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Can't See the Forest for the Stream? In-stream Processing and Terrestrial Nitrogen Exports

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There has been a long-term decline in nitrate (NO_3^-) concentration and export from several long-term monitoring watersheds in New England that cannot be explained by current terrestrial ecosystem models. A number of potential causes for this nitrogen (N) decline have been suggested, including changes in atmospheric chemistry, insect outbreaks, soil frost, and interannual climate fluctuations. In-stream removal of NO_3^- has not been included in current attempts to explain this regional decline in watershed NO_3^- export, yet streams may have high removal rates of NO_3^-. We make use of 40 years of data on watershed N export and stream N biogeochemistry from the Hubbard Brook Experimental Forest (HBEF) to determine (a) whether there have been changes in HBEF stream N cycling over the last four decades and (b) whether these changes are of sufficient magnitude to help explain a substantial proportion of the unexplained regional decline in NO_3^- export. Examining how the tempos and modes of change are distinct for upland forest and stream ecosystems is a necessary step for improving predictions of watershed exports.

Keywords: ecosystem change, HBEF, nitrate, nutrient retention, stream ecosystems

The watershed ecosystem concept as originally formulated stated that "the vegetation of a watershed and the stream draining it are an inseparable unit functionally" (Bormann and Likens 1967). In practice, however, watershed mass-balance studies typically treat the stream ecosystem as nonfunctional with respect to nutrient retention or transformation, using watershed budgets to make inferences about the terrestrial system (e.g., Vitousek and Reiners 1975, Goodale and Aber 2001). Because stream ecosystems can alter the timing, magnitude, and form of nutrient transport (Meyer et al. 1988), treating the stream as a "pipe" may lead to erroneous conclusions about the role of the terrestrial system. A growing body of evidence demonstrates the importance of in-stream processing in regulating nitrogen (N) export (Alexander et al. 2000, Peterson et al. 2001, Bernhardt et al. 2003), suggesting that future watershed studies of N cycling must either explicitly include the stream ecosystem as an integral component in influencing watershed exports, or attempt to separate stream and upland control of export amounts and patterns.

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In neglecting in-stream processing as a driver of watershed N export, it is assumed (a) that in-stream processing of N is quantitatively unimportant, or (b) that the rates, pathways, and processes influencing stream N cycling change in concert with the terrestrial system. It is becoming clear that the first of these assumptions cannot be met, because in-stream processing occurs and can remove large amounts of N relative to watershed export (Bernhardt et al. 2002, 2003, Mulholland forthcoming). However, little attention has been devoted to testing the second assumption, despite a large body of literature examining how ecosystem change in terrestrial ecosystems will affect nutrient losses (e.g, Vitousek et al. 1979, Reiners 1981, Aber et al. 1998). There has been relatively little research on long-term changes in stream ecosystem structure and function in general, and in temperate-zone streams in particular (Fisher 1983). Fisher (1983) suggested that streams are unlikely to undergo long-term change in ecosystem structure and function, since most stream organisms are short-lived and streams are frequently disturbed by floods or droughts. However, when forests are cut, the streams that drain them are also disturbed, and do not return to predisturbance conditions for many years (Webster and Patten 1979, Golladay et al. 1992, Valett et al. 2002). The converse rarely occurs. Disturbance of streams by floods, debris flows, and litterfall deprivation can greatly influence the stream ecosystem without affecting the upland component of the watershed (e.g., Fisher, et al. 1982, Wallace et al. 1997). As a result of these disturbances, stream organic accumulations (and hence N cycling) fluctuate over decadal time scales, potentially causing long-term shifts in export.

Given evidence from recent research showing that biogeochemical processes in stream ecosystems can profoundly alter the concentration and transport of chemicals in streamwater, it is possible that changes over time within stream ecosystems could modify the long-term patterns of element export from a watershed. Long-term studies at the Hubbard Brook Experimental Forest (HBEF) in the White Mountains of New Hampshire provide a unique opportunity to examine whether nutrient cycling in stream ecosystems has changed over time and, if so, how this change has affected watershed export. Stream research at HBEF has taken both comparative and experimental approaches since the 1960s (*www.hubbardbrook.org*). There are almost 40 years of data available at various spatial and temporal scales to evaluate change in stream ecosystem function. Despite the wealth of studies on this ecosystem, gaps exist, and in some instances we rely on anecdotal evidence.

One of the reasons we have become interested in the influence of in-stream processing on landscape-scale N fluxes is the recent discovery of the remarkable decline in nitrate (NO_3^-) concentration and export from several watersheds throughout New England with long-term monitoring records (Aber et al. 2002, Goodale et al. 2003, Stoddard et al. 2003). This decline cannot be explained by current terrestrial ecosystem models (Aber et al. 2002). At HBEF, where streamwater NO_3^- data have been collected weekly since 1963, the lowest levels of annual NO_3^- export on record were observed during the 1990s (figure 1a). This decline is remarkable, because HBEF has not accumulated either aboveground biomass (measured directly) or belowground biomass (estimated by allometric equations) since 1982 (Likens et al. 1994), and atmospheric inputs of N have remained relatively constant since 1970 (Likens and Bormann 1995)—conditions that would be expected to lead to a surplus of N in these watersheds. Indeed, this decline contradicts long-standing theories of forest ecosystem development (which predict that as biomass accumulation slows, N export must increase if N inputs remain the same; Vitousek and Reiners 1975) and of N saturation (which state, in part, that forests have a finite capacity to assimilate N; Aber et al. 1998).

Several potential causes for this N decline have been suggested, including changes in atmospheric chemistry, insect outbreaks, soil frost, and interannual climate fluctuations (Goodale et al. 2003, forthcoming, Huntington forthcoming). Incorporating actual data on atmospheric chemistry and climatic variability into an ecosystem simulation model, however, failed to predict accurately the low NO_3^- concentrations in streamwater during the 1990s (Aber et al. 2002). In fact, Aber and colleagues (2002) found that model estimates of NO_3^- export from the reference watershed (Watershed 6 or Bear Brook) at HBEF exceeded actual export values by approximately 250% during this period (figure 1b). The dramatic declines in streamwater NO_3^- concentration and export at HBEF since 1965, and the inability of current terrestrial ecosystem models to explain these declines, suggest the need to identify new mechanisms to help explain the pattern.

Temporal patterns in nitrate export

During the first decade of the Hubbard Brook Ecosystem Study (1965–1974), streamwater NO_3^- concentrations averaged 0.40 ± 0.18 milligrams (mg) N per liter (L) (an average of the annual volume-weighted concentrations ± one standard error). Throughout the last decade (1993–2002), annual streamwater NO_3^- concentrations fell to 0.09 ± 0.07 mg N per L (figure 2a). There was no change over this entire period in hydrologic yield (figure 3a); thus, the total annual export of NO_3^- from the HBEF reference watershed has declined considerably over the 40-year record, from 3.61 ± 0.64 kilograms (kg) N per hectare (ha) per year during the first 10 years (1965–1974) to 0.85 ± 0.24 kg N per ha per year during the last decade (1993–2002) (figure 2b).

Throughout this long-term record of general decline in NO_3^- concentrations, there have also been dramatic increases in NO_3^- export in response to specific watershed disturbances. These losses of NO_3^- during the 1970s are linked to several factors: (a) a severe drought through much of the 1960s, (b) severe insect defoliation during 1969–1971 (Bormann and Likens 1979, Aber et al. 2002), and (c) a soil freezing event (Likens and Bormann 1995, Mitchell et al. 1996). Another soil freezing event in 1989 contributed to the high export in 1990 (Mitchell et al. 1996). The increase in export in 1998 and 1999 was the result of a severe ice storm in Jan-

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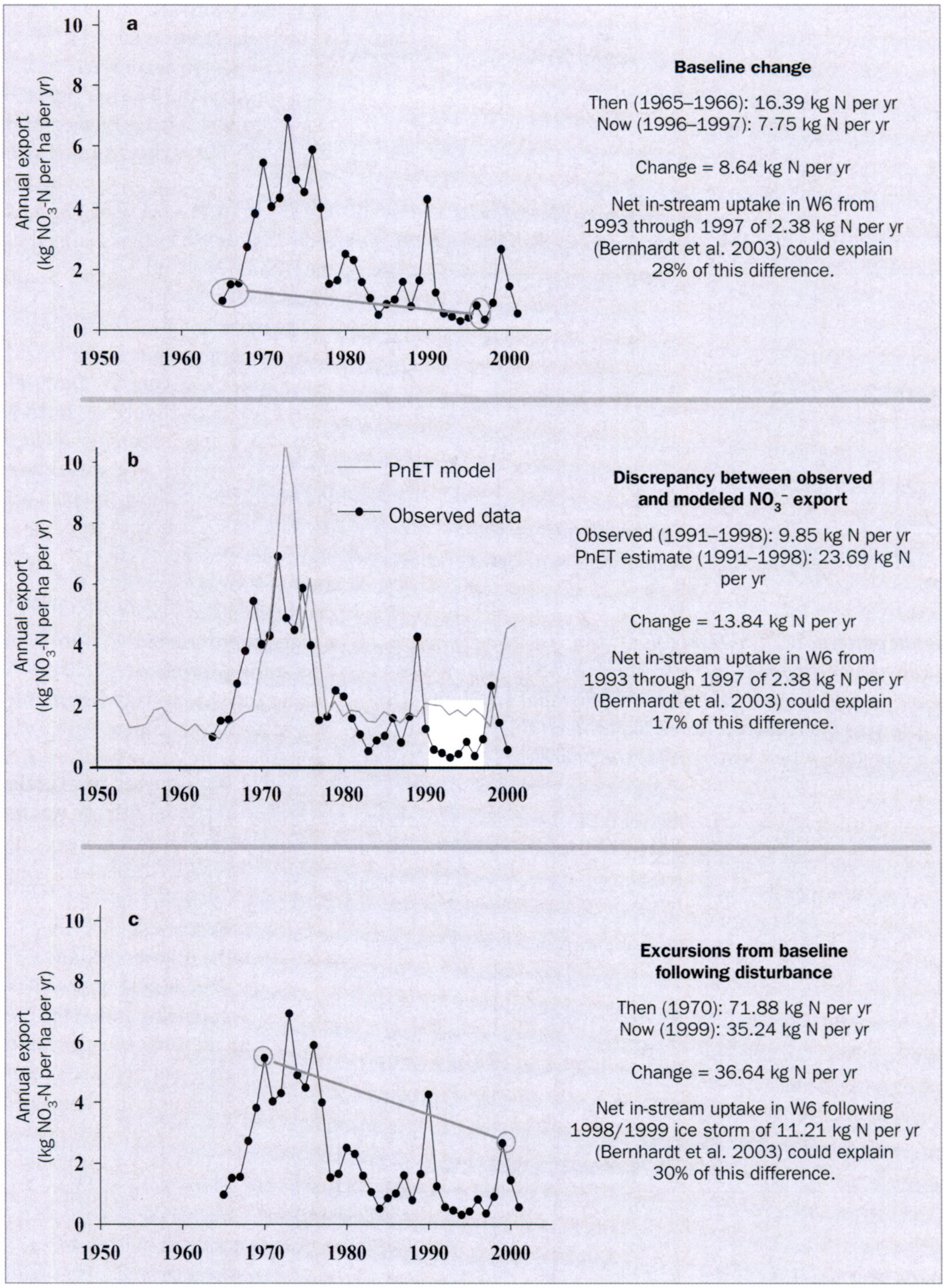

Figure 1. Comparison of estimated changes in stream nitrate (NO_3^-) cycling and different features of the long-term patterns in NO_3^- export, with estimates of what proportion of these differences could be accounted for by incorporating measures of in-stream uptake of NO_3^-. (a) Comparison of NO_3^- export between years in which there was no significant watershed disturbance that exacerbated nitrogen (N) losses. (b) Comparison of observed patterns of NO_3^- export with modeled predictions from the PnET model (Aber et al. 2002). (c) Comparison of declines in disturbance-associated NO_3^- losses and NO_3^- uptake estimates from the years following the 1998 ice storm. Abbreviation: W6, Watershed 6.

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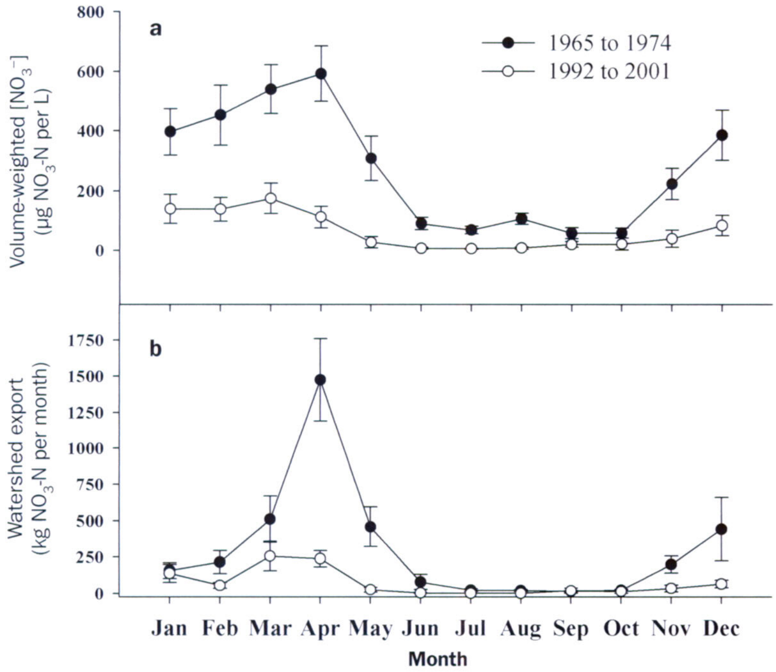

Figure 2. Seasonal patterns of (a) nitrate (NO_3^-) concentration (micrograms of nitrogen as NO_3^- [NO_3-N] per liter) and (b) NO_3^- export (kilograms NO_3-N per month) compared between the first and last decades of the long-term record at the Hubbard Brook Experimental Forest. Note that both decades include major watershed disturbances.

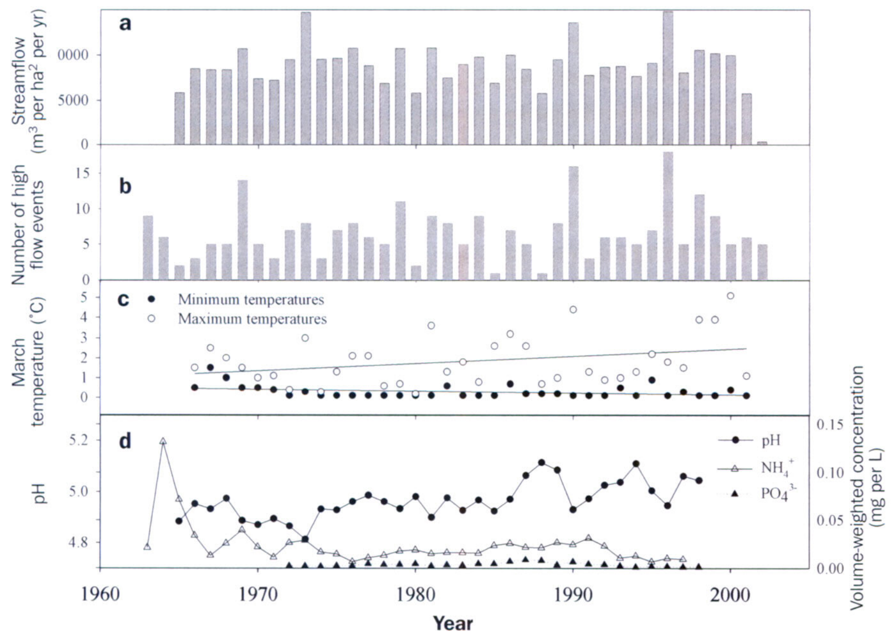

Figure 3. Physical changes in the Watershed 6 stream at Hubbard Brook Experimental Forest: (a) annual streamflow, (b) number of high flow events each year (days in which flow exceeded the long-term average daily flow by more than three standard deviations), (c) change in streamwater minimum and maximum temperatures during March (the only month in which a significant temporal change was detected), and (d) pH and volume-weighted concentrations of ammonium (NH_4^+) and phosphate (PO_4^{3-}).

uary 1998, which substantially damaged the canopy at high elevations within HBEF (Houlton et al. 2003). Floods can also increase NO_3^- losses from the watershed, but these do not appear to drive annual export patterns at HBEF. For example, the two years with the highest annual streamflow, 1973 (14,702 cubic meters [m^3] per ha per year) and 1996 (14,794 m^3 per ha per year) (figure 3a), had annual NO_3^- export values that spanned the full range of the record (30.4 and 3.6 kg NO_3^- per ha per year, respectively).

The majority of each year's export of NO_3^- occurs during spring snowmelt, from March to May, when both NO_3^- concentrations and stream discharge are high (figure 4). In most years, more than 50% of the total annual NO_3^- flux is lost during these 3 months (an average of 68% ± 3%, ranging from a low of 21.6% to a high of 90.6%) (figure 4). The long-term pattern of NO_3^- loss during snowmelt closely matches the declining trends in annual fluxes, with NO_3^- flux declining significantly from the 1960s to the 1990s. Because such a high proportion of the annual yield of NO_3^- occurs during spring, small changes in the N cycle during this season could significantly affect annual watershed N export.

Hypotheses to explain the regional nitrate decline

Several mechanisms have been proposed to explain the long-term pattern of declining NO_3^- concentrations in streamwater at HBEF, and particularly the inexplicably low values during the past decade or so (figures 1, 2). One possibility is that the increased uptake and storage in upland soils and terrestrial plant biomass result in less NO_3^- being leached from the upland to the stream. This may be due to the maturation of vegetation and the buildup of soil carbon (C) pools in this area, following the widespread harvest of forests and the subsequent abandonment of areas cleared for agriculture during the early 1900s (e.g., Likens 1985). The gradual buildup of soil organic matter (SOM) during this recovery process may have increased N storage in soils (Huntington forthcoming), but SOM is a large and spatially variable pool with no quantitative data prior to 1960, and therefore the buildup of N in SOM cannot be evaluated directly. At the same time, forests at HBEF have not accumulated biomass since 1982 (Likens et

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al. 1994), and thus it is unlikely that more N is retained in tree biomass.

Another possible mechanism for declining NO_3^- levels in streamwater is climate change and its relationship to forest disturbance. However, ecosystem models that include local climatic variation have failed to explain the anomalously low NO_3^- export of the 1990s. Thus, climate variation, as currently modeled and interpreted, cannot fully explain the current low streamwater NO_3^- concentrations (Aber et al. 2002). Nonetheless, climate is clearly a complex factor and one that deserves further investigation.

Disturbance of forest ecosystems (e.g., soil frost, defoliation, tree disease, and ice storms) tends to increase streamwater losses of NO_3^- (e.g., Likens et al. 1970). Thus, less frequent or less intense disturbances may reduce disturbance-induced losses of N over time. However, disturbance frequency does not appear to be decreasing. There is no record of soil freezing events decreasing in frequency at HBEF since 1963. Indeed, soils are predicted to freeze more frequently as air temperatures increase because of global warming, since warmer temperatures in the winter will reduce the insulating snow cover that prevents soil freezing (Groffman et al. 2001). There is increasingly widespread tree disease at HBEF, but this disturbance should cause the opposite pattern (i.e., increased NO_3^- concentrations in streamwater). The last major insect defoliation occurred from 1969 to 1971 (Bormann and Likens 1979, Aber et al. 2002), many years before the recent decline of NO_3^-, and has not recurred.

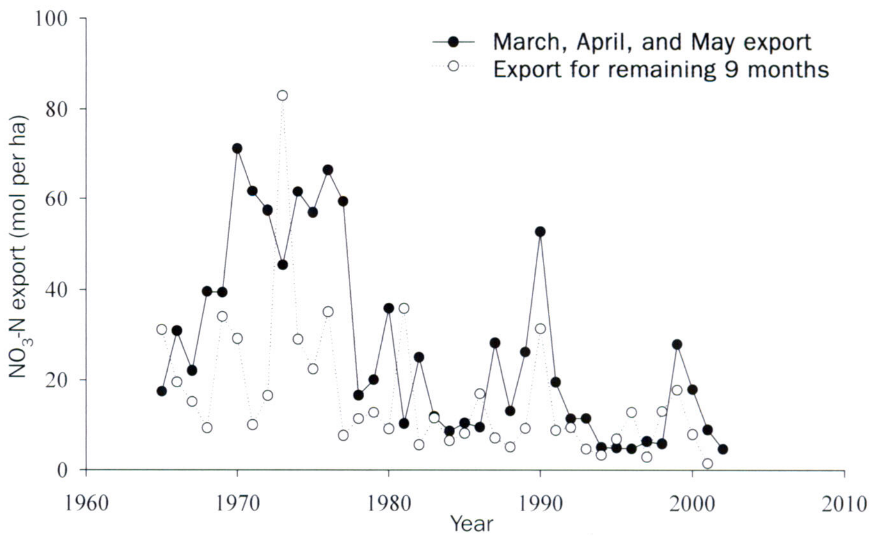

Figure 4. Spring nitrate export (grams of nitrogen as nitrate [NO_3-N] per hectare) compared with export from the rest of the year.

In-stream processing of NO_3^-, although of demonstrated importance in regulating watershed NO_3^- export (Alexander et al. 2000, Peterson et al. 2001), has not been included in current attempts to explain the regional decline in streamwater NO_3^- concentrations across New Hampshire. Despite their small area, streams can be hotspots for N processing (Peterson et al. 2001), with potential for high removal rates of NO_3^-. Gross removal rates of NO_3^- ranged from 0% to 1.5% per m in a survey of North American streams (Peterson et al. 2001). At HBEF, NO_3^- uptake in the small headwater streams is higher because the streams are shallow and slow flowing; removal rates range from 0.4% to 6.5% per m, with an average of 1.5% per m (Bernhardt et al. 2002). Thus, there is high potential for NO_3^- processing along a several-hundred-meter reach of stream at HBEF. For in-stream processing of N to be an important part of the explanation for the long-term NO_3^- decline, there would have to have been a fundamental change in the efficiency of in-stream NO_3^- removal and retention, with streams becoming relatively more effective in net retention in recent years than they were before 1990.

Our objective in this article is to estimate the degree to which changes in stream ecosystem N cycling could account for a substantial proportion of the missing NO_3^- losses. Thus, we address three questions: (1) What changes have occurred in HBEF streams during the past 40 years that may have affected the way that streams retain or transform NO_3^-? (2) Which mechanisms in the stream may have changed in form or function (i.e., rate) that would explain an increased ability to process NO_3^- in HBEF streams? (3) What are the implications of this change in N processing for interpreting the decline in streamwater NO_3^- concentrations and fluxes from streams of HBEF, particularly for interpretations of watershed mass balances?

How have HBEF streams changed?

Bear Brook originates in the 13-ha reference watershed (Watershed 6) at HBEF in the White Mountains of central New Hampshire. Extensive research has occurred throughout the first-, second-, and third-order segments of Bear Brook. The Bear Brook watershed is characterized by second-growth forest (cut ca. 1917) dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). Leaf litter from these trees fuels secondary production in these heterotrophic streams (Fisher and Likens 1973). Discharge varies considerably during the year (from less than 0.5 to more than 100 L per second). The stream channel is characterized by "stair-step" sequences of riffles and pools (Fisher and Likens 1973), and organic debris dams are common features of the channel. Much of the channel has exposed bedrock; thus, the hyporheic zone in this stream is small and shallow.

Bear Brook has changed over the 40-year period of active research. Initial studies found that algae were not present in Bear Brook (Fisher and Likens 1973), but later research found that algae were present throughout the year and that algal blooms now occur during the spring snowmelt period in some years (Bernhardt and Likens 2004). Although there

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may now be additional autotrophic production, there is no evidence to suggest that stream invertebrate biomass has changed appreciably throughout the last four decades. Secondary production estimates conducted in the 1960s derived identical estimates to those conducted in the 1990s (4.2 grams [g] ash-free dry mass per m per year; Fisher and Likens 1973, Hall et al. 2001). Hall and colleagues (2001) documented that predators consume 72% to 92% of the insect production each year. Recent findings that the populations of *Gyrinophilus porphyriticus,* a semiaquatic salamander closely associated with streams, have doubled in abundance between 1972 (0.6 individuals per m^2) and 2002 (1.3 individuals per m^2) could indicate that higher stream insect production is being diverted into predator biomass, but this is not known (Burton and Likens 1975).

Bear Brook may have become more efficient at removing N from the water column during the past 40 years. During the 1970s, there was no evidence of NO_3^- removal for this stream. Indeed, in the 1970s, short-term nutrient release experiments indicated that Bear Brook was a net source of NO_3^-. Ammonium (NH_4^+) added to the stream was rapidly nitrified (oxidized from NH_4^+ to NO_3^-); NO_3^- uptake (assimilation into biota) was low, and not stimulated by C additions (Richey et al. 1985). In contrast, throughout the 1990s, abundant evidence of active NO_3^- removal and transformations was documented (Steinhart et al. 2001, Bernhardt and Likens 2002, Bernhardt et al. 2002, 2003), NO_3^- uptake rates typically exceeded rates of NO_3^- production through nitrification (Bernhardt et al. 2002), and the addition of labile C reduced NO_3^- export from Bear Brook (Bernhardt and Likens 2002). Throughout the long-term record, streamwater NH_4^+ and PO_4^{3-} (phosphate) concentrations have been low (less than 5 parts per billion), and there is no trend with time (figure 3d). Two of us (E.S.B. and W.H.M.) compared the effects of identical releases of leaf leachate on streamwater NO_3^- concentrations in the headwaters of Bear Brook during 1978 and 2000. In 1978, the addition of two labile sources of dissolved organic carbon (DOC)—spruce needle and sugar-maple leaf leachate—did not affect streamwater NO_3^- concentrations or uptake (Richey et al. 1985), whereas in 2000, the addition of similar leachates (at the same concentration) to the same stream immediately lowered streamwater NO_3^- concentrations and increased rates of NO_3^- uptake. This finding suggests that the potential of the stream biota to use NO_3^- and to respond quickly to organic C inputs has changed.

These results suggest that understanding long-term change in stream ecosystems may be fundamental to explaining the long-term decline in NO_3^- export and the overall landscape biogeochemistry of N. We must, however, examine not only whether changes have occurred in in-stream N processing, but also whether those changes are of sufficient magnitude to explain a significant proportion of the long-term decline in NO_3^- export.

In-stream processing of NO_3^- was not measurable in Bear Brook during the early years of the record (Richey et al. 1985). In the late 1990s, repeated measures of NO_3^- uptake in Bear Brook found detectable NO_3^- uptake each time it was measured. We can estimate the gross uptake rate of NO_3^- on an annual basis by multiplying the average mass transfer coefficient for NO_3^- (0.97 millimeters per minute) from 18 nutrient releases conducted in 1998–1999 in Bear Brook (Bernhardt and Likens 2002, Bernhardt et al. 2002) by the daily concentrations of NO_3^- (interpolated between weekly samples) and then summing these daily estimates for an annual estimate. The average annual gross uptake estimate for the years 1993–1999 is 35.5 ± 6.8 g N per m^2 per year, which corresponds to a whole-stream gross uptake rate estimate of 26.7 ± 5.2 kg N per year (assuming a stream area of 750 m^2 from first running water to the weir). This estimate of gross uptake exceeds net annual watershed export for the same period (approximately 10 kg NO_3-N per year). Even if this overestimated in-stream activity greatly (since it is based primarily on NO_3^- uptake measured during the growing season under low flow conditions), it would still suggest that much of the NO_3^- entering Bear Brook is processed multiple times before its export. Thus, even a small change in the fate of that processed N could lead to large changes in N export.

Gross uptake rates cannot be equated with net retention, since NO_3^- may be rapidly transformed and rereleased to the water column. For this reason, it is much more difficult to estimate net uptake rates. Bernhardt and colleagues (2003) used a reach mass-balance approach to estimate a net NO_3^- uptake rate of 2.4 kg N per year in Bear Brook by subtracting NO_3^- flux at the weir from NO_3^- flux at a sampling point 200 m above the weir. These estimates were based on data from samples collected at both stations on the same day at approximately monthly intervals during 1993–1997. This net uptake represents a measure of long-term (at least 1-year) storage or removal of NO_3^- within the stream bed.

If we were to assume that NO_3^- retention was unimportant during the early years of the record (Richey et al. 1985), and that the rate of retention is now approximately 2.4 kg N per year in Bear Brook, then this change in in-stream processing would explain approximately 28% of the total decline of 8.6 kg N per year in NO_3^- export from Bear Brook between the year-long interval beginning in 1965 and ending in 1966 (16.4 kg N per year) and the interval beginning in 1996 and ending in 1997 (7.8 kg N per year) (figure 1a). We have chosen to compare these two intervals because they are years in which there were no major disturbances that increased NO_3^- export, and thus they represent a baseline of NO_3^- export. (Large increases in N export in the long-term record occurred during the years that followed both intervals, because of rewetting that follwed a severe drought [in 1967] and an ice storm [in 1998].)

We can also compare our estimate of in-stream uptake of NO_3^- with the difference between modeled estimates of NO_3^- output and the actual export. The terrestrial ecosystem model PnET (photosynthesis and evapotranspiration) is a suite of three nested models, which simulate the C, water, and N dynamics of forest ecosystems (figure 5). PnET-Day is the instantaneous canopy flux module. PnET-II adds nutrient

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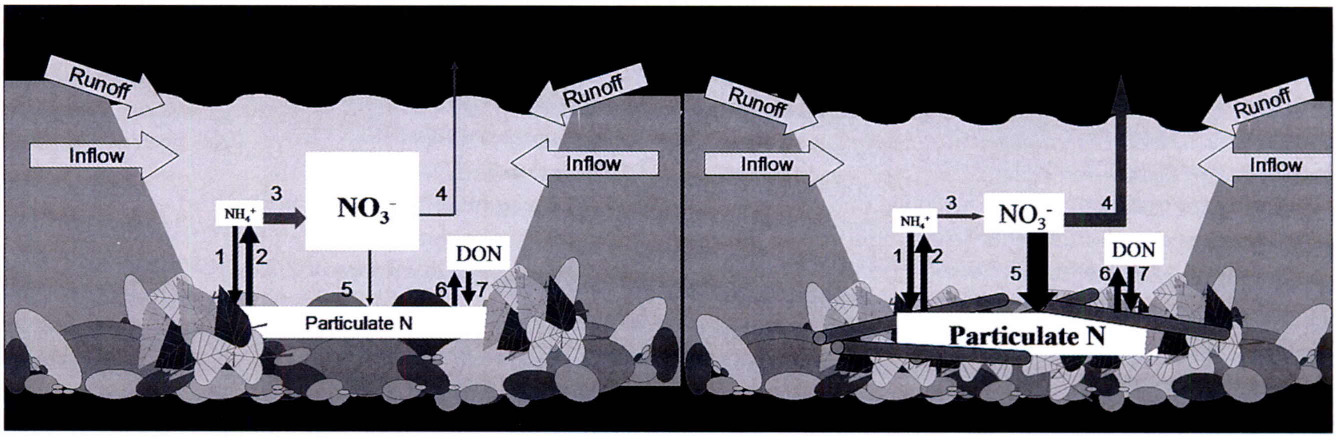

Figure 5. A conceptual model of changes in stream nitrogen (N) cycling as the surrounding forest ages. Transformations between forms of N are indicated by arrows: (1) uptake of ammonium (NH_4^+) through both abiotic sorption and biological assimilation; (2) mineralization of organic N to NH_4^+; (3) nitrification (the oxidation of NH_4^+ to NO_3^- by chemoautotrophic bacteria); (4) denitrification (the reduction of NO_3^- to nitric oxide [NO], nitrous oxide [N_2O], and N_2 by denitrifying bacteria; (5) biotic assimilation of NO_3^-; (6) release of dissolved organic nitrogen (DON) into solution (through leaching of organic material and exudation or excretion of organic molecules); (7) sorption and biological assimilation of organic molecules. In this model we assume that inputs of N to the stream remain constant. If this assumption were met, we would expect faster cycling of N between inorganic and organic forms in streams draining mature forests, due to increased density of debris dams and storage of organic matter. These changes in the channel would increase hydrologic storage and the presence of anoxic zones in the stream bed—conditions that favor storage of particulate N and denitrification of NO_3^-.

allocation, water balance, and soil respiration to produce a monthly time-step C and water model, which is driven by N availability. PnET-CN further extends the soil dynamics component and closes the N cycle by tracking N, along with C, throughout all compartments and fluxes (for more information, see *www.pnet.sr.unh.edu*). This model, which has been applied primarily to temperate-zone forest ecosystems, was used previously to predict N losses from the Bear Brook watershed at HBEF (Aber et al. 2002). An increase in instream NO_3^- uptake of 2.4 kg N per year could explain 17% of the difference (13.8 kg N per yr) between the PnET modeled estimate of NO_3^- output for 1996/1997 (23.7 kg N per year) and the actual export (9.9 kg N per yr) (figure 1b) (John D. Aber, University of New Hampshire, Durham, personal communication, 26 August 2003).

When we consider the major increases in NO_3^- export in the long-term record following major disturbances, we see that there is a similar decline in their magnitude through time (figure 1c). Thus, changes in in-stream processing may be just as important in reducing NO_3^- exports following disturbance (as found by Bernhardt and colleagues [2003]). Nitrate export from Bear Brook in 1970, the earliest year of significant watershed disturbance leading to high NO_3^- export, was 71.9 kg N per year, compared with export of 35.2 kg N per year in 1999, the peak year of NO_3^- loss following the January 1998 ice storm (figure 1c). If in-stream NO_3^- removal rates for Bear Brook increased from 0 in 1969 to 11.2 kg N per year in 1998 (Bernhardt et al. 2003), then the change in in-stream net retention of NO_3^- in response to disturbance would explain 30% of the reduction in magnitude of overall watershed NO_3^- losses following disturbance events (a total reduction of 36.6 kg N per year; figure 1c).

These calculations suggest that (a) gross rates of stream NO_3^- processing (i.e., uptake) are currently high, and (b) changes in stream ecosystem NO_3^- removal may have significantly reduced NO_3^- export in recent years. While these analyses demonstrate the potential importance of long-term change in stream ecosystems, to support this hypothesis, we must examine the potential mechanisms that could cause this long-term change.

What changes in nitrogen retention mechanisms would explain the increased nitrate-processing ability of HBEF streams?

If the annual removal of NO_3^- by Bear Brook increased from 0 to 2.4 kg between 1964 and the late 1990s, there would have to be an increase in N assimilation, with an accompanying increase in the rate of N transformation, in the storage of N within the stream bed, or both (figure 5).

Temporary nitrate uptake mechanisms. The way in which N is processed within streams ultimately determines the fate of NO_3^-. Inorganic N (NO_3^- and NH_4^+) can be removed from the water column if it is (a) immobilized by microbes during the decomposition of organic materials (stored) or (b) assimilated by primary consumers (algae, bacteria, or fungi) and then subsequently transferred to higher trophic levels (assimilated). Even when uptake rates of N are high, turnover of benthic N in stream ecosystems tends to be high, reducing the capacity for long-term in-stream storage of N. Nitrogen stored in the organic matter of a stream bed may be re-

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mineralized and returned to streamwater, or bed materials may be exported as particles during a flood. Longer-term storage of N within hyporheic zones or riparian soils is possible because water moves slowly through these habitats, facilitating uptake by sediment bacteria or terrestrial plants.

We propose that two large changes in HBEF stream ecosystems have occurred, both of which would facilitate N assimilation within stream sediments. The first change is that heterotrophic assimilation of N has increased over time because new organic debris dams have formed as the forest has aged and as tree mortality from disease has increased, leading to higher densities of debris dams in the stream channel. These accumulations of organic-rich sediments serve as hotspots for assimilation and denitrification (Hedin 1990, Steinhart et al. 2001). The increase in flow obstructions within the channel could also potentially increase water residence times, thus increasing opportunities for N removal from the water column (Wollheim et al. 2001, Hall et al. 2002). As the stream channels become geomorphically more complex, benthic storage of N can increase.

An increase in benthic storage could account for a fraction of the missing N. Benthic standing crops of organic matter measured using surface samples average 650 g organic matter per m^2 (Fisher and Likens 1972) or (assuming that 50% of organic matter is C and the average C:N ratio is 30), 10 g of N. Most of this organic material is from leaves originating outside the active stream channel. However, levels of stored benthic N may be much higher. After Bilby (1981) removed benthic wood from the stream draining Watershed 5 at HBEF, particulate N export increased to 31 g N per m^2 of stream bed per year, which provides a minimum estimate of stored N in the channel that was washed out following debris-dam removal. Given this high standing stock, and an observation that the number of debris dams in streams at HBEF is probably increasing (Hedin et al. 1988), there could be net storage of N within the stream bed. Even if this accumulation rate were only 1 g N per m^2 of stream bed per year, it would account for nearly one-third of the 2.4 kg of N processed in the stream each year (table 1). The second major change in streams at the HBEF is that autotrophic assimilation of N has increased, particularly during the period of peak N loss during spring snowmelt. There has been greater algal biomass in HBEF streams within the last decade than was documented previously (Fisher and Likens 1973, Bernhardt and Likens 2004). This change appears to be particularly dramatic during the period of peak N loss (March to May; figure 4). Blooms of filamentous algae, which had not been observed previously, were observed during this period in 1997 and 2000 (Bernhardt and Likens 2004). We suspect that these early spring blooms may be in response to a thinning of the overstory (potentially due to increased tree mortality), leading to higher light levels reaching the stream and warmer temperatures earlier in the spring (higher March streamwater temperature [figure 3] and April air temperature [Likens 2000]). It may be that a slight increase in warmer, brighter conditions before the canopy leaf-out in March allows a window of opportunity for algal populations to bloom. Stream algae may now be acting in concert with forest-floor plants in creating a "vernal dam" (Zak et al. 1990) to reduce losses of N during snowmelt. These warmer temperatures could also increase rates of microbial N uptake during the snowmelt period of peak N loss. An increase in either autotrophic or heterotrophic N uptake could lead to reduced NO_3^- export, either by altering the form of N export (to organic or particulate fractions) or by increasing benthic N concentrations and facilitating denitrification.

Increased N assimilation does not necessarily indicate that the long-term retention of N within the stream channel has increased. Higher assimilation and short-term retention, however, may result in increased rates of N transformation that reduce NO_3^- export. Annual export rates of particulate organic N (PON) for Bear Brook average approximately 1.6 kg per year; however, export in any one year can be highly variable because of flood frequency and magnitude (Bormann et al. 1969, Meyer et al. 1981). For example, PON export from

Table 1. Mechanisms by which nitrogen as nitrate (NO_3-N) may be removed from the water column and lost from the watershed.

Mechanisms of nitrate removal	Total annual rates for Watershed 6 stream	Notes	References
Transformation and loss			
DON export[a]	12 kg	DON was approximately 0.1 mg per L.	Campbell et al. 2000
PON export	0.6–2.7 kg		Bormann et al. 1969, Meyer and Likens 1979
Storage within stream			
Benthic storage[b]	750 g	Losses of 31 g N per m^2 were recorded in the year following debris-dam removal; we assume an accumulation of 1 g N per m^2 per year.	Bilby 1981
Gaseous loss			
Denitrification[b]	11.8 kg	Lowest measured rates of denitrification were found in unamended cores (approximately 1.8 mg N per m^2 per hour).	Bernhardt and Likens 2002

DON, dissolved organic nitrogen; N, nitrogen; PON, particulate organic nitrogen.
a. Assumes an average hydrologic yield of approximately 120,000 m^3 (average water yield for 1965–2001).
b. Assumes a stream-bed area of 750 m^2.

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Bear Brook varied from 0.6 to 2.7 kg per year in two of the years it was measured (Bormann et al. 1969). Given our estimate of in-stream removal of 2.4 kg per year, small increases in PON export could account for a large fraction of N processing in this stream (table 1). Since increasing the frequency of debris dams would most likely reduce particulate export (Bilby 1981), it is unlikely that there has been a persistent increase in PON losses.

Current streamwater concentrations of dissolved organic N (DON) are approximately 0.1 mg N per L (Campbell et al. 2000). An average hydrologic yield of approximately 120,000 m^3 (average of water yield from 1965 through 2001 for the Bear Brook watershed) would result in a DON export of approximately 12 kg per year (table 1). Because no continuous measurements of DON were made during the early years of the HBEF study, it is impossible to determine whether DON loss has increased over the period of record, although the fact that DOC concentrations have not changed suggests that the DON component may have remained relatively constant. However, now that annual export of DON equals or exceeds annual NO_3^- export in streams throughout New England (Campbell et al. 2000), small changes in the percentage of N exported as DON could potentially account for a significant proportion of the 2.4 kg per year removed by in-stream processing.

Permanent removal mechanisms. A permanent sink for N is the denitrification of NO_3^- to N_2O (nitrous oxide) and N_2 gas. Streams can have high denitrification rates (Steinhart et al. 2001), and unlike assimilatory uptake, denitrification represents a permanent loss for N from a stream. Even when denitrification rates are low, over relatively long stream distances much of the stream N may be denitrified. Denitrification is controlled by labile C and NO_3^- availability, and by the extent of anoxic zones within the stream; therefore, streams with high NO_3^- concentrations, coupled with pockets of anoxic sediments or thick microbial biofilms, will have higher denitrification rates. There have been only a few limited measurements of denitrification in Bear Brook (Steinhart et al. 2001, Bernhardt and Likens 2002). Judging from these estimates, in-stream denitrification is sufficient to account fully for a net in-stream removal of 2.4 kg NO_3^- per year (table 1). (The lowest estimates of denitrification potential in unamended stream sediments from Bernhardt and Likens [2002] was approximately 1.8 mg N per m^2 per hour.) If short-term storage of NO_3^- has increased through increased microbial and algal assimilation, as outlined above, there may be more opportunities for denitrification to occur. Alternatively, greater accumulations of organic matter in debris-dam sediments, or higher spring temperatures, may lead directly to higher rates of denitrification. It is likely that all of these explanations may play a role in increasing rates of denitrification over time.

Overall, our calculations and experimental data demonstrate that (a) changes in stream N processing have occurred over the 40-year period; (b) these changes could explain a significant proportion (at least 30%) of the long-term decline in watershed NO_3^- export; (c) this magnitude of change is plausible, given estimates of in-stream denitrification and potential changes in particulate N export and storage; and (d) these changes are distinct from terrestrial changes.

What are the implications for interpreting the long-term decline in streamwater nitrate concentrations and fluxes from streams of HBEF?

Our synthesis of HBEF stream ecosystem research related to N dynamics demonstrates important effects of in-stream processing on watershed N export under current conditions. It also suggests that increasing rates of NO_3^- uptake and subsequent transformation or storage within the stream between the 1970s and the 1990s may have led to significant underestimates of watershed N loss over at least the last decade. Because data on stream nutrient cycling were not collected in any systematic fashion during this period, we cannot move beyond speculation at this point; however, these results suggest a rethinking of how watershed ecosystem studies are designed and interpreted. In-stream N processing can dampen terrestrial signals (Alexander et al. 2000, Steinhart et al. 2001, Seitzinger et al. 2002, Bernhardt et al. 2003, Mulholland forthcoming); therefore, it is important that watershed mass-balance studies not ignore this important component of the watershed ecosystem when drawing inferences about terrestrial processes. To understand the biogeochemistry of a watershed, it is sufficient to compare inputs and outputs of nutrients, but to understand the biogeochemistry of the terrestrial system within that watershed, it is important to tease apart biogeochemical cycling in vegetation, soils, and the stream. Including a stream component in watershed ecosystem models should improve their ability to predict watershed nutrient export. For example, as we have shown above, including an increasing efficiency of N removal in HBEF streams within an ecosystem model (e.g., Aber et al. 2002) would improve the fit to the observed pattern of watershed NO_3^- loss, as well as adding to a better understanding of ecosystem processes overall.

It is no accident that streams are often considered unimportant in watershed interpretations. Stream channels comprise an extremely small proportion of any watershed's surface area and, as a result, have small standing stocks of nutrients relative to terrestrial soils and vegetation. By their very nature, fluxes of nutrients through streams are always much higher than anywhere else in the watershed. These small standing stocks and large fluxes are often misinterpreted as an indication that streams are not capable of influencing export in any substantial way. A number of stream budget studies, however, have documented that streams can remove 5% to 50% of the NO_3^- delivered from the surrounding watershed (e.g., Triska et al. 1984, Burns 1998, Bernhardt et al. 2003). Modeling efforts have resulted in similar estimates. Peterson and colleagues (2001) found that headwater streams have gross removal rates of approximately 60% of their dissolved inorganic N inputs in the first kilometer of length, while Seitzinger and colleagues (2002) estimated that about 20% to 40% of the

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NO_3^- inputs to surface waters are retained within first- to fourth-order streams in 16 large drainage basins in the eastern United States.

An especially difficult aspect of decoupling terrestrial and aquatic subcomponents within watershed ecosystems is determining whether changes in biogeochemical cycling within each subcomponent occur in tandem or follow different trajectories. Long-standing theories suggest that as forests recover from disturbance to a steady-state biomass, they will become less retentive of N (e.g.,Vitousek and Reiners 1975). These theories have undergone adjustment with the growing realization that the early models largely ignored important changes in forest soils that could increase N storage (Aber et al. 1998).

Stream ecosystem recovery from disturbance depends on whether the disturbance primarily affects the stream itself or the surrounding watershed (Valett et al. 2002). Following an in-stream disturbance, such as a flood, stream communities and biogeochemical cycles recover quickly and independently of any slower changes to the surrounding watershed (e.g., Fisher et al. 1982). However, following a whole-watershed disturbance, such as clear-cutting or ice storm damage, stream ecosystems will recover at the same rate as the forest ecosystem, although they might have opposite trajectories with respect to nutrient cycling and retention (Valett et al. 2002). For instance, as debris dams re-form in streams, the increased storage of organic matter should lead to higher net storage of nutrients within streams (Bilby 1981) and may lead to higher gross uptake rates of inorganic nutrients, both from increased hydrologic storage (Hall et al. 2002) and from the increased biological demand of microbes on organic matter (Valett et al. 2002). We propose that following watershed disturbance, patterns of nutrient retention in stream ecosystems may follow different trajectories from that of the surrounding terrestrial catchment. Therefore, we suggest that similar revisions to the original conceptual model for N cycling in forest ecosystems are necessary to accommodate changes in stream nutrient cycling over the course of ecosystem development.

To understand the stream ecosystem's effect on watershed export, future watershed mass-balance studies must work to quantify the amount and concentration of solutes in stream inflow. This information will enable comparisons between nutrient losses for different terrestrial ecosystems as well as for different watersheds. The development of successful conceptual and mathematical models to explain watershed nutrient export will require a new emphasis on in-stream processing and on long-term recovery trends in stream ecosystems.

Conclusions

Stream ecosystems have major and important functional roles within the context of the watershed landscape. Here, we have shown that small headwater streams can alter NO_3^- flux from a watershed ecosystem, and that this rate of alteration can change with time. For example, although stream recovery from disturbance is linked to conditions in the adjacent watershed, the response of nutrient cycling in stream ecosystems to watershed disturbance may be opposite to that of the forest, in that streams retain nutrients as forest ecosystems lose them (Hall 2003). This pattern may occur from short time scales (e.g., increasing primary production takes up nutrients immediately following canopy removal; Sabater et al. 2000) to very long ones (e.g., streams draining old-growth forests had higher levels of debris-dam density, organic-matter storage, and phosphorus removal than those draining second-growth forests; Valett et al. 2002). As watershed ecosystems change with time, the relative importance and the magnitude of interplay between stream ecosystems and upland drainage areas change in myriad and complicated ways. Measuring how nutrient flux and cycling in both stream and terrestrial ecosystems change through time is crucial for analyzing and interpreting nutrient flux and cycling at the overall watershed–landscape scale.

We show that given measured net and gross rates of NO_3^- removal from HBEF streams, processes within the stream channel can lower the export of NO_3^- from watersheds. Changes in terrestrial N cycling could certainly alter watershed N exports; however, current conceptual models suggest that terrestrial systems in New England are likely to be losing more NO_3^- now than they have in the past (Aber et al. 2002). Increased assimilation and transformation of NO_3^- in streams may help explain the regional decline in NO_3^- export that has occurred over the past several decades, and in-stream NO_3^- removal may be of sufficient magnitude to partly resolve the discrepancy between modeled and actual N exports (Aber et al. 2002). Two processes are most likely responsible for NO_3^- removal. One is assimilative uptake by microbes, with subsequent storage or export as PON or DON. The second is denitrification, which may be a large sink, because scaling up its rate suggests it can account for more than 100% of our estimated net in-stream uptake of N. Clearly, additional research is needed to provide accurate measures of denitrification for these streams, as it appears that denitrification is the largest sink for NO_3^- once it reaches the stream. Increases in particulate N export and long-term storage of N in organic debris dams may also represent a fraction of the missing NO_3^- in the stream, but these rates are not likely to be as high as those resulting from denitrification.

Despite the powerful impact of the terrestrial component of the watershed on stream nutrient export (e.g., Likens et al. 1970), it is increasingly evident that processes within the stream ecosystem contribute substantially to—and at times may dominate—watershed N export, thus affecting our interpretation of overall watershed processes. Streams and their catchments can respond along different trajectories during recovery from disturbance. Thus, future watershed mass-balance studies will be improved by incorporating a solid understanding of biogeochemical cycling in both the terrestrial and the aquatic components of the watershed.

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