

Direct and Terrestrial Vegetation-mediated Effects of Environmental Change on Aquatic Ecosystem Processes

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Global environmental changes have direct effects on aquatic ecosystems, as well as indirect effects through alterations of adjacent terrestrial ecosystem structure and functioning. For example, shifts in terrestrial vegetation communities resulting from global changes can affect the quantity and quality of water, organic matter, and nutrient inputs to aquatic ecosystems. The relative importance of these direct and terrestrial-vegetation-mediated effects is largely unknown, but understanding them is essential to our ability to predict the consequences of global changes for aquatic ecosystems. Here, we present a conceptual framework for considering the relative strengths of these effects and use case studies from xeric, wet and temperate, and boreal ecosystems to demonstrate that the responses of aquatic ecosystems to drivers of global changes may not be evident when the pathways are studied separately. Future studies examining changes in aquatic ecosystem structure and functioning should consider the relative contributions of both direct and terrestrial-vegetation-mediated effects of global changes.

Keywords: terrestrial-aquatic linkages, connectivity, global change, carbon cycle, aquatic ecosystem function

Anthropogenic environmental changes such as climate, land use, and species distributions affect terrestrial and aquatic ecosystems worldwide, in turn affecting aquatic processes that provide key ecosystem services to society, such as water supply and food production (MA 2005). Understanding the influence of these changes on ecosystems is difficult because they affect ecosystem processes through numerous pathways at multiple spatial and temporal scales (e.g., McLean et al. 1999, Huxman et al. 2005, Volk et al. 2008). Most research has focused on ecosystem responses to individual environmental changes, yet a more integrated, synthetic approach is essential for understanding and managing the wider effects of environmental changes on aquatic ecosystems.

In aquatic ecosystems, environmental changes directly affect many ecosystem processes. This article focuses on three key ecosystem processes: hydrology, the loading and processing of organic matter (OM), and nutrient dynamics (figure 1, arrows 1 and 2; Schindler 1997, MA 2005). For instance, increases in water temperatures caused by global warming directly increase evaporation rates and decrease discharge from aquatic ecosystems (Schindler 1997), and alter macro-

invertebrate community composition and function (Durance and Ormerod 2007). Higher air temperatures can increase OM processing and nutrient mineralization rates in both terrestrial and aquatic ecosystems (Coûteaux et al. 1995). In addition to such direct effects, these same environmental changes can also alter aspects of terrestrial vegetation at large spatial scales, such as structure, composition, age, and functional type (e.g., Rupp et al. 2000, Van Auken 2000). Such terrestrial vegetation shifts (TVS) are global phenomena, occurring as a result of a variety of environmental change drivers (see appendix 1 in the online supplemental material at <http://hdl.handle.net/1928/9924>). Terrestrial vegetation shifts have indirect effects on aquatic ecosystem processes because adjacent terrestrial plant communities influence aquatic functioning (figure 1, arrow 3; Gregory et al. 1991). For instance, TVS can influence (a) hydrology through alterations of water yield and flow paths from catchments (Huxman et al. 2005), (b) OM loading through alterations of litter quality and quantity (Piccolo and Wipfli 2002), and (c) nutrient dynamics through alterations to nutrient export through changes in nutrient uptake and release by vegetation and OM nutrient

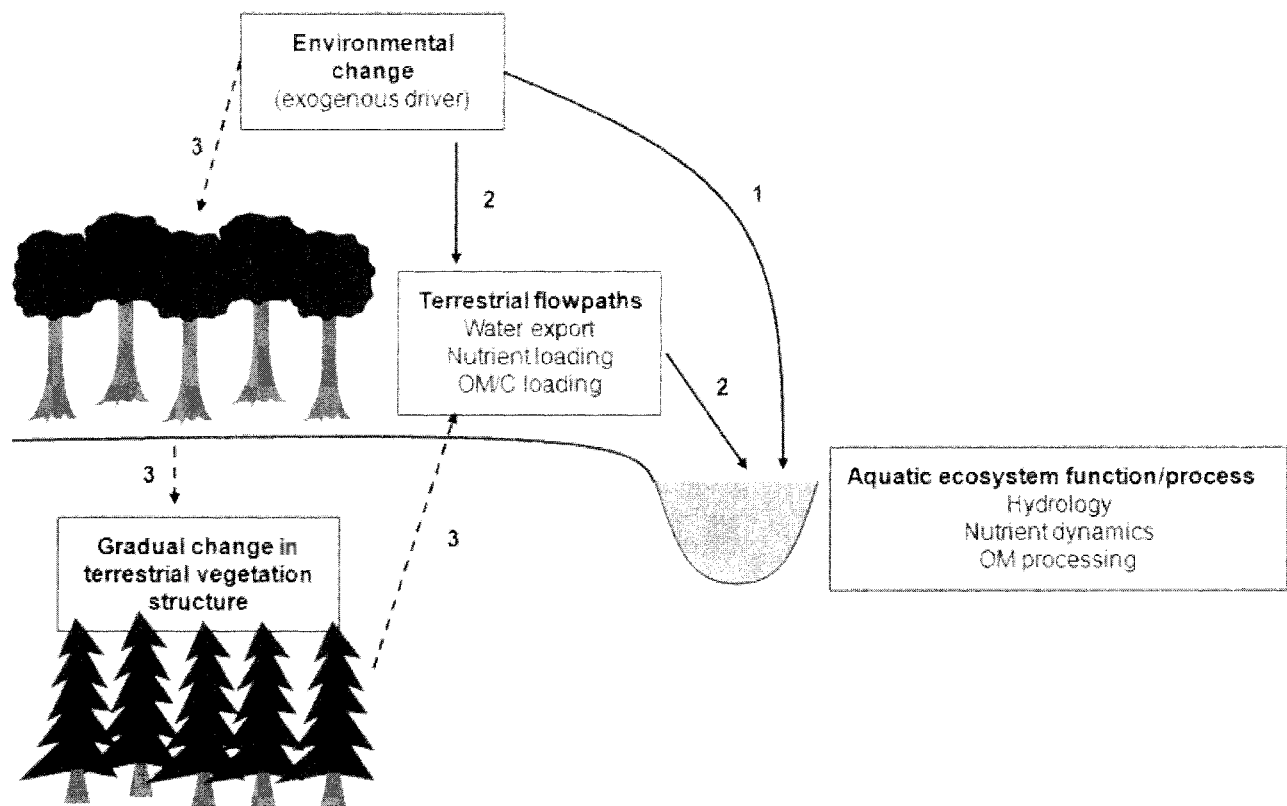


Figure 1. Environmental changes affect aquatic ecosystem processes through two pathways: direct (arrows 1 and 2) and through terrestrial vegetation shifts (TVS; arrow 3). Terrestrial influences, both direct and vegetation mediated, on aquatic ecosystem functioning occur through three main flow paths: water export, carbon (C) and organic matter (OM) loading, and nutrient loading. For example, terrestrial vegetation strongly influences the amount and type of organic matter and C inputs into an associated aquatic system, and therefore the flow of energy. The overall consequences for key aquatic processes will be determined by the net sum of the direct and TVS-mediated pathways.

content (e.g., Cairns and Lajtha 2005). We do not discuss here the many other biological, chemical, and physical factors that change with TVS to influence aquatic ecosystems. For example, TVS can influence invertebrate communities, which will influence aquatic ecosystems through alterations to organic inputs and food-web structure (e.g., Wipfli 1997). However, the three pathways we discuss are of particular interest as they represent key global resource cycles with strong aquatic components for which there is a large body of literature (e.g., Bernhardt et al. 2005, Cole et al. 2007).

The consequences of environmental changes are actually the result of the net influence of both direct and TVS-mediated effects. The relative dominance of direct versus TVS effects on aquatic processes varies both within and among systems. For example, in systems undergoing drastic changes in terrestrial vegetation functional types, such as the afforestation of grasslands through tree plantations (Nosetto et al. 2008), TVS effects are certainly dominant. On the other hand, in systems with limited terrestrial vegetation, such as the McMurdo Dry Valleys of Antarctica (McKnight et al. 1999), TVS effects will appear negligible in comparison with direct effects. However, most ecosystems fall between these

two extremes, and determining the relative importance of direct and TVS-mediated pathways is necessary to evaluate the full consequences of an environmental change. The relative magnitudes of direct versus TVS effects on aquatic processes are difficult to evaluate because they are influenced by so many factors. The spatial scale and proximity of both the terrestrial and aquatic systems will also affect the relative importance of the different pathways. The overall outcome is difficult to predict; the relative importance can be influenced by ecosystem type, the temporal and spatial scale at which the individual pathways occur, the magnitude of the effects, and the possible synergisms between pathways. We argue, however, that failure to address both the direct and TVS effects on aquatic functions may inhibit our ability to accurately predict the effects of disturbances on aquatic systems.

In this article we explore the importance of considering both the direct and TVS-mediated effects of environmental changes on aquatic ecosystem processes (figure 1). Many studies have quantified the effects of environmental changes on either aquatic ecosystem processes or TVS, yet studies of TVS-mediated effects on aquatic ecosystem processes are rare (e.g., McLean et al. 1999, Compton et al. 2003); studies that consider

net effects of both direct and TVS-mediated effects are rarer still (but see Bernhardt et al. 2005). Bernhardt and colleagues (2005) used long-term observations of nitrogen (N) export from a forested watershed to suggest that the increased light availability as forests age interacts with changing vegetation to influence stream function and reduce watershed nitrate (NO_3^-) export. The authors simultaneously considered both the direct (light availability) and TVS-mediated (vegetation succession) effects of forest aging on stream function, and the net outcome of both pathways was evident. However, the individual pathways were not separately identified, and therefore we do not know how important each pathway was to the net effect, which limits our ability to generalize their conclusions beyond this single watershed. We expand upon the few such long-term, watershed-scale studies (e.g., Bernhardt et al. 2003, 2005) by creating a conceptual model that allows us to make predictions about the net outcome of both pathways and to test whether separate studies can be retrospectively interpreted together. To do so, we describe the most likely direct and TVS-mediated effects of environmental changes on hydrology, nutrient dynamics, and OM processing in three case studies, which represent familiar environmental and associated terrestrial vegetation changes, and for which ample data concerning direct and TVS-mediated pathways, separately, are available in the literature. Many more cases exist that cannot be covered here (see online appendixes for additional examples; <http://hdl.handle.net/1928/9924>). We make predictions about the net impact of both direct and TVS-mediated effects on aquatic ecosystem processes to show that the magnitude and even the direction of effects change when both pathways are considered, demonstrating the necessity of considering both pathways to better understand and predict the responses of aquatic ecosystems to environmental changes. These effects may be especially important, and are also more likely to be overlooked, when the direct and TVS effects operate on different temporal scales.

Woody plant encroachment in semiarid grasslands

Woody plant encroachment alters ecosystem structure and functioning in semiarid grasslands and savannas worldwide (Huxman et al. 2005). In semiarid grasslands of the southwestern United States, a combination of land-use practices (intensified grazing, fire suppression, and agricultural abandonment) and climate change (increased temperatures and atmospheric carbon dioxide [CO_2]) has created an environment that favors the success of woody shrubs over native grasses (figure 2; Van Auken 2000). As a result, native shrubs (*Prosopis* spp. [mesquite], *Larrea tridentata* [creosote bush]) and exotic shrubs (*Euroyops multifidus* [resin bush], *Tamarix* spp. [salt cedar], *Elaeagnus angustifolia* [Russian olive]) have become increasingly dominant (Van Auken 2000). We hypothesize that the shift in vegetation composition to dominance by woody species will affect aquatic carbon (C) and nutrient dynamics and hydrologic function, and the net result of activities leading to woody dominance on aquatic systems will be determined by both TVS and direct effects.

The land-use changes driving woody encroachment in semiarid grasslands directly influence aquatic ecosystems in a variety of ways. Soil trampling caused by intensified grazing causes erosion, leading to greater sedimentation in nearby streams and rivers, and manure increases stream OM and nutrient enrichment (table 1, direct; Haan et al. 2006, Soupir et al. 2006). Sedimentation has been shown to reduce invertebrate biomass and alter its composition (Waters 1995, Govedich et al. 1996), but Braccia and Voshell (2006) found no evidence that grazing-induced nutrient enrichment influences in-stream macroinvertebrate assemblage. In contrast, wildfire suppression prevents the erosion and nutrient releases that occur postfire (table 1, direct; Boerner 1982, O'Dea and Guertin 2003), reducing conditions that negatively influence wetland fauna (Bishop and Haas 2005). Fire suppression may also increase C availability for export to streams (i.e., organic C is not returned to the atmosphere as carbon dioxide [CO_2]; table 1, direct; Tilman et al. 2000), but such a process is difficult to measure empirically. Under both forms of land-use change, the direct effects on aquatic systems can be temporally long lasting (as long as the land use persists, which may be decades to centuries; Van Auken 2000), but are spatially limited to the extent of the disturbance. The direct effects of overgrazing begin with the change in land use and last as long as the overgrazing persists. The direct effects of fire suppression might not be evident as quickly or as severely as those of grazing, given that the natural fire regime could consist of a year or more without fire (e.g., as in Tilman et al. 2000), but following their eventual onset, direct effects last as long as fire suppression persists. Notably, fire suppression is not always the dominant change in fire regime. Climate change has the potential to influence fire size and severity (Westerling et al. 2006), which can exacerbate or create different direct influences on aquatic processes, as well as on the terrestrial vegetation composition.

TVS-mediated effects on aquatic ecosystems that result from a shift from grass- to shrub-dominated terrestrial plant communities include altered water availability, resource usage, and allochthonous inputs. Encroaching shrubs often have deeper roots and higher transpiration rates than native riparian vegetation, and they may reduce stream discharge by lowering soil and groundwater levels (table 1, TVS-mediated; Huxman et al. 2005, Wilcox et al. 2005), though reductions do not occur in all cases (Wilcox et al. 2005, Cleverly et al. 2006). The storage of C in woody tissue instead of in more labile grass tissues (Tilman et al. 2000) slows C cycling, most likely reducing the export of soil C to streams (table 1, TVS-mediated; Hibbard et al. 2001, McKinley and Blair 2008). However, shrub leaf detritus may provide pulses of labile organic matter that alter aquatic food webs (Whitcraft et al. 2008). There is potential for N accretion in shrub-dominated ecosystems through storage in recalcitrant woody tissues (Hibbard et al. 2001), but N mineralization may be increased by woody encroachment resulting from greater microbial biomass (table 1, TVS-mediated; McCulley et al. 2004). Nitrogen-fixing leguminous shrubs



Figure 2. Woody shrubs, such as creosote bush (*Larrea tridentata*), encroaching on arid and semiarid grasslands, such as the blue grama (*Bouteloua eriopoda*)–dominated grasslands at Sevilleta Long Term Ecological Research station in the southwestern United States, will most likely drive long-term carbon accretion in terrestrial systems and reduce groundwater recharge, thereby reducing the amount of water and dissolved organic carbon exported to nearby streams. Overgrazing and fire suppression drive woody encroachment, and these land uses potentially directly increase carbon availability to streams and may offset the negative influence of shrub encroachment. Photograph: Mike Friggens.

Table 1. Predictions about the sum effect of direct and TVS-mediated effects of human land-use decisions to influence aquatic processes in arid and semiarid grasslands. Signs refer to a positive (+), negative (–), or neutral (0) effect of the driver on the described aquatic ecosystem process.

Aquatic process	Direct effects	TVS-mediated effects	Sum	Implications
Carbon (C) dynamics/organic matter (OM) processing	+ C availability as a result of increased soil C + OM input from manure	– C release to streams as a result of C storage in woody material	–	Less C import to streams, perhaps attenuated by direct effects
Nutrient dynamics	– nutrient release to streams from burnt plant material and soils + nutrient release to streams from manure	– nutrient release to streams as a result of nutrient storage in low-quality plant material + nutrient availability due to enhanced nutrient mineralization rates	+ / –	Outcome would depend on main driver and the relative magnitudes of direct and indirect effects
Hydrology	0 effect on flow – fire-induced sedimentation + trampling-induced sedimentation	– groundwater recharge as a result of greater transpiration, precipitation interception by shrubs	–	Decreased discharge to streams; sedimentation levels will depend on land use

(e.g., *Prosopis* spp.) will increase soil N pools and alter cycling rates by introducing atmospheric N to soil pools (Geesing et al. 2000). Ultimately, any hydrological alteration caused by encroaching shrubs will interact with changes in C and N cycling to affect the magnitude or timing of C and N inputs to streams. As with the direct effects, the spatial influence of woody encroachment is limited to the area affected by the land use. However, the process of woody encroachment occurs over decades to centuries (Van Auken 2000, Wilcox et al. 2005), so the TVS-mediated effects of fire suppression and overgrazing will begin well after the direct effects. The TVS-mediated effects would also outlast direct effects, given that the presence of woody shrubs would persist beyond a removal of grazing or a return to a natural fire regime.

Overall, the predicted sum of direct and TVS-mediated effects of intensified grazing and fire suppression on aquatic ecosystems depends on the particular function and driver. Further, individual characteristics of encroaching woody species (e.g., litter quality, N sources, water use) will influence specific predictions of how vegetation change will affect

aquatic ecosystem functioning. We predict that heavy grazing and fire suppression in semiarid grasslands, through both direct and TVS-mediated pathways, will most likely result in net increases in C storage on land and decreases in water discharged to aquatic ecosystems (table 1, sum). Although the direct effects would lead to an initial increase in aquatic C availability before woody encroachment occurred, we predict that the TVS-mediated decrease in aquatic C would be of larger magnitude and therefore override the direct effects. This exemplifies that it is essential to consider temporal dynamics, as a short-term study would most likely come to a different conclusion. We would expect no changes in flow on the basis of direct effects alone; however, inclusion of the TVS-mediated pathway leads us to predict a net decrease in discharge to streams. Because of their extensively intermittent water flows, semiarid ecosystems are particularly sensitive to changes in hydrology, with serious consequences for aquatic structure and functioning (Dodds et al. 2004). The implications for nutrient cycling are less clear and depend on the dominant land-use driver (table 1, sum). Given that both



Figure 3. The long-term effects of harvesting Douglas-fir (darker trees, in photograph) and subsequent alder expansion (lighter trees, in photograph), as occurs along the Siletz River in the Oregon Coastal Range of the Pacific Northwest, on stream residents such as salmonids depends on the balance between the benefits of continued high nitrogen inputs from alders and negative impact of reduced woody debris inputs. High stream productivity may increase salmonid populations; however, reductions in habitat quality (debris) may offset these gains. Photograph: Dan Sobota.

Table 2. Predictions about the sum effect of the direct and TVS-mediated effects of forest harvesting on aquatic processes in the Pacific Northwest. Signs refer to a positive (+), negative (–), or neutral (0) effect of the driver on the described aquatic ecosystem process.

Aquatic process	Direct effects	TVS-mediated effects	Sum	Implications
Carbon (C) dynamics/organic matter (OM) processing	– allochthonous (e.g., litter and woody debris) inputs as a result of tree removal	+ leaf litter mass and quality – woody debris residence time	+ / –	Decline in habitat heterogeneity, shift in OM quantity, quality, and residence time will influence secondary production
Nutrient dynamics	+ nitrogen (N) availability from tree removal	+ N availability from N fixation by red alder	+	Long-term maintenance of the short-term pulse caused by disturbance; increased production
Hydrology	+ runoff, sedimentation, channel width – pool frequency + water temperature	– sediment retention, pool frequency, woody debris	+ / –	Outcome would depend on relative magnitudes of direct and indirect effects

the direct and TVS effects can be of relatively long duration, the magnitude of both pathways determines which pathway dominates the net outcome. In the absence of studies that consider both pathways, more research is necessary to clarify and quantify the overall effect of each pathway.

Change in the distribution of red alder (*Alnus rubra*) in the Pacific Northwest

Douglas-fir (*Pseudotsuga menziesii*) is one of several common dominant conifer species in Pacific Northwest forests. However, human activities such as forest harvesting have the potential to influence an array of terrestrial and aquatic properties, including microclimates, material budgets, organic matter inputs, habitat for wildlife (Naiman and Bilby 1998), and forest tree composition (Kennedy and Spies 2004). One important species that can rapidly respond to disturbance is red alder (*Alnus rubra*), in part because alder is an N-fixing species with rapid growth and dispersal (figure 3; Harrington et al. 1994). Red alder can influence soil N concentrations (Binkley et al. 1994), which have been shown to be important in terrestrial ecosystems in the Pacific Northwest (Perakis et al. 2006). However, less is known about how red alder affects stream ecosystems. Forest harvesting is an environmental change driver that is itself a short-term change in terrestrial vegetation. Here, we consider the potential for the direct effects of tree removal to interact with the potential consequences of mixed conifer-alder stands (table 2, TVS-mediated) in a way that influences aquatic ecosystem functioning.

Forest harvesting practices directly influence aquatic primary productivity, sedimentation, and allochthonous inputs. Forest harvesting, especially clear-cutting, raises primary productivity as a result of elevated light levels, N, and water temperature (table 2, direct; Murphy et al. 1981, Naiman and Bilby 1998, Cairns and Lajtha 2005, Gomi et al. 2006, Gravelle et al. 2009). Increased primary production usually supports greater macroinvertebrate and fish production (table 2) and alters aquatic community structure (Naiman and Bilby 1998, Nislow and Lowe 2006), despite reports of a reduction in allochthonous OM and increased

sedimentation (table 2; Murphy et al. 1981, Hartman et al. 1996). Sedimentation and loss of large woody debris lead to greater homogeneity of stream habitat and reduce macroinvertebrate and fish habitat, including salmonid spawning sites (Reeves et al. 1993, Hartman et al. 1996). Additionally, this increased sedimentation causes the stream width to increase and pool frequency to decrease (table 2, direct; Chen and Wei 2008). Direct effects of forest harvesting are immediate and relatively short lived (e.g., Cairns and Lajtha 2005), spatially limited to the area undergoing forest harvesting, and lasting until vegetation reestablishes. For example, the return to preharvesting levels of riparian communities will increase shading and therefore reduce water temperatures, as well as retain nutrients and sediments in the terrestrial system. The composition of the reestablishing vegetative community (TVS), however, may prevent the return to preharvest function.

The TVS-mediated effects of red alder on Pacific Northwest stream nutrient dynamics remain poorly understood. Nitrogen fixation by alder can increase soil fertility through higher rates of mineralization and nitrification (table 2, TVS-mediated; Verburg et al. 2001, Rothe et al. 2002). This leads to greater N leaching (primarily dissolved organic N and NO_3^- ; Compton et al. 2003) to adjacent streams, which could release stream primary production from N limitation (Tiegs et al. 2008, Volk et al. 2008). Forest soils could become N saturated, leading to greater N leaching to streams (Compton et al. 2003). Thus, while forest harvesting increases N export to streams in the short term, the presence of alder maintains a longer duration of elevated N inputs to streams, most likely increasing stream productivity (table 2, TVS-mediated; e.g., Tiegs et al. 2008, Volk et al. 2008).

The presence of alder also alters OM inputs to streams, which influence stream communities, habitats, and nutrient cycling. The more labile tissue of alder relative to the conifers they replace should support greater in-stream invertebrate biomass (table 2, TVS-mediated; Richardson et al. 2004). Piccolo and Wipfli (2002) found greater detritus and macroinvertebrate export from Alaskan headwater streams draining

young, alder-dominated watersheds than from young conifer watersheds. Using a trophic model, Piccolo and Wipfli (2002) showed that streams draining alder stands may support three to four times more salmonid biomass, although the direct negative effects of forest harvesting on salmonids were not considered (Reeves et al. 1993, Hartman et al. 1996). Woody debris provides C and affects nutrient and sediment retention, pool creation, and fish habitat (Harmon et al. 1986, Bisson et al. 1987). Replacing large conifers with smaller, faster-decomposing red alder decreases the residence time of woody debris in streams (table 2, TVS-mediated; Hyatt and Naiman 2001) and reduces the creation of debris dams that help structure streams (Balian and Naiman 2005). As with the direct effects, the spatial influence of increasing alder is limited to the area affected by logging activities. However, the spread of alder occurs over decades to centuries (e.g., Compton et al. 2003), so the TVS-mediated effects of forest harvesting will set in after, and well outlast, the direct effects.

Thus, forest harvesting activities in the Pacific Northwest directly affect stream processes, and they can also indirectly affect streams through TVS. We predict that the presence of alder will reinforce many of the effects of forest harvesting on stream ecosystems (increasing N and primary production [table 2, sum], decreasing large woody debris in streams [table 2, sum]). However, it is when the direct and TVS-mediated pathways have opposing effects that the real importance of considering both pathways becomes obvious. For example, the opposing direct and TVS-mediated effects for hydrology and C dynamics make the outcome harder to predict. The initial decrease in leaf litter would later rebound as trees regrow, but would not return to the preharvest state. Litter inputs would be greater, but both litter and woody inputs would be more pulselike (through seasonal, fast-decomposing alder inputs rather than steady, slow-decomposing fir inputs), leading to an overall shift

in quantity, quality, and residence time of litter in aquatic systems. Likewise, hydrology will be influenced by an initial increase in runoff, which would decrease as trees regrow but potentially would not return to a preharvest state because of differences in water use between coniferous and deciduous species. The relative abundance of alder is another important consideration because it may affect the magnitude of the TVS effects on aquatic function. More research is necessary to quantify the relative magnitudes of direct and TVS-mediated changes for C dynamics and hydrology to allow for confident predictions of the net outcomes for these two aquatic functions. In addition to hydrology, nutrient cycling, and OM, the joint effects of logging and greater alder abundance are also relevant for the management of salmonids. Although forest harvesting initially negatively affects salmonid populations, the presence of alder may raise survivorship because of greater detritus and macroinvertebrate biomass in the streams. In fact, some have suggested that management strategies to encourage mixed conifer-alder stands may ameliorate the influence of forest harvesting activities on salmon (Piccolo and Wipfli 2002).

Increasing dominance of deciduous forest types in the boreal forest

Over the past four decades, arctic and boreal regions have undergone more warming than any other regions on Earth (Chapin et al. 2005). Higher temperatures result in the loss of seasonally or annually frozen ground, thereby directly influencing water movement (Striegl et al. 2005) and storage (table 3, direct; Smith et al. 2005), and also enhancing OM decomposition and dissolved organic C (DOC) release from soils (table 3, direct; Prokushkin et al. 2005, Kane et al. 2006). In part because of these changes, the black spruce forests that currently dominate the North American boreal zone are predicted to be replaced by early successional deciduous trees (such as willow, birch, alder, or aspen) as the climate

Table 3. Predictions about the sum effect of the direct and TVS-mediated effects of climate change to influence aquatic processes in boreal forests. Signs refer to a positive (+), negative (–), or neutral (0) effect of the driver on the described aquatic ecosystem process.

Aquatic process	Direct effects	TVS-mediated effects	Sum	Implications
Carbon (C) dynamics/organic matter (OM) processing	+ dissolved organic carbon (DOC) load as a result of increased terrestrial productivity and OM decomposition – DOC export as a result of lower snowmelt – DOC as a result of greater mineralization in streams	– DOC release to streams due to deeper flow paths and subsurface storage	+ / –	Changes in vegetation composition and flow paths may override the direct effects of warming
Nutrient dynamics	+ dissolved inorganic nitrogen (DIN) and nutrient loading	– nitrogen (N) export to streams due to deeper flow paths, subsurface storage, and increased riparian DIN retention	–	Changes in vegetation composition and flow paths most likely override the direct effects of warming
Hydrology	– as a result of evaporation	– surface runoff as a result of recession of permafrost	–	Ponds and lakes may decrease in continuous permafrost, or increase in continuous permafrost

warms (Rupp et al. 2000). The thick moss and organic layers beneath black spruce stands insulate the soil and buffer frozen layers from thaw (Yoshikawa et al. 2002), and therefore the transition from black spruce forests and loss of the associated moss layers could further decrease the extent of seasonally or annually frozen ground. Therefore, we expect that these environmental changes could contribute to a feedback between permafrost thaw and a shift in forest composition, and we hypothesize that a suite of TVS-mediated effects would influence aquatic ecosystem functioning, in addition to the direct effects of warming.

Unlike the previous case studies, the effects of warming occur at a spatial scale larger than the TVS (global versus regional). Given the nature of climate change, its direct influence on aquatic functioning is immediate and long lasting. Although temperature has been shown to affect within-stream processing of nutrients in other systems (Schindler 1997), little research has addressed the direct effects of temperature on boreal streams. Direct effects of warming on the lability of C and nutrients are most likely to come from increases in the duration of the growing season and decreases in the seasonal snowpack, which largely determine the magnitude and bioavailability of DOC inputs to streams (Finlay et al. 2006). A longer snow-free season with a smaller cumulative snowpack could decrease the flush of labile DOC into streams with snowmelt (table 3, direct). Increasing temperatures raised soil DOC mineralization under laboratory conditions (Neff and Hooper 2002), an effect that could further reduce stream DOC concentrations in a warmer climate (table 3). However, the direct effects of temperature on the accumulation of water-soluble products from decomposition and DOC mineralization may operate in opposing directions, adding to the uncertainty of the net direct effect on stream DOC concentrations. In addition, landscape characteristics (water residence time, catchment drainage, and wetland extent) are also important drivers constraining the quality and internal processing of allochthonous nutrients in boreal aquatic ecosystems (Striegl et al. 2005, Jonsson et al. 2007) and may override any direct effects of increased temperature.

Warming should increase DOC and dissolved inorganic nitrogen (DIN) exports from boreal forests to aquatic ecosystems through changes in terrestrial vegetation composition, productivity, and decomposition. However, previous studies have shown that the presence of permafrost resulted in higher fluxes of DOC and DIN to interior Alaskan streams, with less DOC exported from warmer, hardwood-dominated catchments than from spruce-dominated catchments with permafrost (table 3, TVS-mediated; McLean et al. 1999). Also, DIN retention was greater in the riparian areas of deciduous catchments with little permafrost than in spruce-dominated catchments with extensive permafrost (table 3, TVS-mediated; O'Donnell and Jones 2006). Warmer, more productive sites (e.g., dominated by deciduous species) have increased depths to seasonal ice or permafrost, and thus the water-soluble products of mineralization most likely flow in deeper mineral-associated flow paths rather than being

constrained to the surface or C-rich organic horizons, as in conifer-dominated sites (e.g., figure 4). Deeper water flow paths most likely lead to a decrease in the total solute load of these nutrients to streams (table 3, TVS-mediated). In contrast, concentrations of other dissolved ions in streams (Ca^{2+} , Mg^{2+} , Na^+ , SO_4^{2-} , and HCO_3^-) decreased with increasing permafrost extent, most likely because of the confinement of flow to organic horizons and little interaction between runoff and mineral soil in permafrost-dominated systems (table 3, TVS-mediated; McLean et al. 1999).

Although increased soil temperatures contribute to higher net primary productivity, mineralization rates, and dissolved nutrient loads in the terrestrial environment (table 3, direct; Kane et al. 2006), the thawing of seasonally or annually frozen ground also alters the flow paths for solutes into aquatic environments (Striegl et al. 2005). Thus, the effects of warming in terrestrial boreal ecosystems include greater solute loads, but also include increased mineralization and deeper flow paths with greater storage capacity in the mineral soil (table 3, TVS-mediated). Moreover, the direct effects of warming on within-stream solute concentrations are likely to be either neutral or negative (table 3, direct). The effect of warming on dissolved nutrient loading into aquatic environments in boreal forest catchments is therefore likely to be negative (table 3, sum). The increasing dominance of deciduous trees reinforces the negative hydrological effects of climate warming on stream ecosystems. As with the previous case studies, the rising dominance of deciduous trees occurs over decades to centuries (Rupp et al. 2000), so the TVS-mediated effects will occur after the direct effects, though they are also long lasting. Additionally, the spatial influence of increasing dominance of deciduous trees is more limited in area than the environmental change. Given the uncertainty surrounding direct effects on C dynamics (e.g., DOC production versus mineralization and changes in export flow paths), more research is necessary to clarify and quantify the relative magnitudes of direct and TVS-mediated changes to enable predictions about the net outcome.

A call to simultaneously explore direct and TVS-mediated effects of environmental change

In a time of unprecedented environmental changes, the lack of integration of terrestrial and aquatic perspectives hinders our understanding of broader-scale ecosystem dynamics (Grimm et al. 2003), an understanding that is necessary to predict the impacts of global environmental changes across linked ecosystems. To date, investigations linking terrestrial and aquatic ecosystems have primarily emphasized how changes in one system affect adjacent ecosystems (e.g., Piccolo and Wipfli 2002, Huxman et al. 2005, with a bias toward aquatic consideration of terrestrial changes but not the reverse [Menge et al. 2009]) or have compared processes occurring in both systems (e.g., Wagener et al. 1998). Most studies have not concurrently examined both direct and TVS-mediated effects of environmental changes (but see Bernhardt et al. 2005). Accurately predicting the



Figure 4. South of the Brooks Range of Alaska, seasonal ice and permafrost are directly (negatively) affected by temperature change. Seasonal ice and permafrost change with dominant species cover and constrain primary production, which in turn contribute to the solute loads available for export. Seasonal ice and permafrost also determine the flow paths from terrestrial to aquatic systems. Photograph: Lee Pruett.

effects of global changes on aquatic ecosystem processes requires simultaneous consideration of both direct and TVS-mediated effects, otherwise predictions may inaccurately characterize the magnitude or even the direction of the effects of environmental changes on aquatic processes.

The case studies we present demonstrate that terrestrial vegetation changes can attenuate or exacerbate the direct effects of environmental change drivers on aquatic ecosystem functioning. In several cases, the direct impacts of these drivers on aquatic ecosystem functioning were in the same direction (positive or negative) as TVS-mediated effects. In these cases, considering TVS-mediated effects does not change the direction of the net impact, although the magnitude may change. Of more concern are the cases in which the direct and TVS-mediated effects oppose one another, especially when operating at different temporal scales. Studies that consider only one pathway may inaccurately predict the consequences of a given environmental change. For example, in semiarid grasslands, the direct effect of fire suppression may lead to decreased N export to streams (Boerner 1982), but the TVS-mediated effect of increasing

woody shrub dominance may increase nutrient availability (Hibbard et al. 2001). When direct and TVS-mediated effects are opposite, it is difficult to predict from current data whether the opposing effects will cancel out, or whether one will dominate. Future studies should be designed in a manner that accounts for both pathways to test our predictions and gives a comprehensive forecast of the consequences of an environmental change for aquatic ecosystems. A failure to understand the net consequences of both pathways can lead to incorrect estimations of the consequences of environmental change. For example, Bernhardt and colleagues (2005) demonstrated that solely terrestrial models or consideration of direct effects of N deposition alone are not sufficient to explain changes in NO_3^- export, but that a combination of stream and riparian properties associated with forest aging influence stream N processing, resulting in decreasing levels of NO_3^- export. Without consideration of both pathways through their long-term, watershed-scale study, Bernhardt and colleagues would not have predicted decreasing NO_3^- export for this ecosystem. Such lack of integration concerning the consequences of environmental

change will negatively affect policy and management decisions that rely on existing research.

Notably, the time scale at which direct and TVS-mediated pathways occur may differ. Alterations to terrestrial vegetation as the result of environmental changes can take decades to occur, whereas direct effects can occur within a season. For example, the direct effects of forest harvesting on stream nutrient levels occur with the immediate loss of plant N demand, whereas the TVS-mediated effect of alder expansion may take years to significantly alter N dynamics (Rothe et al. 2002). Therefore, TVS-mediated effects may lag behind the direct effects of environmental changes, causing the interactive influence on aquatic processes to change over time. Some TVS-mediated effects may be overlooked by short-term research considering only direct effects. Also, TVS-mediated effects are inherently long lasting, as changes occur over decades or longer. Thus, from a long-term perspective, TVS-mediated effects may outweigh direct effects when they outlast the driver (i.e., when the direct effect is a pulselike disturbance such as logging, or one that is reversible such as grazing). When the driver is long lasting (e.g., climate change), the relative importance of direct and TVS-mediated impacts will depend on the sensitivity of the ecosystem process in question. For example, shifts to vegetation with highly different water-use efficiencies might allow TVS-mediated effects to outweigh direct effects in water-limited systems (e.g., arid ecosystems), whereas the direct effects of warmer temperatures might outweigh TVS-mediated effects in climate-sensitive systems (e.g., polar and subpolar ecosystems).

These case studies also suggest that direct and TVS-mediated pathways are more likely to have opposing effects on C and OM dynamics than on nutrient dynamics and hydrology (tables 1–3, supplemental online appendixes 2–4). Terrestrially derived OM is the base of many aquatic food webs, and C is the currency of energy flow in these aquatic ecosystems (Wallace et al. 1997). Thus, aquatic ecosystems will be heavily affected by alterations to C and OM dynamics. Our review suggests that it is particularly important to integrate the direct and TVS-mediated pathways when investigating the consequences of global changes for C and OM dynamics. For example, climate warming may increase DOC levels in boreal streams as a result of greater terrestrial productivity and decomposition, or DOC levels may decrease as a result of greater mineralization, reduced snowmelt flush, or changes in soil flow paths and subsurface storage. Uncertainty about the magnitude of the opposing pathways leads to uncertain predictions of the net consequences for aquatic C processing. As part of the “plumbing” that processes and transports terrestrial C, freshwater ecosystems can actively influence regional and global C balances (Cole et al. 2007), making this a particularly pressing relationship to understand.

Conclusions

Given the influence of environmental changes on aquatic ecosystems and the role of aquatic ecosystems as integra-

tors of environmental changes (Williamson et al. 2008), it is important to have a fuller understanding of the consequences of environmental change for aquatic ecosystem structure and functioning. Basic functions of aquatic ecosystems, such as nutrient cycling, OM processing, and hydrologic function, will be affected by global environmental changes and associated TVS. Understanding and predicting the consequences of global changes for aquatic ecosystems is of utmost importance to preserve the integrity of the ecosystem services they provide. Inland freshwater ecosystems are key providers of water’s provisioning and supporting services that are important to human well-being (MA 2005). Their roles in providing the basic necessities of life (food, water) and cultural amenities (recreation, aesthetics), as well as their links to disease dynamics and severity of natural disasters, inseparably link aquatic ecosystem health to human health. An integrated understanding of the direct and TVS-mediated influences on aquatic processes is therefore imperative for maintaining human well-being.

The case studies we present demonstrate the importance of simultaneously considering both the direct and TVS-mediated effects of global changes to better predict the outcome of global changes for aquatic ecosystem functioning. However, few studies have simultaneously considered both the direct and terrestrially mediated influences of environmental changes. Although both direct and TVS-mediated effects of global environmental changes have been investigated separately, the combined result of the two may not be predictable using current data, especially when the directions of effects are opposite. We suggest that future research examining the influence of environmental changes on aquatic ecosystems must incorporate both the direct and TVS-mediated effects simultaneously to accurately project the consequences of global changes. To do so will require long-term monitoring, manipulative experiments, and modeling of systems undergoing both the environmental change and the associated TVS (e.g., Bernhardt et al. 2005). Field research at this scale is expensive (e.g., sustained maintenance and management) and difficult given time constraints (e.g., funding cycles, lengths of student degree programs; Likens 2004). The need for research at this scale highlights the importance of long-term research networks, such as the LTER (Long Term Ecological Research) network, NEON (National Ecological Observation Networks) and its associated stream component (STREON), and the global lake component (GLEON) that provide the infrastructure for long-term site maintenance in a variety of ecosystems around the world. Future studies that test the predictions we have laid out for these case studies (tables 1–3 and online appendixes 2–4), or other cases involving other processes than those presented here, will demonstrate whether the net consequences for aquatic systems of an environmental change and the associated TVS are predictable from retrospective studies, or whether individual studies for every TVS are necessary.

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