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FOCUS ARTICLE

Unexpected ecological advances made possible by long-term data: A Coweeta example

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In the 1970s, Forest Service and academic researchers clearcut the forest in Watershed 7 in the Coweeta Basin to observe how far the perturbation would move the ecosystem and how quickly the ecosystem would return to its predisturbance state. Our long-term observations demonstrated that this view of resistance and resilience was too simplistic. Forest disturbance triggered a chain of ecological dynamics that are still evolving after 40 years. Short-term pulses in dissolved inorganic nitrogen (DIN) (3 years) and streamflows (4 years) were followed by several years in which the system appeared to be returning to predisturbance conditions. Then however, changes in forest composition triggered a regime change in DIN dynamics from biological to hydrological control as well as persistent high stream DIN levels mediated by climatic conditions. These forest composition changes also led to later reductions in streamflow. These long-term observations of streamflows, stream DIN concentrations, stream DIN exports, and stand composition have substantially advanced our understanding of forest ecosystem dynamics; and they demonstrate the value of long-term observational data in revealing ecosystem complexities and surprises, generating new hypotheses, and motivating mechanistic research. Shorter observational records from this experiment would have produced incomplete or erroneous inference.

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1 | INTRODUCTION

Long-term observations of ecosystem responses to disturbance often reveal system behaviors that were neither hypothesized nor predicted, and these unexpected responses can lead to new insights, hypotheses, and research directions. Long-term data can identify and illuminate ecosystem responses to slow ecological processes, highly variable processes, subtle or complex phenomena (Dodds et al., 2012), episodic phenomena (Gooseff et al., 2017), and climate or landscape management changes (Edmondson, 1991; Goldman, Jassby, & Hackley, 1993). The Coweeta Basin Watershed 7 (WS7) Long-term Ecological Research (LTER) experiment provides several examples of complicated hydrological and biogeochemical responses to disturbance that have not reached equilibrium 40 years after road building, timber harvest, and natural regeneration across the entire watershed. It appears the watershed shifted to a new and persistent regime of elevated nitrogen export and reduced

water yield (Swank, Knoepp, Vose, Laseter, & Webster, 2014; Webster, Knoepp, Swank, & Miniat, 2016). These findings would not have been revealed without long-term monitoring, and our understanding of system behavior would have been erroneous or incomplete if observations had ceased at any earlier times.

The original goal of the experiment was to conduct a watershed-scale timber harvest with new logging roads to examine ecological resistance and resilience across a suite of macroscopic ecosystem properties including streamflow, stream nitrogen exports, soil carbon and nutrients, forest species composition, and stream basal resources and macroinvertebrate communities. It was expected that the forest disturbance would push hydrological and biogeochemical processes from their preharvest state for a period of years and then the system would return to something like the preharvest state (Monk et al., 1977). The experiment sought to quantify how far different ecosystem processes and states would shift after disturbance, and how quickly they would move back. This manipulation of WS7 was conceived and initiated in the early 1970s under the International Biological Program and became the signature experiment around which the Coweeta Long-Term Ecological Research program (LTER) was conceptualized and funded in 1980.

Results from this study are well documented (see Swank & Webster (2014) for a full overview). Here, we focus on unanticipated findings and insights revealed by the long-term time series of stream flows and dissolved inorganic nitrogen (DIN) concentrations and exports. In conjunction, we examine long-term forest composition and soil chemistry data as they support interpretations of biogeochemical processes within the watershed and streams. We also point out erroneous or incomplete inferences we might have drawn if observations had terminated earlier.

2 | STUDY DESCRIPTION

The research was conducted in the USDA Forest Service Coweeta Hydrologic Laboratory in the Nantahala Mountains of western North Carolina. The climate features cool summers, mild winters, and abundant rainfall in all seasons. Less than 5% of precipitation falls as snow. Hydrological and biogeochemical responses were assessed using the paired watershed experimental design (Hewlett, Lull, & Reinhart, 1969; Wilm, 1943) and were summarized by Swank et al. (2014) and Swank, Vose, and Elliott (2001) The strength of this design is that treatment effects can be isolated by accounting for year-to-year variation in climate using the reference, watershed. WS7 (treatment) and WS2 (reference) were instrumented with permanent 90° v-notch weir structures in 1964 and 1935, respectively. The duration of the calibration period was 11 years beginning in 1966. Weekly grab sampling of water chemistry samples for both WS7 and WS2 began in 1971 and continues today. Flow-proportional samples were collected from 1975 to 1981. All samples were analyzed according to established protocols (Coweeta, 2016).

At the time this watershed-scale forest harvest was conceived, forestry best management practice (BMP) programs had not been formalized. Consequently, the watershed manipulation reflected the practices and forestry questions of the time. In 1976, gravel-bedded forest access roads were constructed along contours at toeslope, midslope, and ridgetop positions. In January 1977, the watershed was clearcut from ridge to ridge with no riparian buffer; and logs were cable-yarded upslope to landings along the access roads. Cable yarding was little used in the Appalachian Mountains, so a major motivation for this study was to examine the practicality, economic feasibility, soil disturbance, and erosion associated with this yarding system. During yarding, large wood was removed from the stream channel. Following timber removal, the roadbeds were seeded with grass and fertilized. This hardwood forest watershed was allowed to regenerate naturally, as was common then and now in hardwood silviculture.

Prior to harvest, the reference and treatment watersheds (Table 1) featured mixed hardwood forests with some pitch pine (*Pinus rigida* Mill.). Stands varied by landscape position and included cove hardwoods, mesic mixed-oak, and dry mixed-oak communities. Clearcutting shifted species composition from a forested watershed dominated by oaks (*Quercus* spp.) and

TABLE 1 Characteristics of treatment (WS7) and reference (WS2) watersheds

	WS7 (Big Hurricane Creek)	WS2 (Shope Branch)
Drainage area (ha)	59.5	12.3
Elevation range (m)	724–1060	716–991
Average slope (%)	57	60
Aspect	South	South-southeast
Stream type	Second order, perennial	First order, perennial
Soils	Typic Hapludults, Typic Dystrudepts, and Typic Humudepts	
Mean annual precipitation (mm)	1890	1810
Mean annual flow (mm)	1060	990
Range in annual flow (mm)	760–1490	590–1300

hickories (*Carya* spp.) to one dominated by shade-intolerant, fast-growing species such as tulip poplar (*Liriodendron tulipifera* L.) and black locust (*Robinia pseudoacacia* L.), subdominant red maple (*Acer rubrum* L.), and shade-tolerant understory shrubs (Figure 1) (Boring et al., 2014). The early proliferation and dominance of black locust, a nitrogen-fixing tree species, was unexpected. Later in succession (10–15 years), black locust density declined substantially due to locust borer infestation (Boring et al., 2014; Boring, Swank, Waide, & Henderson, 1988); however, it is still present in the watershed (Figure 1). Although the basin had been harvested before at the turn of the century, *Robinia* was a negligible component of the preharvest forest. These shifts in forest species composition from expectations appeared to drive changes in DIN exports and watershed water budgets discussed below. These unexpected observations led to further studies on species-specific effects on biogeochemistry and hydrology (Caldwell et al., 2016; Elliott et al., 2017; Knoepp, Coleman, Crossley, & Clark, 2000; Knoepp & Swank, 1998; Knoepp, Vose, & Swank, 2008).

3 | UNEXPECTED BIOGEOCHEMICAL AND HYDROLOGICAL BEHAVIOR REVEALED BY LONG-TERM DATA

Forests in the southern Appalachians are generally N-limited (Swank & Vose, 1997) as evidenced in this study by the low stream DIN concentrations and export in both pretreatment and reference watersheds (Figure 2). Prior to harvest, there was little variation in the DIN or water budget dynamics of the treatment watershed relative to the reference (Figure 3). For the first 3 years after harvest, DIN concentrations and water yields behaved as expected in WS7 according to ecological resistance and resilience ideas (Webster, Swank, Vose, Knoepp, & Elliott, 2014; Webster, Waide, & Patten, 1975). DIN yields increased after harvest due to N release by soil microbial mineralization and reduced plant uptake (e.g., Vitousek and Melillo (1979)), and water yield increased due to reduced interception and evapotranspiration of the young forest (Figures 2 and 3). From 1980 to 1988, the initial effects on DIN and water yield had greatly diminished, and the watershed biogeochemical dynamics appeared to be heading back to preharvest conditions, indicating relatively rapid ecological resilience.

Terminating the experiment at this time (1988) would have led to the conclusion that clearcutting a southern Appalachian produces only short-term changes in forest evapotranspiration and nitrogen cycling, and that the system moves on a relatively direct path to preharvest conditions. The more interesting stories of the biogeochemical dynamics spurred by forest disturbance and succession, however, would never have been observed. The long-term cycles of stream DIN trends illustrate the danger of fitting and extrapolating trends that appear clear from the data at hand, a danger illustrated by Argerich et al. (2013) who showed that at many forested reference watersheds the length and period of record determined whether trends in stream nitrate and ammonium showed increases, decreases, or no change.

The expected recovery trend in DIN reversed course 12 years after harvest, moving the watershed into a persistent period of elevated DIN concentrations (Figures 2 and 3) described by Webster, Knoepp et al. (2016) as a functional regime shift. We hypothesize that the continued high stream DIN concentrations are related to the large component of *Robinia* (black

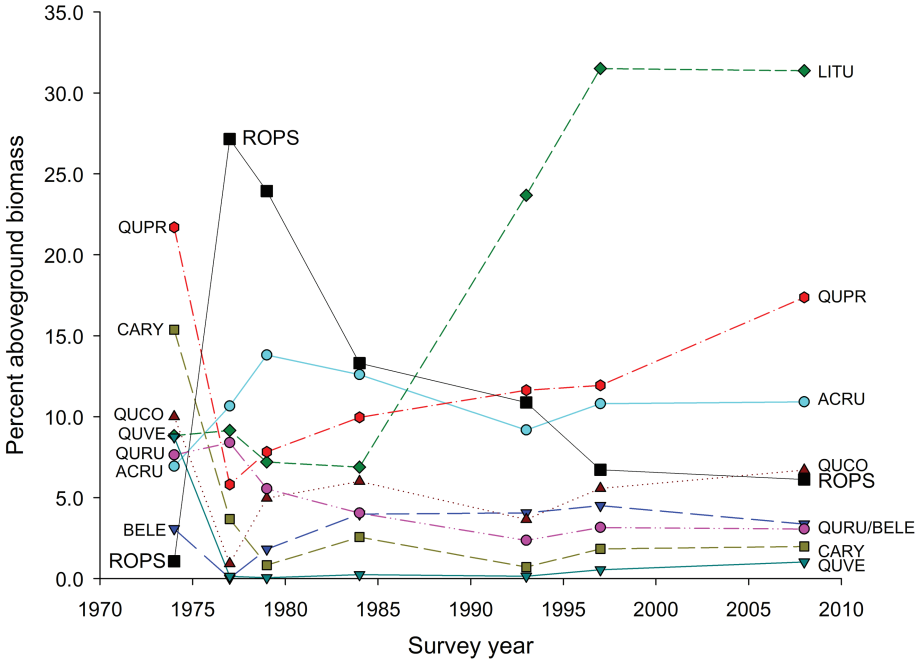

FIGURE 1 Percent aboveground biomass for the whole watershed in WS 7 through time (Boring, Elliott, & Swank, 2014). Species code are ACRU, *Acer rubrum*; BELE, *Betula lenta*; CARY, *Carya* spp.; LITU, *Liriodendron tulipifera*; QUCO, *Quercus coccinea*; QUPR, *Quercus prinus*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*; and ROPS, *Robinia pseudoacacia*. *Robinia* became dominant early in succession then diminished substantially but remained well above preharvest levels 30 years after harvest

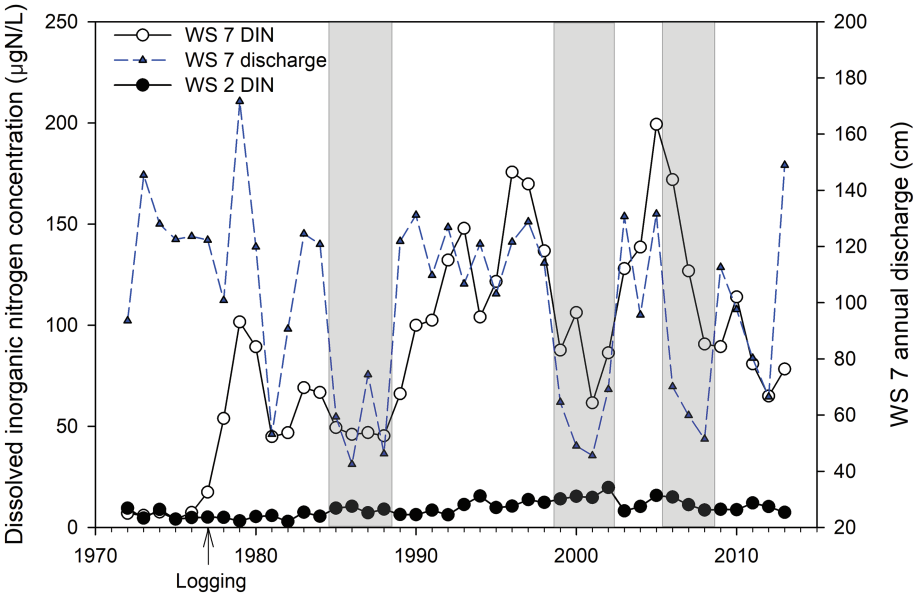

FIGURE 2 Mean annual disolved inorganic nitrogen (DIN) concentration in Coweeta watersheds 7 (WS 7, logged 1977) and 2 (WS 2, reference) and annual discharge from WS 7. The gray bars represent periods of drought.(Reprinted with permission from Webster, Knoepp et al. (2016)

locust) in the early successional forest. The rise in DIN, however, lagged several years behind the peak of *Robinia* as a fraction of above-ground biomass (Figure 1). This lag could reflect a delay generated during the buildup of soil N or by the long transit times required for the movement of DIN into the soil water and groundwater or possible obfuscation by the apparent effects of drought on DIN movement and export. The secondary increase in DIN followed several years of severe drought (1984–1988) and was attributed to the infestation of *Robinia* by a native pest, the locust stem borer, leading to widespread *Robinia* mortality within the harvested watershed (Boring et al., 2014; Elliott, Boring, Swank, & Haines, 1997). Again a relatively rapid recovery was expected (Swank & Vose, 1997). However, by 20 years postharvest, stream DIN was twice as high as the original pulse. In fact, this period of high DIN export (for a forested watershed) persisted more than 20 years, until at

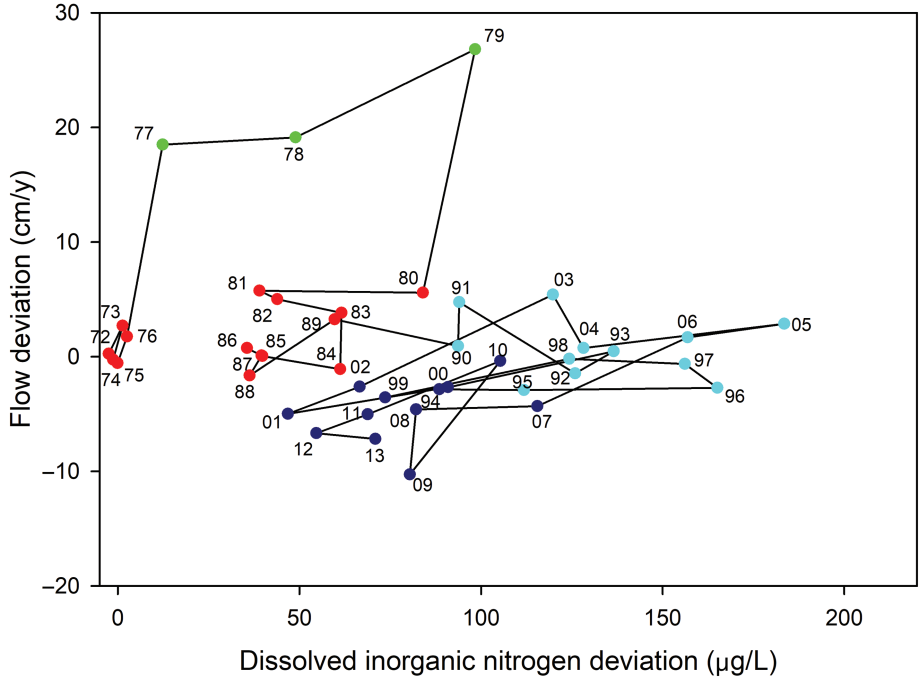

FIGURE 3 Progression of annual DIN and discharge deviation between Coweeta Watersheds 7 (treatment) and 2 (reference) from 1973 to 2013. The discharge deviation is the difference between the observed WS7 flow and that predicted from WS2 based on the pretreatment model. The DIN deviation is WS7 DIN–WS2 DIN. Each point is marked by the last two digits of the year. Symbol colors denote separate clusters identified by k-means clustering by year. Green points encompass the initial watershed response (1977–1979) featuring large increases in water yield and moderate nitrogen release after harvest. Red points encompass the preharvest period (1972–1976), but also a period when the watershed seemed to be returning to preharvest conditions (1980–1988) after the initial response. Light blue points encompass the period of high DIN concentrations (1990–1998) due to nitrogen fixation following the emergence of *Robinia* as a dominant forest tree. Dark blue points encompass the most recent period (1999–2013) featuring lower streamflows and DIN. These latter two periods suggest interactions between droughts and DIN. The data do not yet indicate a move back to the initial condition

least 2008 (Figures 2 and 3). Long duration of elevated DIN export suggests either (a) large pools of N in soil or wood are slowly converting to nitrate over time, (b) groundwater DIN transport times are long, or (c) the remaining stands of *Robinia* are well connected to the stream system and still fixing nitrogen. These alternate explanations are not mutually exclusive. *Robinia* does not produce nitrogen-fixing nodules when nitrogen is not limiting, so it is currently unknown if and when *Robinia* quit contributing to elevated DIN exports, and this question has motivated ongoing research.

One of the problems of paired watershed studies, such as the WS7 logging study, is separating responses to the initial disturbance from responses to long-term changes in external drivers, which may not be adequately addressed by the paired watershed response. The large swings in DIN concentration in WS7 (Figure 2) suggest a relationship between DIN concentration and drought periods in 1984–1988, 1999–2001, and 2006–2008. The large swings in DIN concentration in WS7 following several years of high or low precipitation (Figure 2) probably occurred because biological nitrogen uptake became nitrogen saturated (Aber, Nadelhoffer, Steudler, & Melillo, 1989) both terrestrially and in the stream (Webster, Newbold, & Lin, 2016). This relationship with precipitation trends is not evident in WS2, the reference watershed, due to high nitrogen retention.

During this period of persistently high DIN concentrations with significant increases following drought, the relationship between stream DIN and streamflow suggests the watershed shifted to a regime in which DIN export is regulated by hydrologic not biogeochemical (soil N production, plant uptake, and stream production and uptake) processes (Webster, Knoepp et al., 2016). This is evident by the reversal of the DIN versus flow relationship (Webster, Knoepp et al., 2016) and suggests that the short-lived profusion of black locust followed by a shift in the overstory species composition pushed the watershed into a condition of N-saturation and hydrological control of DIN export. Under hydrological control, DIN concentrations were positively correlated with streamflow, and this was true at short-term, seasonal, and annual timescales (Webster, Knoepp et al., 2016). The lowest DIN concentrations occurred during seasonal low flows and during droughts. Interactions of drought with stream DIN export became somewhat apparent following the 1984–1988 drought and became more accentuated with each drought until 30 years postharvest, when two extreme droughts occurred (1999–2001 and 2006–2008, Figure 2). Conversely, in both preharvest and reference watersheds, annual DIN concentrations were negatively correlated with annual precipitation and streamflow. Without 37 years of data, we would have been unable to distinguish the long-term, biologically driven increase of WS7 DIN concentration and export from the response to approximately decadal precipitation cycles.

Long-term collections of soils in both the clearcut and reference watersheds suggest that changes in soil organic matter are occurring. Following harvest, surface soil (upper 30 cm) total C and total N increased along with soil-available N (upper 10 cm) (Knoepp, Swank, & Haines, 2014). The increase was short lived and was followed by declines in total C and N in the 10–30 cm layer until the 1990s, and then stabilization. The long-term decline in total C and N suggests a change in soil organic matter quality over time. Interestingly, this decline also occurred in the reference watershed; neither watershed had a change in the soil total C:N ratio. Evidence of organic matter movement within the soil profile coupled with evidence from ^{15}N signatures in tree core segments in the treated watershed (Knoepp, Taylor, Boring, & Miniat, 2015) suggests long-term increases in soil N availability in the harvested watershed compared to the reference. The large inputs of N due to *Robinia* N-fixation along with logging residue inputs coupled with changes in the vegetation community may have worked together to change soil organic matter chemistry and shift patterns of N retention and export in the clear-cut watershed.

Streamwater nitrate-N varies spatially within the treatment watershed's stream network (Figure 4) perhaps lending insight into the source of elevated DIN measured at the WS7 outlet over time. Throughout repeated surveys from 1977 to 2008 in the postlogging period, stream nitrate-N concentrations were consistently highest at the top of the main stream channel, with variable inputs from tributary streams, and generally decreasing concentrations going downstream. The spatial arrangement of streamwater nitrate-N suggests that a large part of the N signal was coming from a relatively small area in the upper portion of the watershed, above the start of the main channel. Visual surveys of this area reveal a surviving stand of *Robinia* at this location. This point represents a hotspot (McClain et al., 2003) of nitrogen production in the terrestrial system, suggesting the headwaters area may be a major source of stream nitrate.

Even though slow groundwater dynamics at Coweeta may not be responsible for explaining long-term trends in stream nitrate concentrations, long transit times associated with flow through deep soils and saprolite may be complicating interpretations of DIN in WS7. Except for the highest elevation ridges, Coweeta catchments tend to have deeply weathered soils and saprolite. Soils can range in depth from 1 to 2 m with another 6 to 23 m of saprolite layered between these soils and bedrock (Knoepp et al., 2015; Swank & Douglass, 1975; Velbel, 1988). Together with deep colluvium deposited in convergent landscape positions (Price et al., 2011), these subsurface environments have the potential to store and conduct large amounts of water relative to the small size of Coweeta's first-order catchments (on the order of 10 ha) and their steep slopes (average catchments slopes range from approximately 20 to 30°), all properties that produce continuous streamflow and long-term responses to precipitation. Foundational experiments at Coweeta recognized the large subsurface storage capacity of Coweeta

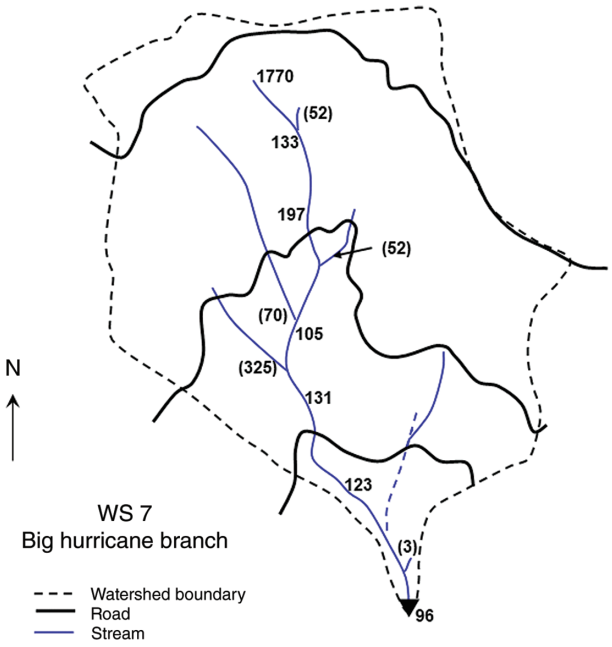

FIGURE 4 Map of WS7 nitrate-N concentrations (μg/L) across the stream network in 2008. Numbers in parentheses are tributary concentrations, and numbers not in parentheses are concentration in the main stream. Patterns were basically the same in sampling that occurred in post treatment sampling in 1977–1978, 1999, 2004, and 2008. The increase in nitrate at the headwater spring was first observed in April 1977, just after logging in January–February. The 2004 samples were taken as part of the LINX project(LINX Colaborators, 2014)

catchments and linked this property to streamflow generation and long-term responses to precipitation (Hewlett & Hibbert, 1963, 1967).

Motivated by this earlier work at Coweeta, Nippgen, McGlynn, Emanuel, and Vose (2016) analyzed 20 years of hydroclimatic data from Coweeta and found that streamflow responses lagged behind precipitation inputs by time periods ranging from a few months to 1 year in deep-soiled, low elevation catchments. The same study found that antecedent catchment water storage (i.e., the relative storage state at the beginning of a year) helped explain deviations from a simple, linear relationship between annual precipitation and annual streamflow. A high-elevation catchment at Coweeta with shallower soils and steeper slopes did not exhibit the same lag behavior and explanatory power in antecedent water storage (Singh, Emanuel, & McGlynn, 2016), emphasizing that subsurface water storage, and the slow release of this water to streams, are key factors responsible for lag and memory effects on rainfall-streamflow behavior in the lower elevation portions of the Coweeta basin. Analysis of the isotopic composition of baseflow within the same low elevation south-facing catchments revealed that the entire catchment did not contribute proportionately to baseflow through time (Singh, Emanuel et al., 2016). Rather, topographic characteristics (e.g., area, length) helped determine the extent to which an individual hillslope influenced the overall composition of baseflow at a particular point in time. Given that stream DIN originates from soil water that can have long travel times in catchments (Nippgen et al., 2016) and that these travel times are influenced by the topography of hillslopes in which those soils are situated (Singh, Emanuel et al., 2016), it comes as no surprise that the hydrological drivers of DIN dynamics are complex.

Forest harvest and subsequent changes in species composition and tree growth continue to affect annual water yield (Q) from WS7, 40 years after harvest. Immediately after harvest, annual Q increased 266 mm (28%) above that expected had the harvest not occurred (Figure 5) (Swank et al., 2014). The increase in annual Q quickly declined over 5 years as vegetation reestablished, and for 10 years, flows were within prediction intervals based on reference stream flows. However, a reduction in stem density and leaf area due to competition, pests, and diseases (Boring et al., 2014) occurred in water year 1992 (15 years after harvest), resulting in a single year in which Q was significantly greater than expected (+68 mm, 8%). For another 15 years, annual flows fluctuated within prediction intervals. Beginning in water year 2007 (30 years after harvest) and continuing to 2016 (39 years after harvest), Q was less than expected every year and significantly less in four of the 10 years. These early and intermediate results are consistent with other examinations of water yield changes observed after watershed clearcutting and regeneration in which Q increases quickly after harvest and then declines quickly as the forest regrows (Andreassian, 2004; Bosch & Hewlett, 1982). Q typically returns to pretreatment levels in 3–10 years depending on climate and forest type. However, only a few water yield studies have run long enough to examine water budget changes in later seral or management states. Others have also observed late-stand reductions in growing-season Q (Adams & Kochenderfer, 2014; Perry & Jones, 2017), but the number of such observations is too small and the range of responses too large (Adams & Kochenderfer, 2014; Hicks, Beschta, & Harr, 1991) to generalize about conditions leading to reductions in Q later in stand development. Again, terminating the research at any time within the first 30 years after harvest would have produced an incomplete story about the potential effects of forest succession on water yield.

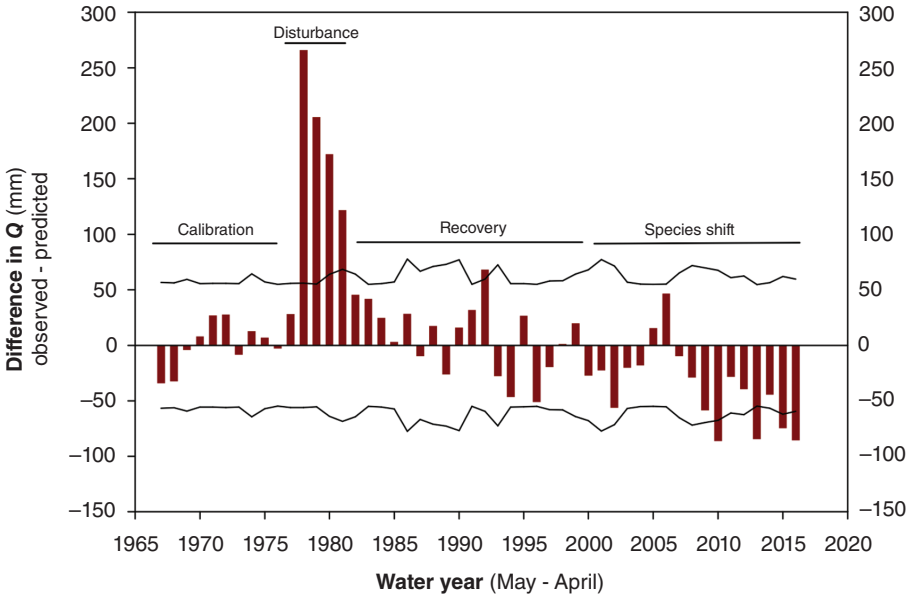

FIGURE 5 Changes in annual water yield (Q) from WS7 between water years 1967 and 2016 (bars), and the prediction intervals evaluated at $\alpha = .05$ (lines). Changes in Q that lie outside prediction intervals are significant. Predicted WS7 yield in the absence of treatment was estimated by fitting a linear model of treatment to reference watershed Q during the calibration period and using this model to predict what would have been WS7 Q in the posttreatment period. Data are previously published (Swank et al., 2014) but updated to include 2013–2016

The recent reductions in Q are consistent with the long-term changes in forest species composition observed in WS7 (Figure 1). Water use differs among tree species due to differences in age, size, and sapwood characteristics. Species with a ring-porous xylem anatomy (e.g., *Quercus*) have less functional sapwood area and thus transpire less water for a given stem diameter than species with a diffuse-porous xylem (e.g., *Liriodendron* and *Acer*), semi ring-porous xylem (e.g., *Carya*), and tracheid xylem anatomies (e.g., *Pinus*) (Ford, Hubbard, & Vose, 2011; Ford, Laseter, Swank, & Vose, 2011). Thus, the changes in species composition in WS7 resulted in increases in ecosystem water use and decreases in Q. This pattern has borne out on other catchments with disturbance histories that shift species to those with higher water use (Boring et al., 1988; Hornbeck, Martin, & Eagar, 1997). Even in unmanaged reference watersheds, slow, subtle species shifts to those that use more water have been shown to reduce Q (Caldwell et al., 2016).

The long-term records of Q (Figure 5) and vegetation dynamics (Figure 1) provide an opportunity to examine the cumulative effects of reforestation on surface water supplies; rather than simply the effects of clearcutting. For example, had Q measurements been discontinued 10 or even 30 years following harvest, it could have been logically assumed that Q had returned to preharvest levels and would remain there in perpetuity, and that the changes in species composition had a negligible effect on Q. Only by continuing measurements beyond 30 years was it shown that the changes in species composition through early- and later-successional dynamics that differed from the reference watershed led to an eventual significant decline in Q relative to what would be expected had the harvest not taken place.

4 | SELECT MANIPULATIVE RESEARCH MOTIVATED BY THESE LONG-TERM DATA

By practical necessity, watershed-scale manipulations tend to have a black-box quality. There are not enough resources for monitoring at high enough spatial and temporal resolution to clearly define internal watershed processes contributing to the observed time series of water and solute exports. Furthermore, it is difficult to hypothesize about mechanisms before seeing the watershed response. To elucidate the mechanisms behind dynamic biogeochemical responses to watershed-scale disturbance, more focused experiments and observations were required as exemplified below.

Clearcutting WS7 caused major changes in the stream macroinvertebrate community, including a decrease in production by detritus-consuming insects and an increase in production by insects that feed on algae (Gurtz & Wallace, 1984; Wallace & Ely, 2014). Because of the multiple effects that logging had on the stream, however, it was unclear whether the community changes were due to the alteration of detrital inputs, increased stream nutrients, increased sediment, altered light inputs, channel position, or some other factor (Wallace & Ely, 2014). The uncertainty about mechanisms driving stream invertebrate responses was a major motivation of an experimental exclusion of litter inputs to a small stream (Wallace, Eggert, Meyer, & Webster, 1997, 1999). Without leaf detritus, macroinvertebrate production in mixed stream substrates declined to near zero within a few years but also rebounded quickly after leaf reintroduction (Wallace, Eggert, Meyer, & Webster, 2015). Litter exclusion had strong bottom-up effects on macroinvertebrate communities, which propagated from detritivores to predators.

The WS7 experiment also indicated that elevated nutrients had effects on leaf litter and basal resources. Subsequent, experimental additions of N and P into streams (Rosemond et al., 2015) revealed that nutrient addition reduced C:N and C:P

ratios of leaf litter and accelerated breakdown rates, increased carbon losses, and altered the timing of basal resource availability (Manning et al., 2015, 2016).

5 | LONG-TERM RESEARCH CHALLENGES

Observations from long-term experimental manipulations often suggest that additional measurements would have been helpful to understanding the system. Since there is no way to recover things you should have measured before you started, long-term experimentalists are limited by their initial hypotheses. In the case of WS7, hindsight would have expanded the suite of measurements to include other variables including stream sediment particle size distributions and groundwater chemistry determined from well samples (no wells were installed). Additionally, long-term research must be coupled with short-term studies that help elucidate mechanisms behind trends observed in long-term data.

The conceptual idea behind paired watershed experiments is that stream exports and biogeochemical dynamics integrate processes across the whole watershed, but these processes may be highly spatially variable. Regarding biogeochemical exports, the experimental design did not allow resolution of the effects of spatial heterogeneity in soils, vegetation, and topography (Bailey, Brousseau, McGuire, & Ross, 2014; Ford, Hubbard et al., 2011; Gillin, Bailey, McGuire, & Gannon, 2015; Singh, Emanuel et al., 2016). Synoptic sampling of DIN across the WS7 stream network indicates that a large amount of the DIN originates in a single hotspot where subsequent observations revealed a stand of surviving *Robinia.* Planning for long-term experiments should balance the need to coordinate measurements on multipurpose plots while minimizing sampling effects on these plots. In the WS7 experiment, vegetation plots and soil plots were not co-located, impeding our ability to connect vegetative and soil changes.

Changes in monitoring technology and analytical techniques are a challenge for all long-term experiments (Dodds et al., 2012). A recent analysis of 25 years of stream DOC from Coweeta's Watershed 27 serves to illustrate. Approximately halfway through the study, researchers migrated analytical methods from persulfate oxidation to high temperature combustion (Meyer, Webster, Knoepp, & Benfield, 2014; Singh, Reyes et al., 2016). Researchers used more than 100 samples collected over a 1-year period and analyzed using both techniques to build a robust empirical relationship between methods, but the method change itself added new uncertainty to analyses and interpretations involving long-term dynamics.

During the long-term monitoring of WS7 and its reference stream, WS2, unplanned and unanticipated disturbances affected both watersheds, complicating inference. Our long-term data suggest that ongoing climate change is affecting the seasonality and variability in precipitation and increasing annual air temperatures (Laseter, Ford, Vose, & Swift, 2012), rendering it difficult to isolate water balance responses to forest changes (Kelly, McGuire, Miniat, & Vose, 2016). Furthermore, we have observed mesophication of the forests in the region, with increasing dominance of tulip poplar and red maple (Caldwell et al., 2016). For currently unexplained reasons, DIN concentrations in the reference stream crept upwards during the monitoring period.

Focused manipulation experiments provide apparently strong inference by controlling covariates and isolating specific effects, but this inference may not be scaleable to whole ecosystems (Schindler, 1998). Large-scale manipulations, like the WS7 experiment, cannot be replicated but have the advantage of directly incorporating ecological interactions and indirect effects operating at larger spatial and temporal scales (Schindler, 1998). If we want to understand larger-scale ecosystem behaviors, we need conceptual frameworks and analytical tools that embrace the interactions. With respect to forest demographics, the Coweeta LTER has made some progress in this area (Clark, Bell, Kwit, & Zhu, 2014; Clark, Nemergut, Seyednasrollah, Turner, & Zhang, 2017), but understanding interactions and indirect effects in other types of data remains a challenge.

6 | CONCLUSIONS

For the first 12 years following watershed road building, forest harvest, and forest regeneration, streamflows and DIN concentrations temporarily increased and then began returning to preharvest behavior, in accordance with ecosystem resistance and resilience ideas. Then the surprises emerged. Unexpected successional changes in forest composition interacted with pests, diseases, drought cycles, and climate change to shift the biogeochemical system into an alternate nitrogen-cycling regime featuring persistently high DIN concentrations and hydrological rather than biological control of DIN exports. Thirty years after harvest, these later forest composition changes also increased evapotranspiration and reduced water yields. These ecosystem dynamics, and the novel manipulative mechanistic research they inspired, were only revealed because of long-term monitoring. Suspension of monitoring at any time in the first 40 years after disturbance would have produced incomplete and erroneous inference. While not allowing for replication, this large-scale manipulation incorporated abiotic and

biotic interactions and complexities beyond what would have been possible in replicated plots. Although long-term and large-scale research certainly features challenges, such as changes in technologies, unplanned disturbances, and drawing inference without replication, long-term and larger-scale approaches are critical for understanding the effects of perturbations on ecosystem dynamics and the effects of management on water quality and quantity.

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Conflict of interest

The authors have declared no conflicts of interest for this article.

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