pre-commercial thin is applied to the stand early in development, which slightly increases light and associated processes in the stream. Then, when the full-scale timber harvest occurs light increases more dramatically but because of a riparian buffer the increase is not as large as occurred in association with historic forest management (per Kiffney et al. 2003). Stream nutrient processing is driven primarily by autotrophic demand through much of this time period but later, as forests in the buffers mature, wood recruitment becomes increasingly important and promotes additional nutrient retention via increases in carbon retention and changes in hydrologic flow paths.

important in creating stream shade and the non-stand-replacing event releases the growth of understory shrubs and trees, which enhances shading (Fig. 4). This is reflective of what has been suggested for some areas of the southeastern USA in response to the loss of eastern hemlock (*Tsuga canadensis*), in which the loss of canopy trees allows understory rhododendron (*Rhododenron* spp.) to thrive and shade smaller headwaters (Webster et al. 2012, Northington et al. 2013).

4. In the fifth scenario (Fig. 5), we explicitly consider one possible human management option in and around the riparian zone. While regulations in many states and on federal land

restrict forest management directly adjacent to the stream, other areas allow greater riparian intrusion. We present a scenario in which the forest was initially cut to the stream and then replanted at a high density (reflecting historic forest management and therefore the conditions under which many riparian forests across the country have more recently developed). In this scenario, riparian forests are then thinned, which initially increases light and also accelerates the transition to a gap-dynamic phase. Next, the upland outside the riparian zone is harvested with a riparian buffer in place (reflecting current forest management regulations in many regions). Forest

management outside the buffer can impact light somewhat (Kiffney et al. 2003), but it does not lead to a "reset" of the riparian forest. The latter parts of this scenario reflecting management adjacent to the riparian zone that affects light could also represent some of the recent efforts at managing riparian forests to emulate smaller periodic non-stand-replacing natural disturbance events (Kreutzweiser 2012, Sibley et al. 2012).

IMPLICATIONS AND CAVEATS

Understanding how long-term trajectories of stand development and recovery from stand-replacing disturbances translate to changes in stream light and associated stream ecosystem function in forested ecosystems informs current research, our interpretation of past stream ecosystem studies, and projected changes to forested freshwater ecosystems in the coming century (Skelly et al. 2002, Kreutzweiser et al. 2012, Davis et al. 2013). Placing research on forested headwaters in a temporal context can enhance our understanding of the structure and function of these ecosystems and how processes may change in the future depending on where along a developmental continuum the systems currently occur. For example, a classic paradigm in stream ecology is that forested headwater streams are heterotrophic, with food webs supported almost entirely by allochthonous material from the adjacent riparian forest (e.g., Fisher and Likens 1973), and see review by Tank et al. (2010). In the past few decades, a number of studies have challenged this paradigm (McCutchan and Lewis 2002, Brito et al. 2006, McNeely et al. 2007, Li and Dudgeon 2008, Lau et al. 2009*a*, Schmid-Araya et al. 2012) by showing that consumer communities are disproportionally reliant on autochthonous carbon, even when algal standing stocks are low. We suggest that results from early research that demonstrated strong dependence on allochthonous carbon for stream consumers may partially be a product of when in the trajectory of riparian forest development the work was conducted. Early- and mid-successional second-growth forests encompass the period in stand development when light fluxes to the forest floor and associated streams are at a minimum. With

limited light, primary production is likely constrained, increasing the relative importance of allochthonous litter in fueling secondary production. External food resources are clearly critical to forested headwater streams, and these systems are not expected to shift to net autotrophy as stands develop. The consumption of heterotrophs by secondary consumers may even increase as light increases because elevated light levels can enhance allochthonous carbon assimilation and growth by bacteria (Lagrue et al. 2011, Danger et al. 2013, Kuehn et al. 2014). Overall, however, as riparian forests transition from mid-successional to mature and ultimately to late-successional status, light is likely to increase and the relative availability and importance of autochthonous carbon at the base of many food webs may increase substantially. Therefore, stand structural development can influence our interpretation of stream ecosystem function because the age and stage of stand development affect stream light, which affects subsequent patterns of nutrient demand and energy flow to higher trophic levels (Skelly et al. 2002, Finlay et al. 2011, Julian et al. 2011, Wootton 2012, Lesutiene et al. 2014).

Although factors such as nutrient availability, grazing pressure, and substrate stability can also influence stream primary production, a number of studies found that small-to-moderate changes in stream light fluxes (< 40% change in canopy cover) can promote productivity of stream periphyton with subsequent increases in nutrient demand, grazing macroinvertebrate abundances, and the biomass of aquatic predators (Kiffney et al. 2003, 2004, Hill et al. 2010). Quinn et al. (1997), for example, observed increases in primary production, algal standing stocks, and invertebrate biomass in streams when the percentage of maximum ambient sunlight increased from as little as 2–10% and then again from 10% to 40%. In a series of headwater streams in British Columbia, Canada, Kiffney et al. (2003) found that even with fully forested 30-m-wide buffers, the small increases in ambient light associated with removal of trees outside the buffer zone led to a significant increase in stream periphyton biomass and accrual rates relative to nearby fully forested reference reaches. Hill et al. (2010) demonstrated that the growth rate of stream grazers was closely associated with the amount

of primary production in the stream and followed patterns of seasonal light availability. In a ^{13}C addition study, Lesutiene et al. (2014) found that elevated light led to greater primary production and to more efficient assimilation of the instream primary production by consumers, which they attributed to greater availability of high-quality food. Studies using stable isotope analysis also provide evidence that many stream consumers acquire a majority of their energy from instream production despite low algal standing stocks (Finlay 2001, McCutchan and Lewis 2002, Brito et al. 2006). Forty to eighty percent of consumer production was supported by instream primary production, even though autochthonous material represented only <2–40% of total available carbon in Colorado headwater streams (McCutchan and Lewis 2002). Fewer studies have explored how changes in stream light affect higher trophic levels, but there is evidence that in forested headwaters moderate increases in light can promote the growth and production of fish via bottom-up processes (Murphy et al. 1981, Kiffney and Roni 2007, Mellina and Hinch 2009, Kiffney et al. 2014). Overall, these studies highlight the potential for small increases in stream light that occur in association with the transition to late-successional stand structure to indeed result in notable changes in headwater stream ecosystems.

There are six published models that address riparian forest recovery from a stand-replacing event and specifically including stream light, and associated bottom-up driven changes aquatic ecosystem biota and/or ecosystem function: (1) Sedell and Swanson (1984), (2) Gregory et al. (1987), (3) Minshall et al. (1989), (4) Gresswell (1999), (5) Mellina and Hinch (2009), and (6) Romme et al. (2011). In all cases, ecosystem recovery reflects some variation of scenario one in the conceptual models described here, with high stem density and low stream light after canopy closure. Sedell and Swanson (1984), Gregory et al. (1987), and Mellina and Hinch (2009) focus on stand development following forest management in the coastal, humid Pacific Northwest ecoregion. All three of these models include or imply increases in light later in stand development as canopy complexity increases. The Minshall et al. (1989), Gresswell (1999), and Romme et al. (2011) models address ecosystem recovery from stand-replacing fires in the dry Intermountain West region of North

America. The Romme et al. (2011) model is a modification of Minshall et al. (1989), which was based on observations following 20 yr of stand recovery from the Yellowstone fire of 1989. There are no specific conceptual models for how changes in stand development and its influences on light are likely to affect stream ecosystems in other regions for other forests. Nislow (2005) and Brooks et al. (2012) do explore in prose the relationships between various stages of stand development, stream light, and stream fish production in deciduous hardwood forests. They focus primarily on a trajectory that is most constant with scenario one above as well. Overall, the models presented in this paper are not intended to supplant existing models, but to (1) highlight the potential for alterative development trajectories and processes of stand development that could be considered across multiple systems, and (2) provide new components and new perspectives on how changes in stand structure over time and the associated influences of changing structure on stream light will affect ecosystem processes.

To place our current models in the context of the earlier studies that presented fish biomass as a key response variable, we developed projections of fish (salmonid) biomass over time in a set of headwater streams under each of the five scenarios (Fig. 6). Key assumptions for these responses are that (1) habitat is not degraded—including pool habitat, wood cover, and sedimentation, (2) temperatures remain below thermally stressful levels for the dominant salmonid, (3) GPP is not strongly nutrient limited, and (4) the macroinvertebrate species that increase in response to greater primary production under higher light are a quality food resource for trout. Mellina and Hinch (2009) demonstrated that stream cleaning (intentional wood removal following timber harvest) and an associated loss of habitat was an important factor leading to a negative response of fish to forest management. Current management does not clean streams, so this assumption is reasonable when considering future management. Removing all riparian vegetation and increasing light flux increases stream temperature (Johnson 2004). If temperatures reach stressful levels, we would expect declines in salmonid abundance but in many headwater streams and systems where groundwater inputs dominate, or in cases where light increases but adequate shade

is maintained, temperatures may be limited and can remain below thermally stressful levels (Groom et al. 2011). Increases in primary production that are consumed by inedible or low-energy macroinvertebrates will decouple an autotrophic response to increasing light from a response in stream fish. This was articulated in the conceptual models of Power and Dietrich (2002) addressing the influence of snails on stream food webs and stream energy flow in the context of large river vs. small headwater streams.

Ultimately, the early conceptual diagrams of changing stream light over time as well as the set of alterative trajectories presented here provide useful broad frameworks for considering how stream function can change over time as riparian forest structure changes; however, caution

should be used in applying a specific stand age to these trajectories. The characterization of forest structure and the processes that influence structure remain an ongoing and important area of research and in the field of forest ecology. Studies are increasingly moving toward describing forest structural changes through time as continuous rather than using developmental stages or assigning ages to approximate when changes will occur (Donato et al. 2012, Lorimer and Halpin 2014, Reilly and Spies 2015). Lorimer and Halpin (2014), for example, used the basal area of live trees of different size classes to categorize forests into different structural stages and focus on alternative trajectories and drivers of the transitions between these stages. Alternatively, Reilly and Spies (2015) focus on tree density and stand
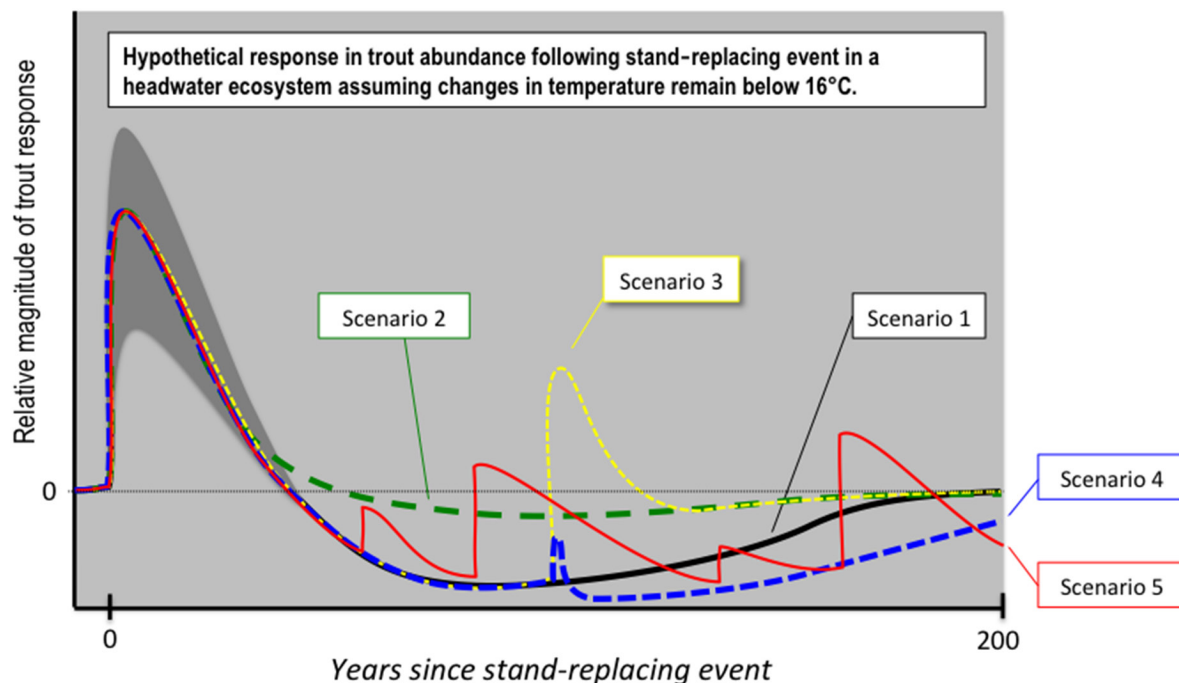

Fig. 6.   Applying projections of trout biomass responses to each of five stand development trajectories. (Scenario 1: stand development under high density tree recruitment; Scenario 2: stand development under low density tree recruitment; Scenario 3: stand development with non-stand replacing disturbance and limited understory shading; Scenario 4: stand development with non-stand-replacing disturbance and release of understory shading; and Scenario 5, forest management with a small riparian buffer and two entries into the adjacent upland–pre-commercial thinning and later harvest.) Gray area around the initial increase reflects and highlights potential variability in the magnitude of a hypothesized initial positive response. While opening the canopy increases temperature as well as light, all scenarios here assume that the initial increases in light do not increase temperatures to stressful levels for headwater trout (>16°C). Substantial increases in temperature, changes in sediment loading, and the fate of stream wood will all affect how fish in these systems ultimately respond to a stand-replacing event (Mellina and Hinch 2009).

biomass to create multiple stand developmental categories and highlight the potential for forests to transition between a stages as a function of stand productivity, climate, disturbance history, and rates of tree mortality. Changes through time are a key theme to all of this work, and overall, there is often strong alignment between contemporary models of stand development and historic projections of changing stand structure over time—especially following a stand-replacing event. The key differences are consideration of complexity, particularly alterative development trajectories and a recognition of the importance of moderate disturbance events as drivers of long-term structural dynamics. Headwater ecosystems which are strongly influenced by the structure of the riparian forest can therefore also progress under multiple changes in stream function over time.

Conclusion

For centuries, trees have been removed from riparian zones in temperate regions for timber, fuel, agriculture, residential development, and industrial land development. However, beginning in the mid- to late 20th century, land-use changes and improved forest management practices in North America reduced the amount of riparian forest clearing leading to a period of reforestation (Foster et al. 1998, Pan et al. 2011, Brooks et al. 2012, Richardson et al. 2012). As a result, many mid-size and small headwater streams across North America currently flow through heavily forested landscapes that are dominated by stands in the mid-seral, stem-exclusion phase of development (Pan et al. 2011). Given the age and structure of these forests, we anticipate substantial changes in the amount and distribution of light in many headwater streams the next 50–100 yr. As stands mature and experience small-scale disturbances, canopy structural complexity and in-turn, light availability beneath the canopy will increase (Emborg 1998, Franklin et al. 2002, Bartemucci et al. 2006). In most regions, we expect increases in light, but even in systems where the total flux does not change, we still anticipate increases in the spatial variability of stream light, and light is a key variable influencing key stream processes. Across North America, and indeed globally, ecosystems are in flux and changes in forest structure associated with recovery from historic and current forest management will influence and interact with impacts of a changing climate to affect stream function. We therefore stress a consideration of the past as well as the future as we evaluate stream ecosystems in the coming century.

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