Distinctive Connectivities of Near-Stream and Watershed-Wide Land Uses Differentially Degrade Rural Aquatic Ecosystems

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The water-quality effects of low-density rural land-use activities are understudied but important because of large rural land coverage. We review and synthesize spatially extensive studies of oligotrophic mountain streams in the rural Southern Appalachian Mountains, concluding that rural land-use activities significantly degrade water quality through altered and mostly enhanced landscape–stream connections, despite high forest retention. Some connections (insolation, organic inputs, root–channel interactions, stream–field connectivity, individual landowner discharges) are controlled by near-stream land-use activities, whereas others (reduced nitrogen uptake and cycling, enhanced biological nitrogen fixation, nutrient subsidy, runoff from compacted soils, road runoff delivery) are controlled by basin-wide land use. These connections merge to alter basal resources and shift fish, salamander, and invertebrate assemblages toward species tolerant of higher turbidity and summer temperatures and those more competitive in mesotrophic systems. Rural water quality problems could be mitigated substantially with well-known best management practices, raising socioecological governance questions about best management practice adoption.

Keywords: aquatic ecosystems, ecology, hydrology, land-use management, connectivity

Stream ecosystems are products of the landscapes they drain (Hynes 1975), and therefore, rural low-density watersheds create water quality conditions unique to that land use. Understanding the relationships between human land use and freshwater ecosystem structure and function has been a major area of research for several decades. Such studies typically employ land-use gradients encompassing highly urbanized watersheds; across such gradients, the ecological effects of low-intensity rural development are masked by the larger effects of high-intensity development. Consequently, the effects of low-density rural land uses on water quality and aquatic ecosystems are little studied and poorly understood. In the present article, we are interested in rural environments with a significant component of low-density residential land use, as opposed to largely agricultural or forested landscapes. Such low-density residential rural lands cover 15 times more land area than do the more intensely studied urban lands in the United States (Brown et al. 2005). In rural landscapes, the actions of each individual private landowner or the sediment-laden runoff from a particular unpaved road segment can have significant ecological effects on small streams (e.g., Reid and Dunne 1984, Coats and Jackson 2020, Grudzinski et al. 2020). Mitigating the water quality effects of large areas of rural development will only be possible through a more detailed process understanding of how low levels of rural development affect stream water quality.

The Southern Blue Ridge Mountains provide a laboratory to examine how oligotrophic cold-water stream ecosystems vary across rural basins differing in the amount and spatial arrangement of forest conversion. A mosaic of forested hillslopes, rural residential valleys with small-scale agriculture, scattered modern hillslope housing developments, and commercial corridors along major highways characterizes the Southern Blue Ridge Mountain ecosystem (figure 1). The valleys feature rural residences, often with large lawns, small farms, ornamental ponds, and altered riparian conditions. The slopes are steeper than in many rural areas, so hydraulic gradients carrying sediment from roads are higher, but the valley topography is gentle, with slopes common to rural

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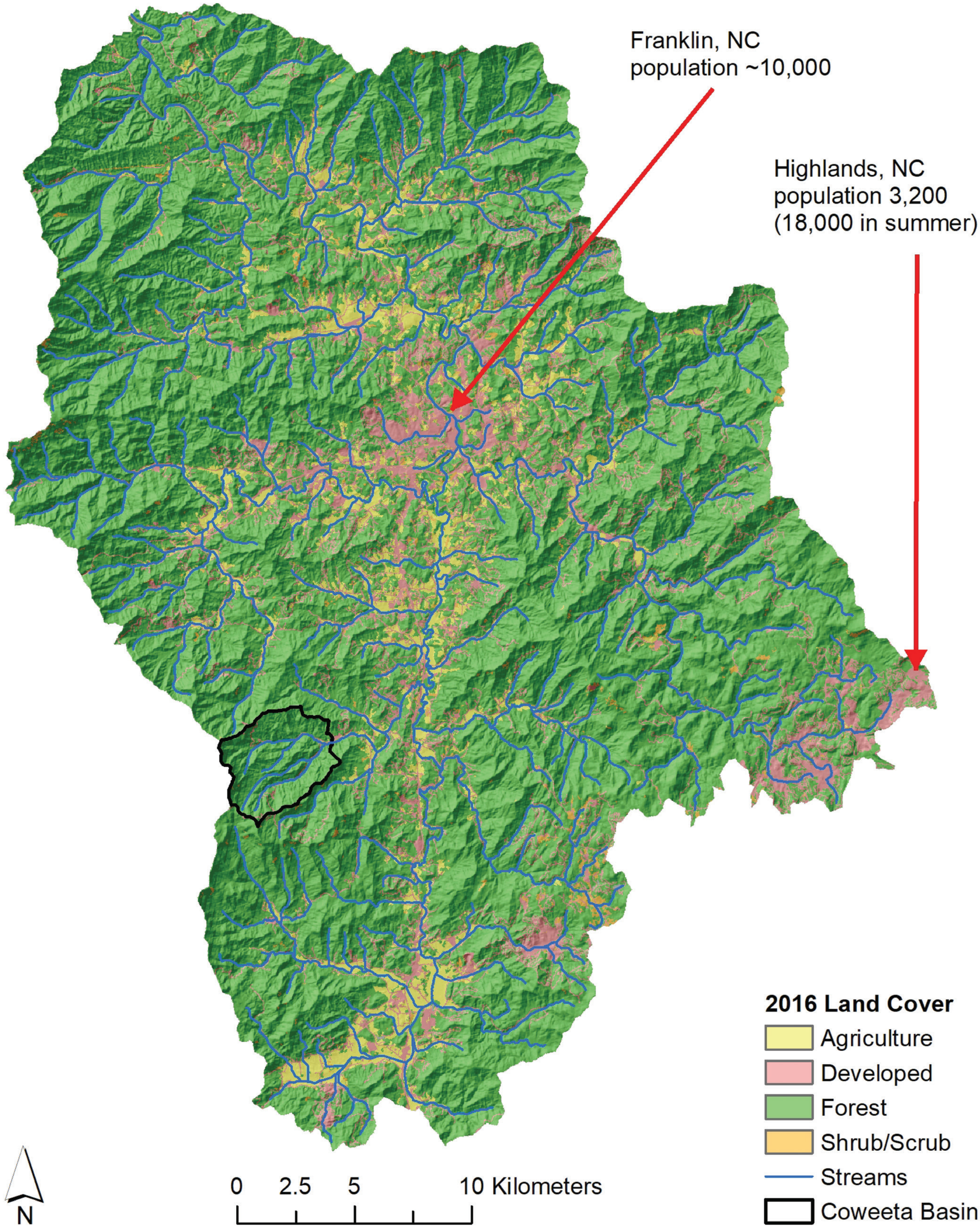

Figure 1. Land uses across the focal study area of the Upper Little Tennessee River Basin above the US Geological Survey Needmore gage.

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valley environments. The average basin forest cover is 80%, with developed land cover well below 10% in the great majority of the regions' watersheds (Webster et al. 2012). Land cover conversion in the study area is limited by the fact that the US Forest Service manages large amounts of mostly higher-elevation lands (46% of Macon County). These low development levels are below previously identified impervious thresholds for comprehensive water quality degradation (e.g., Miltner et al. 2004, Snyder et al. 2005, Schueler et al. 2009). Therefore, one might expect the area's streams to feature healthy native aquatic species assemblages and relatively pristine water quality. In some respects, this supposition is correct: The river water in the region meets drinking water standards, baseflow turbidities and total suspended solid (TSS) concentrations are low, and parts of the stream network maintain habitat for native endemic aquatic species. However, simple land-cover thresholds for water quality degradation developed from more urban contexts are too coarse to illuminate the importance of hydrologic connectivity, watershed context, the behavior of some stressors that show no threshold behavior, and sensitive taxa that respond to lower levels of watershed disturbance (e.g., Booth et al. 2002, Wenger et al. 2008).

In the 1990s, researchers at the Coweeta LTER site (CWT; LTER stands for *long-term ecological research*) became curious about how stream ecosystem responses to forest disturbance compared with the effects of rural land uses affecting the stream system at broader scales. In the present article, we synthesize findings from over 30 regional stream studies conducted by CWT, mostly across the Upper Little Tennessee River Basin, to characterize water quality effects of low levels of rural and exurban development in a landscape in which almost all basins are more than 70% forested. We frame these studies against smaller-scale manipulative studies conducted within the US Forest Service Southern Research Station's Coweeta Hydrologic Laboratory. This synthesis incorporates studies of sedimentation, hydrology, channel morphology, stream chemistry, basal resources (algae and terrestrially derived organic matter), aquatic animal assemblages (invertebrates, salamanders, and fish), and the spatial and temporal scales of stressors and responses. Taken together, these studies indicate that rural land uses alter—and generally increase—landscape–stream connectivity and that these connections and their effects differ between near-stream and basin-wide land uses. Hydrologic alterations to soils, forest loss, importation of fertilizer, and riparian forest removal increase the transport of overland flow, sediments, nutrients, organic matter, and light energy to streams, and decrease the input of organic detritus. Each of these water quality effects is generated and transported (and eventually mitigated) differently from watershed-scale and stream-adjacent riparian land uses (figure 2). These near-stream and basin-wide alterations to landscape–stream connectivity initiate a cascade of hydrologic, geomorphic, and biogeochemical responses that merge within the channel (*sensu* Burcher et al. 2007). Overland flow from compacted valley soils and road networks alter hydrology and transport sediment and phosphorus to streams. Nutrient subsidies increase groundwater contributions of nitrogen to streams. Riparian forest removal increases insolation and summer stream temperatures, alters geomorphic processes, but also reduces inputs of wood and organic matter. The cumulative effect of these changes in rural landscape connectivity is to shift basal resources from detritus to algae dominated; raise summer stream temperatures; increase turbidity, specific conductivity, and nutrient concentrations; narrow and simplify channels; and shift competitive balances of aquatic organisms. These morphological and biological effects are mediated by network position, geology, valley slope, and past land use. Based on these observed connections, we suggest mitigation strategies, borrowed from existing agricultural and forestry best management practices (BMPs), as well as from nongovernmental organization and government programmatic strategies that would improve regional water quality with little negative effect on rural lifestyles.

Study area

The focal area for these regional stream studies is the Upper Little Tennessee River Basin above Lake Fontana, North Carolina (specifically, above the Needmore US Geological Survey gage, no. 0350300) draining 1130 square kilometers (km^2) of the highly weathered and mostly forested Blue Ridge Mountains in western North Carolina and northeastern Georgia. The rugged topography features gentle alluvial and colluvial valleys below steep hillslopes. The elevations range from 537 to 1661 meters. The climate is cool and wet. Orographic effects drive high spatial climate variability both within and across the area's basins. The average annual rainfall ranges from 2050 millimeters (mm) per year in the southwest to 1350 mm per year in the northeast (PRISM Climate Group). The valley air temperatures average around 7.9 degrees Celsius (°C) from January to April, 21.2°C from May to August, and 12.1°C from September to December (Oishi et al. 2018). The complex topography, climate variability, and absence of past glaciation have produced high regional biodiversity and endemism in plants, amphibians, and fish (Whittaker 1956, Pickering et al. 2003).

In this landscape, the aquatic ecosystem effects of modern land-use practices are layered on the enduring effects of historic land-use activities. European settlers moved into the Southern Appalachians in the early 1800s and forcibly removed most of the native Cherokee Indians by 1825. The Europeans entered a landscape in which the valleys were already cultivated and the forested hillslopes were used for hunting and gathering, with frequent ground fires set to improve habitat productivity (Bartram 1791, Bolstad and Gragson 2008). In the mid- to late 1800s, the settlers clear-cut the forest from ridge to ridge, leaving only hard-to-reach coves unlogged (Gragson and Bolstad 2007, Bolstad and Gragson 2008). For much of the 1900s, the forests naturally regenerated on the hillsides, and the residences, farms, and paved road networks were concentrated in the valleys. In the late 1900s, exurban immigrants attracted by environmental

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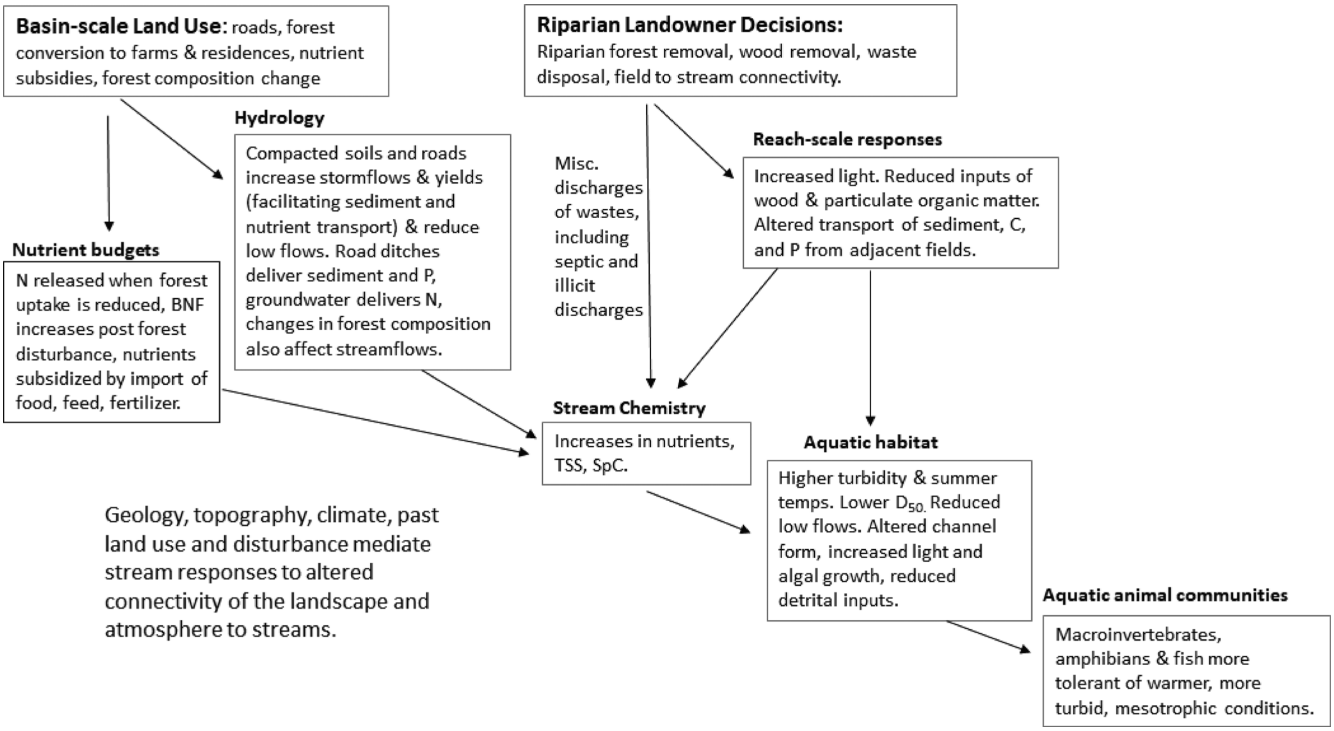

Figure 2. Differential and merging cascades of rural watershed and riparian land-use effects on landscape–stream connectivity, stream water quality, and aquatic assemblages.

amenities rather than employment fueled home construction in the region (Kirk et al. 2012). Some exurbanites began building residential subdivisions on hillslopes with views. This was a novel land use; the long-term residents deemed mountainside living to be impractical because of snow, heavy rain, and the difficulty of maintaining roads and ditches on steep slopes. This new type of mountainside development created new water quality issues, increasing both suspended sediment and nutrient concentrations above those observed in watersheds with only valley development (Jackson et al. 2017, Webster et al. 2019).

Physical channel responses to land-use activities, past and present

Land-use activities have substantially altered the physical habitat template of streams particularly sedimentation, hydrology, riparian condition, and stream temperature.

Sedimentation. Widespread timber harvest and hillside cultivation during the late nineteenth and early twentieth centuries resulted in extensive soil erosion (Glenn 1911). The ensuing postsettlement floodplain accretion rates have been about an order of magnitude faster than the presettlement rates (currently 1–10 mm per year; Leigh 2016). Therefore, most of the alluvial bottomlands are draped by a distinctive stratum of postsettlement alluvium that buries the presettlement landscape (figure 3). The rapid postsettlement accretion of tributary bottomlands ultimately transitioned to incision, terracing, and new floodplain formation following reforestation after the 1920s that reduced upland sediment yields. However, the bottomlands of the main stem rivers generally lack historical terraces and new floodplains and, instead, continue to accrete bottomland sediment at rapid rates in accord with the distributed sediment budget concept of Trimble (1994). That is because tributary streambank erosion and erosive new home and road development generate sediment that funnels through the low-order streams and accretes along the main stems.

The presettlement stream channels had lower sediment yields, greater sinuosity, gentler gradients, and smaller cross-sections than the modern streams. Historically, the channels were mechanically straightened (channelized), which steepened their gradients, and the cross-sections grew larger to accommodate greater flood runoff from the uplands, with lowered infiltration rates caused by deforestation, crop cultivation, pastures, and home development. Contrary to previous studies (Walter and Merritts 2008), the presettlement streams with catchments larger than approximately 20 km^2 had single-channel meandering planforms, as is evidenced by infilled meander scars on alluvial bottomlands (Leigh 2016). Radiocarbon dates indicate that the meandering paleochannels range in age from several hundred to several thousand years, spanning the entire Holocene (Leigh 2010, 2016). In 1775, William Bartram (1791) also noted the meandering pattern of tributaries and the main stem of the Little Tennessee River.

Hydrology. The conversion of forests to lawns and pastures has altered the region's hydrologic behavior, specifically

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Figure 3. Upper Little Tennessee River floodplain stratigraphy at Riverside Park along the upper Little Tennessee River near Otto, North Carolina, showing massive deposition of postsettlement alluvium following forest clearing and initiation of row crop agriculture after regional settlement by nonindigenous people in the late nineteenth and early twentieth centuries (from Leigh 2016). The top of the buried A horizon marks the very stable presettlement land surface occupied and cultivated by Native Americans.

increasing overland flow during storms, reducing low flows, and increasing water yields. The forested soils tend to have high porosity and low bulk density, and, therefore, infiltration rates into the forested soils are so high that they are rarely exceeded by precipitation rates. The lawn and pasture soils are much denser, with lower porosities (Price et al. 2010). Therefore, the surface infiltration rates of lawns and pastures are about one-tenth of those found in the forested soils and are commonly exceeded by precipitation rates (Price et al. 2010). Soil compaction due to forest conversion also appears to reduce overall hydrologic storage in these watersheds, with the effect that late summer and fall low flows are lower in watersheds with less forest cover (Price et al. 2011).

These hydrologic changes have facilitated the transport of pollutants to streams and reduced late summer stream capacity for assimilating increased nutrients and light. However, the streamflow changes due to rural development are small relative to the high degree of hydrologic variability caused by the regional variability in climate and topography. For example, because of the regional rainfall variability, unit-area peak flows and annual yields in the most urban stream in the region (Crawford Branch in Franklin, North Carolina) are still substantially lower than the unit-area peak flows in the fully forested Ball Creek, which is much higher, steeper, and wetter (Jackson et al. 2017).

Riparian condition. The region's valley residents and farmers frequently manage their fields or lawns to the stream edge, such that approximately 33% of the valley streambanks feature grass or pasture growing to the streambanks, 14% feature other nonforest cover, and 19% of the streambanks feature a narrow tree buffer less than 3 m wide (figure 4; Sanders 2019). Riparian removal typically occurs for one of three reasons: to allow more sunlight to reach crops restricted to alluvial valleys, to allow cattle access to water, and because residents want to maintain access to streams (Evans and Jensen-Ryan 2017, Sanders 2019). Furthermore, some landowners remove wood from channels because they think wood looks “messy” and worry that it will block bridges and culverts during floods (Sanders 2019).

Riparian forest removal and manipulation has altered the habitat structure of the valley stream segments. Because grasses have denser and shallow root networks, the conversion of forested riparian zones to grass and pasture streambanks causes the active and bankfull widths of stream channels to become narrower for streams less than 20 m wide (Hession et al. 2003, Anderson et al. 2004, Faustini et al. 2009, Leigh 2010, Jackson et al. 2015). In this basin, active channel widths for grass-banked streams are generally about one-third as wide as forested streams for the same basin area and valley slope (figure 5; Jackson et al. 2015, Leigh 2010). Furthermore, forested streams have greater wood abundance, and this wood increases habitat complexity by creating jams and steps in channels (Jackson et al. 2015, Jensen et al. 2014). Flow obstruction frequency and the diversity of channel depths and velocities increase with forested buffer width (Jackson et al. 2015). Streams without any forested buffer (figure 6) have almost no in-channel wood because of low recruitment and wood removal by stream-adjacent landowners (Evans and Jensen-Ryan 2017). Even narrow forest buffers of only 1 m width (i.e., a single row of streambank trees) are associated with wider channels and increased stream habitat complexity relative to grass and pasture streambanks (Jackson et al. 2015).

Stream temperature. The forested streams in this region rarely experience summer water temperatures above 18°C because of high canopy cover and extensive shade (Swift and Messer 1971, Long et al. 2014, Jackson et al. 2017), but the streams in agricultural and residential valleys often record summer temperatures that are 4°C–5°C warmer, in the range of 22°C–23°C (Jackson et al. 2017, Coats and Jackson 2020). Such temperatures are stressful to salamanders and trout adapted for cool mountain streams (e.g., Hoffacker et al. 2018). Furthermore, the streams in basins with mountainside housing developments have warmer temperatures than the streams in basins with only valley development (Jackson et al.

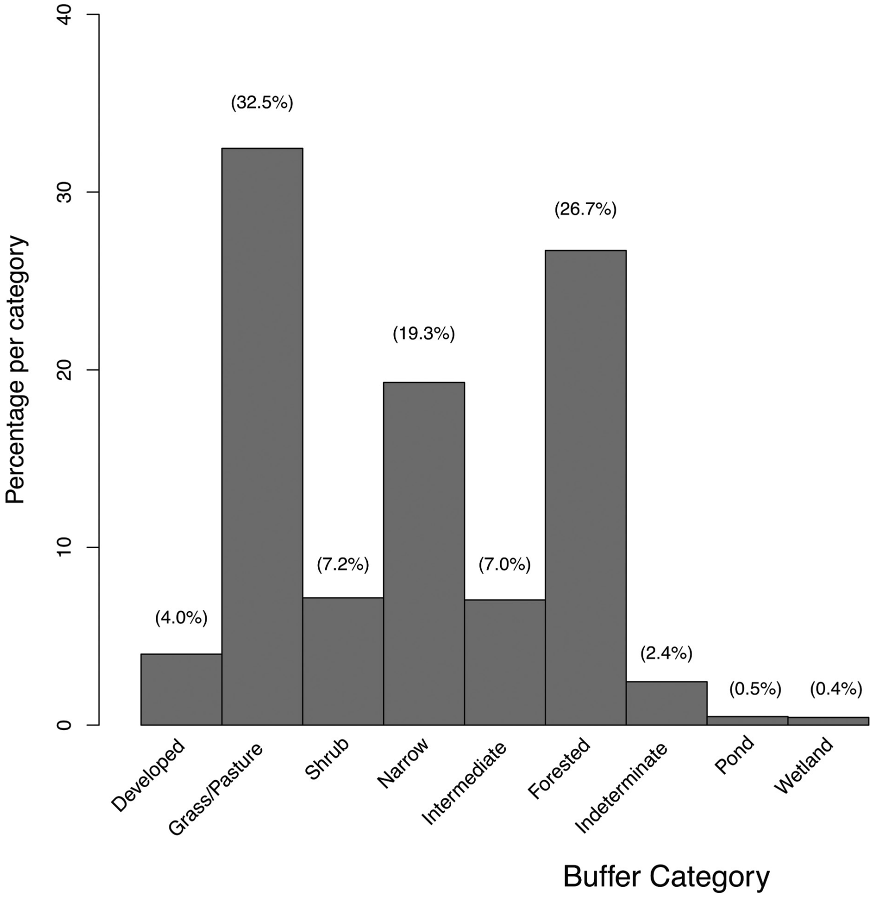

Figure 4. Upper Little Tennessee riparian vegetation conditions on private lands in valleys, from analysis of 659 km of streambank using 2015 aerial photography. Narrow indicates less than 3 m of woody vegetation along channels, forested indicates more than 10 m of woody vegetation along channels, and intermediate indicates between 3 and 10 m. Indeterminate indicates aerial photograph quality was not sufficient to discern riparian condition. Two-thirds of all valley stream banks feature either grass or pasture, shrub, or developed cover or a narrow strip of trees. Source: The data are from Sanders 2019.

2017). Even understory rhododendron removal, leaving an intact overstory with greater than 82% canopy cover, leads to 1°C–3°C increases in summer temperatures in small streams (Raulerson et al. 2020). Longitudinal surveys of summer stream temperatures above, within, and downstream of riparian canopy openings have revealed that smaller streams are more sensitive to changes in canopy cover, and these small streams can cool down rapidly after returning to forested riparian conditions (Coats and Jackson 2020).

Stream chemistry responses

Because lawn and pasture soils produce overland flow much more frequently than do forested soils (Price and Jackson 2010), they are often sources of sediment and soluble surface contaminants, such as fertilizers, manure, and pesticides (e.g., Law et al. 2004, Weston et al. 2009, Romeis et al. 2011, Yang and Toor 2016). Road runoff from unpaved roads and unvegetated roadside ditches also contributes sediment to streams (figure 6). The total length of federal, state, and county roads has not increased appreciably over the past 50 years in Macon County; however, private roads, roads in subdivisions, and driveways expanded 361% between 1954 and 2009, from 790 to 3644 kilometers (km; Kirk et al. 2012). These private roads often suffer from poor design and maintenance. Although Southern Appalachian forest streams are famous for their clear and clean water, with median TSS concentrations around 8–10 milligrams per liter, small amounts of rural and agricultural development are associated with substantial increases in baseflow suspended solids and suspended sediment loads (Price and Leigh 2006a, 2006b, Jackson et al. 2017). In the basins with both valley development and mountainside development, the median TSS concentrations are about four to six times those in forested streams and similar to the one urban stream in the region. The TSS concentrations in the larger river segments of the Little Tennessee River Basin are highly variable, with median values similar to those in the small stream segments draining mountainside development, indicating that the ongoing bank erosion of historical floodplain sediments in the big river valleys contributes to sediment loads leaving the basin.

Nutrient and other chemical concentrations in the streams of the Southern Appalachians are generally very low, reflecting the highly weathered crystalline geology, deep forested soils, and efficient nutrient cycling. However, the concentrations of many solutes, indicated by specific conductance values, increase with even small levels of watershed disturbance (Jackson et al. 2017). The basin forest land cover explains 65% of the variation in specific conductance (Webster et al. 2012), with developed watersheds and main stem river sites in the region featuring median specific conductance values two to five times those observed in reference forest watersheds (Jackson et al. 2017). However, median specific conductance is highly idiosyncratic, with high variability among watersheds with similar land uses and land-use patterns, possibly because of differences in road salting, poorly treated septic effluent, or agricultural amendments (Jackson et al. 2017). All rural residents use septic systems, but the placement and functioning of these systems is unknown and likely highly variable. In small tributary watersheds, there

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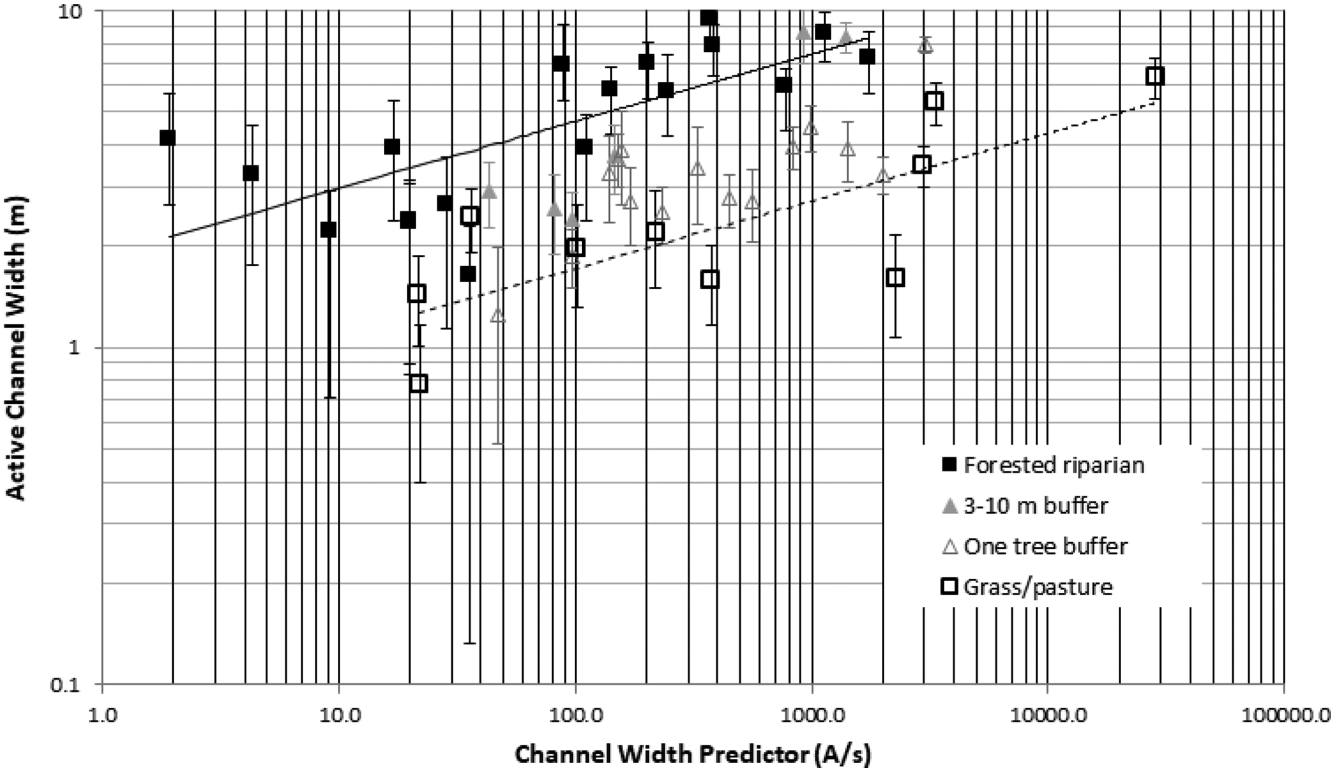

Figure 5. Channel widths of streams varying in riparian conditions as a function of the drainage area (in square kilometers) divided by the channel slope. Regressions fit to the endpoints of fully forested (r^2 = .52) and grass or pasture (r^2 = .61) streams. Widths of streams with grass or pasture riparian conditions are only 33% to 40% of those with full forest buffers. Source: Reprinted with permission from Jackson and colleagues (2015).

Figure 6. (a) Road ditch runoff with high suspended sediment concentration along paved county road in the Bates Creek watershed, Upper Little Tennessee River Basin. (b) Riparian landowner in the study area removing trees, tree roots, and shrubs from a streambank and stream edge.

may be only a few dozen streamside landowners, and some engage in behaviors that affect stream chemistry disproportionately to their portion of total watershed area. The observed near-stream activities likely to have high relative impacts on water quality include direct livestock access, mysterious small-pipe discharges, streambank composting, the diversion of stream water to clean a dog kennel, cow patty disposal on streambanks, the diversion to and return from ornamental ponds, and others (Jackson et al. 2017). The ability of basin or riparian land cover alone to explain stream chemistry is limited by the effects of such near-stream activities often unique to individual landowners.

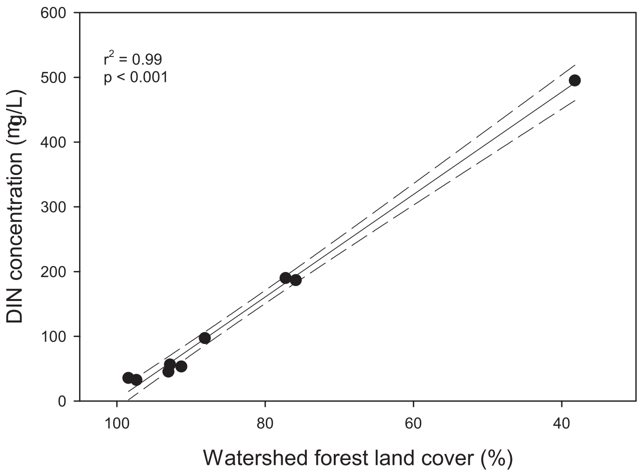

Figure 7. Stream dissolved inorganic nitrogen (DIN) concentrations across a gradient of forest cover. Basin forest cover explains 99% of the variation in stream DIN. Source: Adapted with permission from Webster and colleagues (2019).

Excess nitrogen concentrations are an important water quality issue in this region because of nutrient subsidies and losses in assimilative capacity. The nitrogen inputs to the watersheds have increased greatly in the last century because of fossil fuel combustion and the use of fertilizer created by industrial nitrogen fixation (e.g., Swank and Vose 1997). In the forested watersheds, nitrogen is strongly retained (Swank and Waide 1988, Swank and Vose 1997, Groffman et al. 2004, Adams et al. 2014, Webster et al. 2016), with stream export often representing less than 2% of the atmospheric inputs. Forest disturbance and clear-cutting greatly increase the export of nitrogen (Swank 1988, Adams et al. 2014, Webster et al. 2016, 2019). The increased exports are partly attributed to the loss of tree uptake and changes in soil cycling but mostly to fertilizer subsidies and elevated inputs by biological nitrogen fixation associated with postdisturbance abundance of black locust (*Robinia pseudoacacia*). Consequently, the loss of forest vegetation to agricultural and urban development accelerates increases in stream concentrations and loads (Webster et al. 2012, 2019). There is a very strong negative correlation (linear regression, $r^2 = .99$, $p < .001$) between stream nitrogen concentration and forest land cover (figure 7; Webster et al. 2019), a result backed up by extensive synoptic sampling (Webster et al. 2012). In agricultural watersheds, inputs from fertilizer and septic systems are probably the dominant sources of elevated nitrogen (e.g., Fraterrigo and Downing 2008) and in developed watersheds, lawn fertilizer (e.g., Law et al. 2004, Yang and Toor 2016), and leakage from sewer systems may be significant sources. However, throughout the area, the predominant source of nitrogen to the watersheds is atmospheric deposition, and the dissolved inorganic nitrogen (DIN) within the streams is determined by the degree with which DIN deposition is retained in the forest soils. The timescales of stream responses to these nitrogen cycle perturbations are variable and can be quite long, sometimes confounding the interpretation of stream concentration time series (Jackson et al. 2018).

Phosphorus concentrations in the region are so low that they have inhibited studies of attribution. Even in the streams draining agricultural or urban watersheds, phosphorus concentrations are often near or below the levels of detection. On the basis of the data of Swank and Waide (1988) and Swank (1988), phosphorus retention is high in the region (76%–77%) in both forested and managed watersheds, and the soluble reactive phosphorus levels are low in all stream in the region (Webster et al. 2012). In the larger streams and rivers, agricultural land cover and parcel ownership longevity together explain about 38% of the variability in soluble reactive phosphorus, but these factors explained little of the variability in the small streams (Webster et al. 2012). Scott and colleagues (2002) found significant correlations between soluble reactive phosphorus concentration and land cover and land cover change. However, the information on phosphorus export is incomplete, because most phosphorus export occurs as particulates, and there have been very few studies of particulate phosphorus transport.

Basal resources

The rural land uses in the region affect basal resource quality and quantity via increased nutrients, decreased shading, altered leaf litter inputs, and increased sediment. The quantity and type of food resources in the streams are critical to macroinvertebrate, fish, and salamander production. Terrestrially derived organic matter, such as leaf litter and wood (detritus), is the main source of energy in the forested headwater streams (Wallace et al. 1997, 2015, Walther and Whiles 2011, Venarsky et al. 2018) over which canopies limit light penetration and algal growth (e.g., Hagen et al. 2010). Forest conversion and landscaper fertilization may result in a decreased quantity of detritus via factors that affect inputs, decomposition rates, and retention; either an increased or a decreased quantity of algae via factors that affect growth rates and retention; and changes to the quality of both detrital and algal resources. These changes generally result in simplified basal resources dominated by algae versus detritus and higher in nutrients relative to carbon content (Hagen et al. 2010, Manning et al. 2015). Such shifts in nutrient to carbon ratios lead to greater production of some organisms (Demi et al. 2018) and result in altered food web structure (Davis et al. 2010).

Increased solar insolation due to riparian forest removal, coupled with increased nutrients, usually leads to increased algal biomass (McTammany et al. 2007, Gardiner et al. 2009), but agricultural sediment inputs (Jackson et al. 2017) may inhibit autochthonous production, especially where livestock have direct access to streams (Price and Leigh 2006a, 2006b, Hagen et al. 2010). Following agricultural abandonment, the rapid regrowth of riparian vegetation

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results in reduced autochthonous production. In streams of forested watersheds, over 98% of the total carbon supply is from allochthonous sources, and even light and moderate agriculture streams receive over 90% of their carbon input from allochthonous sources (Hagen et al. 2010). In contrast, high intensity agricultural streams receive only 21%–50% of their carbon from leaf litter, with the majority coming from autochthonous algal production stimulated by increased light and nutrients.

Rural land use invariably results in reductions in stream detritus and altered diets of stream organisms, most obviously because reduced riparian forest results in reduced inputs of organic matter (England and Rosemond 2004). The loss of allocthonous litter inputs reduces the total numbers and composition of macroinvertebrates at all trophic levels, with effects varying across geomorphic habitat type (Wallace et al. 1997); affects the abundance and feeding of a predatory salamander (Johnson and Wallace 2005); and reduces dissolved organic carbon production in streams (Meyer et al. 1998). Higher nutrient concentrations, higher light levels, and higher stream temperatures can all accelerate leaf litter breakdown (Greenwood et al. 2006, Hagen et al. 2006, Benstead et al. 2009, Lagrue et al. 2011, Rosemond et al. 2015, Manning et al. 2017). Rapid leaf litter breakdown can lead to a paucity of food resources in late summer or early fall, affecting the macroinvertebrate community (Rosemond et al. 2015). Stream discharge also controls the retention of detritus (Rosemond et al. 2015), such that increased storm flows due to land-use change may also reduce detrital availability to organisms.

Elevated stream nutrient concentrations increase the nutrient content of basal resources. This is partly because of the shift from detritus to algae but also because the microbial uptake of nutrients increases the nutrient-to-carbon ratios of detrital resources in high-nutrient streams (Manning et al. 2015). These shifts in food nutrient content benefit some macroinvertebrate taxa that can exploit high-quality food resources but negatively affect others (Demi et al. 2018). Shifts in food web structure have been observed, in which increased growth of primary consumers fails to propagate to higher trophic levels (Davis et al. 2010).

Alterations of biotic assemblages

The distribution and abundance of aquatic and semiaquatic animal species are influenced by biotic and environmental factors that operate over a range of spatial and temporal scales (Frissell et al. 1986, Poff 1997, Fausch et al. 2002). Therefore, animal assemblages are typically hierarchically structured and sensitive to perturbations occurring over broad scales. In general, anthropogenic land developments occurring in a watershed can have a long-lasting cascading effect on multiple processes that maintain the physical characteristics of local stream environments and their animal assemblages (figure 2; Harding et al. 1998, Burcher et al. 2007). Extensive research has was shown that urban and agricultural land cover occurring in the Upper Little Tennessee River and French Broad River Basins is often associated with lower occurrences or abundances of highland endemic fishes (Scott and Helfman 2001, Scott 2006, Kirsch and Peterson 2014) and amphibians (Cecala et al. 2018) and altered assemblages of benthic macroinvertebrates (Harding et al. 1998, Frisch et al. 2016). In addition, anthropogenic land cover has been related to higher occurrences of algae (Gardiner et al. 2009), benthic grazing macroinvertebrates (Frisch et al. 2016), and generalist fishes (Scott 2006). Although these effects collectively resulted in highly altered biotic assemblages, variation in animal diversity at sites with small changes in forest cover is dependent on topology, topography, and the proximity, intensity, and type of human activity in and adjacent to streams (figure 2).

Macroinvertebrates. The macroinvertebrate assemblages in the region show high sensitivity to low levels of human land-use activities, with taxon-specific responses to riparian change and watershed-scale land use. For example, Frisch and colleagues (2016) quantified the presence or absence of four focal stream taxa (three macroinvertebrates and a fish) representing different life histories and functional roles across 37 streams varying widely in catchment and reach characteristics and found taxon-dependent sensitivity to aspects of land cover and water quality changes commonly observed in subbasins across the watershed. The probability of detecting the algae-grazing snail *Pleurocera proximum* was most strongly predicted by calcium concentration (necessary for shell construction) but decreased with increasing forest cover, suggesting that forest cover reduced algal resources. Conversely, the presence of the shredder *Tallaperla* sp. was positively correlated with basin forest cover but negatively correlated with nitrogen concentrations. The presence of the omnivorous crayfish *Cambarus* sp. was negatively correlated with agricultural land cover and positively correlated with wood debris. Each taxon had a different story but each responded to low levels of land-use change according to their ecological role. Gardiner and colleagues (2009) examined invertebrate assemblages across streams varying in land use. All agricultural and residential watersheds supported much more diverse diatom assemblages, including shade-intolerant diatoms relative to the forested streams that supported fewer diatom species, most of which were associated with shady, oligotrophic streams. This clear shift in diatom assemblages reflects the variation in riparian cover across these watersheds. The forested and less developed sites had higher macroinvertebrate species richness and greater proportions of Ephemeroptera, Plecoptera, and Trichoptera taxa.

Amphibians. Stream-breeding amphibians of this region rely heavily on both in-stream and riparian habitats (Crawford and Semlitsch 2007, Peterman et al. 2008, Cecala et al. 2018). A decrease in the quality of either habitat will cause stream amphibians to decline. Forest conversion had a strong and negative impact on occupancy of both larval and adult

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stream breeding amphibians, as well as diversity (a 30% reduction in watershed forest cover corresponds to a 2.2-fold decline in the probability of occupancy; Cecala et al. 2018). Mechanistically, these distribution changes are the result of shifts in local stream conditions (Cecala et al. 2018, Weaver and Barrett 2018). Even fine-scale changes in well-forested catchments result in lower occupancy when riparian forest loss interacts with shade-seeking behaviors of salamanders resulting in avoidance of sunny regions with high temperatures, low organic matter inputs, and different prey and predator communities (Cecala et al. 2014, 2017, Cecala and Maerz 2016). Stream salamanders exhibit altered habitat selection, aggressive social behaviors, and reduced growth in warm and deforested reaches (Cecala et al. 2014, Bliss and Cecala 2015, Hoffacker et al. 2018, Bissell and Cecala 2019). Regardless of the watershed context, small riparian losses in forest cover disproportionately affect salamander population dynamics.

Fishes. The Little Tennessee and French Broad rivers are occupied by over 150 native fish species, many of which are locally endemic and imperiled (Warren et al. 2000). These streams are occupied primarily by species dependent on drifting or rock-associated aquatic insects for food, on clean rocky bottoms for spawning, and on relatively cold water (Scott and Helfman 2001). As was discussed earlier, deforestation and anthropogenic land development can degrade these habitat attributes by decreasing macroinvertebrate abundance and diversity (Harding et al. 1998, Sponseller et al. 2001, Frisch et al. 2016) and increasing nutrients, fine sediment, and water temperature (Swift and Messer 1971, Jones et al. 1999, Sponseller et al. 2001, Scott et al. 2002, Sutherland et al. 2002).

Multiple studies in the Southern Appalachians have revealed a strong influence of land cover on fish distributions and abundance. Reductions in forest cover within the riparian corridor upstream of a site have been related to lower abundances of fishes that require clean cobble and gravel for spawning and higher abundance of fishes that are tolerant of sediment (Jones et al. 1999, Sutherland et al. 2002, Burcher et al. 2008). Furthermore, more than one kilometer of deforestation in upstream riparian corridors within fully forested watersheds has resulted in fewer benthic cool-water fishes (Jones et al. 1999). Similarly, deforestation and rural development throughout the watershed has largely been associated with the reduced occupancy or abundance of highland endemic species (native cold-water and cool-water specialists) and increased occupancy or abundance of cosmopolitan species (widely distributed, often tolerant taxa; Jones et al. 1999, Sutherland et al. 2002, Scott 2006, Burcher et al. 2008, Kirsch and Peterson 2014). The negative relationship of the endemic:cosmopolitan ratio to forest cover suggests that rural watershed development contributes to an expansion of generalist species at the expense of regional endemics, potentially leading to increasingly homogenous assemblages across the landscape that are depauperate in highland endemic fishes (Scott and Helfman 2001, Scott 2006, Petersen et al. 2021). For example, streams with more than 15% urban land cover in their watershed tend to have no more than 25% endemic species, whereas streams with nearly fully forested watersheds can have up to 90% endemic species (Kirsch and Peterson 2014). However, there is mixed empirical evidence for an increase in fish community homogenization through time as was indicated by decreasing beta diversity (Petersen et al. 2021). Furthermore, there is evidence that historic (1950s) land use in the watershed and in the riparian corridor is a good or better predictor of fish richness and diversity than current land use (Harding et al. 1998, Burcher et al. 2008), indicating a long-term legacy effect of agriculture and deforestation on fish communities.

Legacy land-use effects

Confounding the effects of current land use on water quality, aquatic and terrestrial ecosystem studies indicate that current stream ecological conditions partly reflect legacy effects of past land uses. For example, stream macroinvertebrate and fish assemblages show impacts of prior land use 30 years after reforestation (Harding et al. 1998, Burcher et al. 2008). The stream sedimentation history described above continues to affect channel form and sediment dynamics in the present. Similarly, current soil characteristics tend to reflect past land use. For example, within the neighboring French Broad River Basin, forests abandoned from agriculture a century ago have elevated levels of phosphorus and potassium relative to forests lacking a history of intensive land use (Fraterrigo et al. 2005). They also show reduced spatial heterogeneity of soil carbon, nitrogen and calcium, and increased heterogeneity of phosphorus, potassium, and magnesium. Although these changes were likely initiated by past agricultural practices, their persistence is thought to be the result of shifts in vegetation composition that emerged following abandonment. Specifically, increases in the relative abundance of disturbance-adapted tree species such as tulip poplar (*Liriodendron tulipifera*) may have led to greater and more uniform inputs of high-quality (low carbon to nitrogen ratio) litter. This in turn could have sustained the elevated levels and evenness of soil resources in postagricultural forests. Such shifts in forest composition may contribute to higher nutrient levels in streams because tulip poplar litter breaks down relatively rapidly compared to other species (e.g., Kominoski et al. 2009). Available soil carbon is lower in previously agricultural forest stands, altering soil nitrogen dynamics by increasing ammonium availability and facilitating potential nitrification rates (Keiser et al. 2016). Past clear-cutting can also result in long term increases in stream dissolved inorganic nitrogen by favoring establishment of black locust (*Robinia pseudoacacia*), a nitrogen fixer (Jackson et al. 2018). The legacy effects of past land uses and human actions likely contribute to the noisiness of functional relationships between current land uses and stream ecosystem states and processes.

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Differential but merging effects of watershed and riparian land uses on landscape–stream connectivity

Connectivity is a dynamic and spatially variable watershed property, and stream ecosystems respond to either increases or decreases in connectivity. Stream responses to rural land uses depend on the differential alterations to the supply and routing of water, solutes, and energy caused by riparian- and basin-scale land uses (figure 2). Together, these studies show the vegetation, soil, and hydrologic changes wrought by even low levels of forest conversion to low density residential development and small farms generally increase the transport of nutrients, other solutes, light, and sediments to streams. Previously, Burcher and colleagues (2007) hypothesized that land cover changes affected stream biota through an abiotic cascade running from and through hydrologic, geomorphic, erosional, and depositional processes that affect streamflows, channel form, suspended sediment, and bed particle size distributions, but this conceptualization did not consider the differential routing of nonpoint pollution from near-stream and basin-wide land uses.

In this broader assessment of water quality effects of rural land uses, we find that near-stream and basin-wide land uses affect different aspects of landscape–stream connectivity. Some of the processes affecting rural water quality changes are controlled by near-stream land use and activities (e.g., solar insolation, streambank dynamics, channel roughness, riparian biogeochemical cycling, stream–field hydrologic connectivity, individual landowner discharges), whereas others are controlled by basin-wide land use (e.g., nutrient subsidy, runoff from roads and disturbed soils and roads, streamflow changes). As examples, stream nutrient concentrations largely reflect basin-wide land use, whereas summer stream temperatures reflect mostly local riparian conditions but also network position. We also have observed various idiosyncratic water quality perturbations by individual stream adjacent landowners that degrade water quality including illicit discharges, poor waste and manure management, and channel manipulation. Such landowner-specific behavior may partially account for the individuality of each watershed with respect to average specific conductance values. Channel morphological conditions reflect both basin-scale changes in streamflows and riparian-scale effects of bank mechanics and wood inputs. All of these connections and their effects are mediated by local topography, geology, climate, and the legacy effects of past land use. Without consideration of mobilization and transport processes, it is difficult to distinguish the riparian and watershed land-use effects on stream conditions, because their effects merge within the channel (figure 2). Distinguishing between the riparian and watershed processes affecting stream ecosystems is critical to the formulation of strategies to improve rural water quality conditions.

In these rural watersheds, many water quality measures are sensitive to small changes in land use without any apparent threshold response. Dissolved inorganic nitrogen concentrations are nearly linearly related to forest loss (figure 7), channel morphology is responsive to small differences in forested buffer width, summer stream temperatures are sensitive to small changes in total canopy cover, and suspended sediment concentrations are very responsive to changes in watershed land cover. Some aspects of stream biota responses to rural land use indicate threshold behaviors (e.g., Johnson et al. 1999, Kirsch and Peterson 2014), but in the present article, we see that even small increases in near-stream and watershed connectivity to streams have significant effects on important aspects of water quality.

Mitigation potential and implementation issues

The water quality problems observed in this rural, low human density mountain landscape could be substantially reduced through the implementation of well-known and well-studied BMPs previously developed for the forestry and agricultural communities for reducing landscape–stream connectivity (Theobald et al. 2005). Applicable BMPs include restoring wooded riparian zones, reducing sediment delivery from road runoff, fencing livestock from streams, and implementing nutrient management plans on farmlands. Riparian restoration would shade the streams, reduce summer temperatures detrimental to cold water species, and increase leaf litter inputs. Undisturbed riparian forests would filter sediment and phosphorus carried from adjacent farm fields and would promote denitrification, reducing nitrogen loads in streams draining fertilized watersheds (Sweeney and Newbold 2014). Riparian forest restoration would also widen stream channels, increasing aquatic habitat area, and create more complex and diverse aquatic habitat (Jackson et al. 2015). The cumulative effects of riparian forest restoration would push stream ecosystem processes closer toward their forested state, mitigate many aspects of rural water quality, and provide resilience to global warming (Burrell et al. 2014, Turunen et al. 2019, 2021).

There is currently no comprehensive governance system in this region to address the multiple subtle but significant rural stream water quality issues related to riparian forest loss, runoff from row-cropping to the stream bank, sedimentation from eroded banks with free cattle access, lack of regular and comprehensive testing for septic systems, and direct runoff from thousands of kilometers of private roads in steep mountainous terrain. However, organizations and programs in the region are attempting to reduce landscape–stream connectivity. These include the USDA Natural Resources Conservation Service (NRCS) and the US Fish and Wildlife Service working (USFWS) with landowners, the Macon County Soil and Water Conservation District (MSWCD), and conservation nonprofits such as the Mainspring Conservation Trust (MCT).

NRCS programs are primarily directed toward riparian exclusion fencing and alternative water sourcing for livestock through the North Carolina Agricultural Cost Share Program. The USFWS Partners for Fish and Wildlife Program provides technical or financial support to private landowners, organizations or local municipalities to implement voluntary riparian and stream habitat restoration or stream road crossing improvement projects in locations that would benefit federally listed or at-risk species. Between 1995 and 2014, the MSWCD also offered streambank stabilization funding to nonagricultural landowners through a program unique to the district. Over $900,000 in state and federal funding was secured, resulting in over 17.5 km of riparian buffers planted and over 4.5 km of revetments installed at 86 sites in Macon County (Chesky-Smith 2016). The MCT has also promoted a Shade Your Stream initiative (http://shadeyourstream.org) that provides resources to private landowners that are otherwise ineligible for NRCS funding (Brownson et al. 2020). As a nonprofit, the MCT can often negotiate voluntary conservation agreements in a community in which individuals have a strong commitment to private property rights, frown on additional regulations, and may distrust public agencies (Evans and Jensen-Ryan 2017, Brownson et al. 2020). From 2015 to 2020, the MCT opportunistically worked with landowners to restore 2.7 km of riparian buffers on 27 different streams through light touch activities such as planting trees and live-staking species such as silky dogwood (*Cornus amomum*) and black willow (*Salix nigra*; Jason Meador, Mainspring Conservation Trust, personal communication, 3 March 2021). Through the land trust a total of 46.4 km of riparian buffers have been protected through fee simple purchases or conservation easements in Macon County from 1999 to 2015. These activities have been accomplished in part by appealing to a documented shared value among landowners to be a good neighbor, which leads many landowners to conserve and restore their land through the voluntary programs offered by the MCT (Sanders 2019).

Sediment inputs from road runoff could be reduced through targeted implementation of well-known rural road BMPs (e.g., Kocher et al. 2007, Ramos-Sharrón 2012), including diverting road runoff to forested slopes where it can be infiltrated, vegetating roadside ditches to reduce sediment mobilization from ditches themselves, installing and maintaining sediment traps on ditches, and paving well-traveled gravel roads (Clinton and Vose 2003, Turton et al. 2009). The Regional Erosion and Sediment Control Initiative, a consortium of federal, state, and conservation nonprofits, previously provided training for private landowners and heavy equipment operators on proper road building and road maintenance techniques, but lack of funding and support ended this initiative. Fencing livestock out of streams would provide multiple benefits including reduced streambank erosion and reduced transport of manure and sediment to streams during storms (Platts and Wagstaff 1984). County extension and NRCS agents work with farmers to enroll them in cost-share programs to fence out cattle from streams while providing alternative watering sources for livestock. These same agencies also help farmers to develop fertilizer and manure management plans that decrease nutrient loading to streams. Identifying and addressing illicit discharges could further reduce nutrient and carbon loads.

On the basis of nearly three decades of observations and research in our study area, we conclude that improving rural water quality is a matter of motivating and incentivizing BMP implementation through programs and policies that balance ecological, social, and economic considerations. Landowners who understand BMP benefits and who view voluntary conservation programs positively nevertheless demonstrate low program enrollment rates (Armstrong and Stedman 2012, Chapman et al. 2019). Landowners are also often unwilling to contribute their own funds toward BMP installation and cite cost as a limiting factor (Napier et al. 2008). Therefore, programs targeting agricultural landowners in rural areas such as Macon County can improve enrollment rates with strong financial incentives, whereas residential landowners prefer tax subsidies (Napier 2000, Corbett 2002, Napier 2008). Flexible contract term length and shorter contract duration options also improve program interest (Yeboah et al. 2015, DeAngelo and Nielsen-Pincus 2017). Increasing the range of options in voluntary conservation programs is important because a single incentive approach might not be relevant for all landowners in a region (Napier 2000).

Many nonadopters believe that they are already good stewards of the resource, even when their management practices conflict with BMP guidance or ecological science (Corbett 2002, DeAngelo and Nielsen-Pincus 2017). Voluntary conservation programs can link BMP adoption with local stewardship values using language that resonates with local people to successfully attract nonadopters who place high importance on protecting natural resources (Yeboah et al. 2015).

Conclusions

Even modest amounts of forest conversion (less than 30%) to small valley farms and rural residential lands increases landscape–stream connectivity and results in higher nutrient and suspended sediment concentrations, increased insolation and summer stream temperatures, higher specific conductance, lower wood frequency, and reduced litter inputs, all with attendant effects on stream food webs. Suspended sediment, DIN, and specific conductance levels increase with forest loss, with no apparent threshold behavior. Cumulatively, low-density rural development shifts cold-water oligotrophic rural streams from wide, complex, shady, cold, clear, litter-dependent systems to narrow, simple, well-lit, warm, turbid, nutrient-subsidized, algae-dependent systems. Consequently, cold-water fish, amphibian, and macroinvertebrate communities are shifted toward species more tolerant of warmer, more turbid, and mesotrophic conditions.

Watershed-scale land uses and riparian land uses differentially affect landscape–stream connectivity and the transport of nonpoint pollutants to streams. At watershed scales, road runoff and sediment from roads can be routed long distances via conveyance ditches, bypassing riparian vegetation. Similarly,

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nitrate mobilized by reduced forest uptake and subsidized by fertilizers and food and feed imports can move by groundwater from ridges to streams. In the near-stream environment, riparian forest removal increases solar insolation to streams and summer stream temperatures, often beyond tolerances of cold water species; increases sediment and overland flow transport from fields to streams; reduces wood and detritus inputs; alters root–channel interactions; and creates simpler and narrower channels. The effects of these watershed and riparian scale connectivity changes are merged within the channels, making it difficult to separate their effects without considering mobilization and transport processes.

Most water quality responses to rural land uses are noisy and complicated, reflecting the high degree of topographic, climatic, and geologic heterogeneity across these mountain watersheds, as well as the nonuniform effects of prior land-use history. Biological responses to rural land-use activities show threshold behaviors and are mediated by topography, geology, climate, network position, and past land use. Studies of the hydrologic and water quality effects of low density rural development are inherently challenged by a low signal to noise ratio, but nevertheless we saw similar responses consistent with transport process understanding over this region. These findings should be generally applicable to low-density rural environments, although some effects are likely to be more muted in flatter topographies.

Application of known BMPs previously developed for forestry and agriculture could greatly reduce water quality effects of low density rural development, and riparian forest restoration could mitigate the effects of a warming climate, but the socioecological governance question is how to promote and incentivize BMP application in multiple landowner and multiple use watersheds with few local tax resources. Developing and testing effective governance systems for rural water quality is critical given the significant water quality effects of such low-density rural development and the wide spatial coverage of such land uses.

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