

Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response

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A current pine beetle infestation has caused extensive mortality of lodgepole pine (*Pinus contorta*) in forests of Colorado and Wyoming; it is part of an unprecedented multispecies beetle outbreak extending from Mexico to Canada. In United States and European watersheds, where atmospheric deposition of inorganic N is moderate to low (<10 kg·ha⁻¹·y), disturbance of forests by timber harvest or violent storms causes an increase in stream nitrate concentration that typically is close to 400% of predisturbance concentrations. In contrast, no significant increase in streamwater nitrate concentrations has occurred following extensive tree mortality caused by the mountain pine beetle in Colorado. A model of nitrate release from Colorado watersheds calibrated with field data indicates that stimulation of nitrate uptake by vegetation components unaffected by beetles accounts for significant nitrate retention in beetle-infested watersheds. The combination of low atmospheric N deposition (<10 kg·ha⁻¹·y), tree mortality spread over multiple years, and high compensatory capacity associated with undisturbed residual vegetation and soils explains the ability of these beetle-infested watersheds to retain nitrate despite catastrophic mortality of the dominant canopy tree species.

nitrogen biogeochemistry | streamwater chemistry | nitrate loss | watershed disturbance

Bark beetles have infested 1.6 million hectares of coniferous forest in Colorado and Wyoming during an outbreak that began in 1996 and accelerated after 2004 (1). Although several species of bark beetle are harmful to North American conifers, the native mountain pine beetle (*Dendroctonus ponderosae*) has caused the most damage since 1996, particularly through its infestation of lodgepole pine (*Pinus contorta*), which often grows in nearly monospecific stands dominated by trees of similar age. The Colorado/Wyoming outbreak is part of a severe general upsurge in infestation affecting dominant conifer species from northern Mexico to British Columbia (2). Beetle infestations have been present historically in western montane forests of North America, but climate change (drought, warming) and stand uniformity appear to have increased vulnerability of forests to extensive bark beetle outbreaks (2, 3).

Timber harvest and other watershed-scale canopy disturbances often affect the amount of runoff, water quality, and ecosystem metabolism of streams and rivers (4–10). One of the strongest responses is increased export of nitrogen, especially in the form of nitrate, which moves readily to streams via subsurface drainage.

Although nitrate released in response to forest disturbances can be taken up by stream autotrophs (11, 12), removal of nitrate in streams typically is greatly exceeded by nitrate release following strong disturbances of the terrestrial ecosystem. Release of nitrate to streams can be caused by reduced vegetative uptake of nitrate that follows damage to or removal of vegetation. In addition, decreased uptake of ammonium caused by tree mortality

may facilitate or increase production of nitrate by soil microbes, which contributes to increased nitrate concentrations in streams (4, 5, 9, 10). We show here that extensive tree mortality caused by the mountain pine beetle in Colorado has, contrary to expectation, not been accompanied by any large increase in streamwater concentrations of nitrate; we offer an explanation for the retention of nitrate in beetle-infested forests.

Often, pine beetle infestation in a given watershed is established first at locations that are more xeric than the watershed as a whole because water-stressed trees are less able to defend themselves against the beetles (2). Furthermore, the mountain pine beetle preferentially infests large trees, which have a large phloem volume for growth of larvae as well as thick bark that may protect beetle larvae from potentially lethal winter temperatures (13, 14). Thus, the initial infestation is spatially heterogeneous (14).

During infestations, beetles spread widely from ideal sites to less favorable sites and to smaller trees over a period of multiple years (13, 15), but their dispersal may be affected by winter air temperatures or soil moisture in a given year. Infestation ultimately may cover entire watersheds (e.g., 60% of lodgepole, 90% of large lodgepole) (15, 16).

Methods and Study Sites

Changes of nitrate concentrations in Colorado streams within watersheds dominated by mature lodgepole pine with a range of beetle-induced mortality were documented in three concurrent studies at 65 sites over a range of 150 km in Colorado's Rocky Mountains (*SI Text 1*). The Fraser Experimental Forest (FEF) study included weekly measurements of streamwater nitrate concentration beginning before 2003, prior to the onset of beetle infestation, and extending through 2011, by which time beetle mortality had reached 20–90% of the canopy trees (*SI Text 1*) (16). The Willow Creek Study (WC) consisted of monthly measurements of nitrate concentration from June to September 2009 in 11 watersheds with varied intensity of beetle infestation. A spatially distributed study (SD) documented bimonthly nitrate concentrations at 53 sites in central Colorado during the ice-free season of 2009. A nitrogen assimilation study (NA) for noninfested trees was based on measurements of foliar nitrogen, an index of compensatory N uptake from groundwater (17), for lodgepole pine-dominated sites with varied degrees of pine beetle infestation (*SI Text 1*).

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concentrations, in contrast to the beetle-infested watersheds, which showed either a very small increase or no detectable increase in nitrate concentrations for streams.

More broadly, the literature on nitrate concentrations for unpolluted streams in paired watersheds that are undisturbed (no extensive mortality) and disturbed (with extensive mortality or physical disturbance) can be compared with streams in Colorado watersheds showing beetle-induced mortality (Fig. 2 and *SI Text 3*) (4, 19–27). Wet DIN deposition is shown for each of the sites; only watersheds with low-to-moderate DIN deposition ($<10 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$) were chosen for inclusion in Fig. 2. For this group of watersheds there is no statistical relationship between DIN deposition and the proportional increase in stream nitrate concentrations following disturbance ($r^2 = 0.04$, $P = 0.50$) (i.e., atmospheric deposition does not explain the trend shown in Fig. 2).

There is a strong relationship between stream nitrate concentrations before and after disturbance, but there are four strongly divergent outliers (all four outside the 95th percentile confidence limits) (Fig. 2). The first of these, which is well above the trend line, is for the classic study at the Hubbard Brook Experimental Forest (HBEF) involving catchment clear-cut harvesting of an entire watershed followed by 3 y of herbicide treatment, which removed postharvest demand by plants for inorganic nitrogen (4). This experiment produced the highest postharvest export response on record, probably by an acceleration of nitrification in soil following cessation of plant uptake of ammonium and by absence of residual vegetation that otherwise would have taken up inorganic nitrogen (4, 5). Numerous other studies have confirmed the importance of residual vegetation in sequestering nitrate following removal of vegetation (10). In addition, above the trend line but less extremely so, is a whole tree harvest of an entire watershed at HBEF, which may be divergent because of greater disturbance required for removal of all aboveground tree biomass (20).

The Colorado watersheds with beetle-induced mortality (pooled for Fig. 2), along with a partial tree harvest, including buffer strips in a Swedish forest (21), are outliers below the trend line. Beetle kill is unlike the HBEF harvest/herbicide watershed treatment in that it involves no physical disturbance and leaves much residual vegetation. The partial tree harvest in a Colorado watershed near the beetle-kill study sites (*SI Text 4*) falls near the trend line with 550% increase in nitrate export (19) (Fig. 2). Comparable data for beetle-induced mortality from other forest types are not yet available (*SI Text 3*).

The lack of a large streamwater nitrate response after extensive canopy mortality caused by bark beetles may be explained by some combination of two factors. Heterogeneous mortality (spatial and temporal) would be expected to reduce the amount of nitrate loss at any given time over the progression of infestation. In addition, compensatory responses by residual live vegetation are likely to respond to the increased resources available following overstory mortality. Multiple studies have documented increased foliar N content in the remaining live trees after surrounding trees were killed by bark beetles (NA study) (28). Increased establishment of new seedlings and faster growth of understory trees further demonstrate compensatory responses to the bark beetles (16). An estimate of the relative role of (i) temporal and spatial heterogeneity of mortality and (ii) compensatory response through accelerated uptake of DIN can be obtained by use of process modeling, the starting point for which is the deviation between the expected release of nitrate from disturbed watersheds based on the regression line shown in Fig. 2 and the observed (negligible) nitrate loss from Colorado watersheds with extensive beetle kill.

A common pattern of watershed nutrient release in response to disturbance of vegetation is captured in a conceptual model proposed by Vitousek and Reiners (29) and elaborated with modifications by others (5); it incorporates a spike in stream

nutrient concentrations following a disturbance, a steep subsequent decline in concentrations extending below the original baseline that reflects recovery of vegetation, and slow return to an asymptote equal to the baseline (Fig. 3). Data on nitrate export following disturbance in numerous watersheds shows the model to be conceptually realistic, but the onset of nitrate release and breadth of the concentration peak vary considerably from one disturbance type or forest type to another (10), and the model may lose its realism over multiple decades because of changes in climate, occurrence of other disturbances, or nutrient processing by streams (12). It is possible to calibrate the model with empirical data for disturbances other than beetle mortality, then modify it sequentially to account for observed negligible loss of nitrate from watersheds with extensive beetle kill (Fig. 3). The basis for the model modifications is a hypothetical, spatially

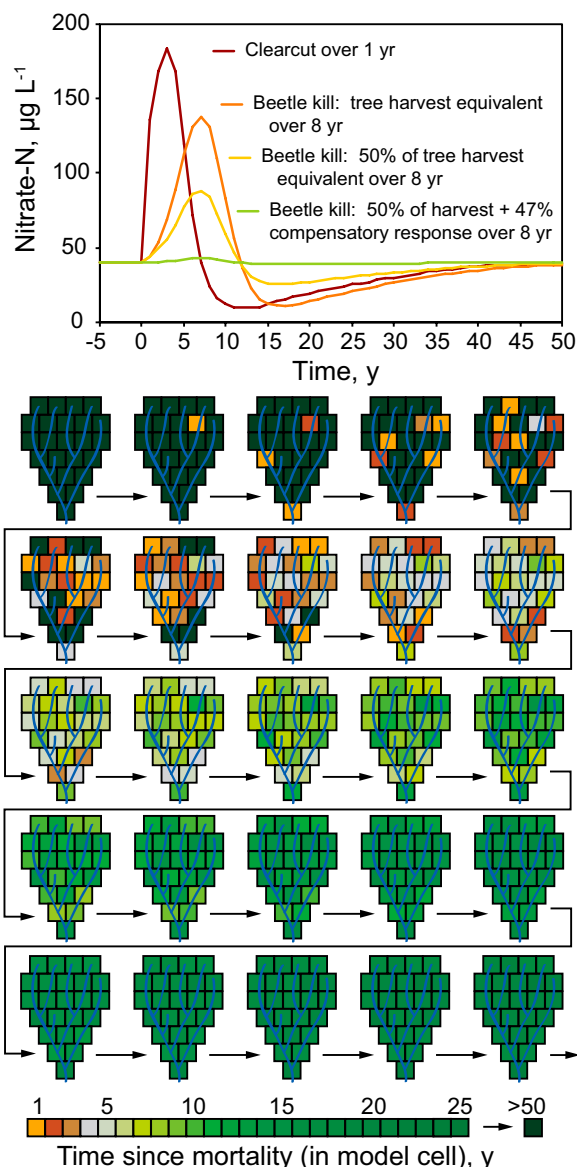


Fig. 3. (Upper) Modeled nitrate release for Rocky Mountain forests calibrated for tree harvest, to which three factors that differ between harvest and beetle kill are added sequentially, based on field studies. (Lower) A 25-y spatial sequence of canopy mortality for a hypothetical watershed with beetle kill spread over 8 y terminating at 100% cumulative infestation, as used in deriving the modeling results shown above.

segmented watershed consisting of watershed blocks; individual blocks are assumed to experience beetle-induced mortality on an incremental basis over a defined period that can be adjusted to mimic typical progressions of infestation (*SI Text 5*). For simplicity, any given watershed block experiencing beetle kill is assumed to show complete loss of nitrogen uptake by the canopy trees during the year of infestation. Cessation of water uptake by lodgepole pine shortly after beetle infestation (28) and the increase in soil nitrogen availability beneath recently killed pines (18) justify this assumption.

The first step in adapting the general model to beetle-induced mortality of trees is based on the assumption that beetle-kill response for nitrate is the same as the tree harvest response except that it is spread through time over an interval of 8 y (*SI Text 5* gives results of modeling for other durations). The temporal distribution of beetle kill reduces predicted maximum nitrate concentrations (Fig. 3), but the reduction is not nearly sufficient to account for the observed extreme difference between harvested and beetle-infested watersheds.

A second step in adaptation of the model is to assume that beetle-induced mortality, although killing much or most of the original canopy, does not disturb beetle-resistant overstory trees and the understory vegetation that would be lost or damaged during tree harvest. Based on data for Colorado forests, residual vegetation is estimated for modeling purposes at 50% of the original vegetative cover (16) (*SI Text 5* shows the effect of other assumptions about percent residual canopy) and would include some scattered large lodgepole (e.g., 20% of the original stand) as well as numerous small lodgepole, other beetle-resistant tree or plant species, and a mixed species strip of riparian vegetation. Presence of this residual vegetation, with the baseline assumption that its nitrogen demand remains at preinfestation levels, reduces the expected increase in nitrate concentrations considerably, but not to the extent reported by field studies (Fig. 3).

A third and final step in the sequence of modeling modifications is to attribute the residual difference between the modeled and observed nitrate concentrations associated with beetle kill to factors that can be designated collectively as “compensatory response.” In this way, the model predicts the quantitative significance of the increased nitrogen uptake by remaining vegetation

when canopy is removed and microbial processes (e.g., suppressed nitrification caused by deficiency of labile carbon following loss of fresh litterfall and root exudates) that may work against the mobilization of nitrate in response to beetle kill (30–32).

Modeling indicates that the magnitude of compensatory response as defined here accounts for about half of the suppression of nitrate release from forests with beetle kill; spatial and temporal heterogeneity of beetle kill accounts for the other half. Thus, compensatory response can provide potent water quality protection against adverse effects of elevated concentrations of inorganic N (33) in these western forests, but only if substantial vegetation (e.g., 50%) survives overstory mortality, as it does in the case of beetle kill.

Compensatory response deserves more detailed study given its potentially strong effect on nitrate release following canopy damage. Quantification of the understory component in particular has implications for harvest management. The close relationship between nitrate concentrations before and after tree harvesting or other severe canopy damage that involves collateral damage to understory is useful as an index of compensatory response. Because harvesting of beetle-killed forests stimulates regeneration of new seedlings (34), careful logging has the potential to mitigate increases in streamwater nitrogen concentrations. Ideal management that involves cutting would seek a mode of tree removal that produces nitrate concentrations significantly below the canopy-damage trend line (Fig. 2) by coupling canopy removal with protection of soils and residual vegetation.

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Supporting Information

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SI Text 1

Three of the studies [Fraser Experimental Forest (FEF) study, Willow Creek study (WC), and the spatially distributed study (SD)] were based on measurement of nitrate concentrations in streams showing varying degrees of conifer mortality caused by mountain pine beetle. Streams included in these studies extended over a distance of 150 km in the Colorado Rocky Mountains on both sides of the Continental Divide at elevations of 2,600–3,900 m above mean sea level (Fig. S1). Baseline concentrations of nitrate (concentrations in watersheds unaffected by beetle-induced mortality) are low in these streams ($< 150 \mu\text{g/L NO}_3^- \text{-N}$; median $\sim 40 \mu\text{g/L NO}_3^- \text{-N}$) and show high seasonal variation. Nitrate concentrations in the presence or absence of beetle kill are highest in winter and lowest during the warm months and in fall when the rate of nitrate movement to streams is low and uptake of nitrate by attached algae, which reach peak biomass at this time, may remove a significant proportion of nitrate from streams. Fig. 1, *Upper*, which is for the FEF study, shows typical seasonal patterns in concentrations for streams included in the three studies of nitrate concentrations in streams (FEF, WC, SD).

Estimates of mountain pine beetle infestation intensity in the FEF, WC, and SD studies were calculated from an overlay of the GIS coverage of watershed boundaries (US Geological Survey digital elevation data) on digital mountain pine beetle infestation maps from the US Department of Agriculture Forest Service (1) (surveys of this type may underestimate percent mortality) (2). Nitrate concentrations for all three studies were measured on filtered samples with ion chromatography at detection limits of $1\text{--}2 \mu\text{g/L NO}_3^- \text{-N}$. Samples typically were frozen before analysis.

The FEF is located 100 km west of Denver on the western edge of Colorado's Front Range. East St. Louis Creek, for which data are reported in this article, has a watershed area of 941 ha, 30% of which is alpine. The canopy consists of pine, spruce, and fir; lodgepole pine is predominant. The stream is gauged at its lower end, which allows continuous estimation of stream discharge. Samples were taken weekly.

For the WC study, samples were taken from one station on upper Willow Creek and from stations at the mouths of 10 tributaries to Willow Creek (Fig. S1) monthly between June and September over the interval of seasonally declining flow (peak discharge occurred in May). Over the entire WC watershed, 75% of canopy showed beetle-induced mortality (range, 43–97% for the 11 sites). Information used in statistical analysis for the 11 watersheds included watershed area, mean elevation, mean percent gradient, aspect, and percent canopy mortality.

The SD study was based on sampling at 53 sites during 2009 (Fig. S1). Samples were collected for nitrate analysis from each site two or three times between June 23 and October 9; mean concentration of nitrate at each site is the basis for statistical analysis. Stream discharge was estimated for each site on each sampling date on the basis of current meter measurements at multiple locations over the stream cross-section (3). Independent variables for this study included elevation, slope, aspect, mean stream discharge, and percent canopy mortality.

A fourth study, the nitrogen assimilation study (NA), was designed to give empirical information on compensatory uptake of nitrogen by live trees in response to beetle-induced mortality of nearby trees. Sampling of live pine needles was conducted in 53 plots, each 25 m^2 , at 12 sites on both the eastern and western side of the Continental Divide (Fig. S1). There were four control sites (no mortality) and eight treatment sites with varying severities of infestation.

At each site, a plot of 25 m^2 was located adjacent to a stream. A foliar sample was collected from the lower branches of each living coniferous tree over 0.5-m tall within the plot. Directly upslope from the first plot, another plot of 25 m^2 was sampled by the same method. A third plot was located 5-m upslope of the second, a fourth plot was located 15-m upslope the third, and a fifth plot was located 25-m upslope of the fourth. Measurements were made of diameter at breast height for each tree in each plot as well as elevation, slope, percent ground cover, aspect, counts of live and dead trees, and tree type (lodgepole, spruce, or fir). Mortality of trees in plots was quantified as the ratio of dead lodgepole to the total tree count (live and dead). Live tree density was measured as the number of live trees divided by the total area (25 m^2) for each plot. Leaf samples ($n = 201$) were freeze-dried and ground to powder. Foliar nitrogen was estimated by use of an elemental analyzer as percent of nitrogen per gram dry mass.

SI Text 2

The 30% difference in nitrate export before and after beetle infestation at the FEF St. Louis Creek watershed cannot be attributed confidently to beetle kill. Interannual variation in nitrate concentrations in the Colorado Rockies depends strongly on amount and timing of runoff, which shows great interannual variation that complicates the interpretation of variation in nitrate concentration across years (4, 5). The main point of interest for the purposes of this article is that partial (30%) harvest in a watershed of the same FEF study area yielded a substantial increase in stream nitrate (6). Thus, the FEF watershed with beetle-induced mortality showed a response that was either nil or far smaller than the response that followed partial harvest in a nearby watershed. Although the percent increase following patch clear-cut as calculated from Stottlemeyer's (6) data were 550%, this estimate can be considered only approximate because the duration of the study was not sufficiently long to produce a precise estimate of percent increase in nitrate concentrations. Percent increase as calculated from Stottlemeyer's data does align well, however, with expected percent increases for numerous watersheds elsewhere in response to complete or partial timber harvest (Fig. 2).

Table S1 shows results for the statistical analysis of data from the SD study relevant to relationships between stream nitrate concentration and percent mortality of canopy trees, as well as other variables. Nitrate concentration was not significantly related to percent mortality of trees. Slope explains about half of the variance, discharge (reflecting watershed area and other factors) explains a smaller but substantial (Table S1) amount of variance, and nothing is a statistically significant but small contributor to explained variance.

The WC study showed statistical results similar to those of the SD study (no significant relationship for percent mortality; Spearman's $r = 0.55$ for mean slope, -0.54 for aspect). Statistically significant but minor additional components of variance included elevation and watershed area. Watershed area is a surrogate for a cluster of potentially relevant variables including discharge.

The NA study showed a relationship of significant slope between percent mortality and foliar nitrogen content of conifer needles (Fig. S2). Percent variance in foliar nitrogen explained by percent mortality was low (18%), even though the relationship was highly significant statistically. Distance from the stream was not a significant covariate. The low r^2 value indicates that numerous variables

other than mortality influenced the degree of foliar nitrogen response of living trees in a given plot relative to mortality of nearby trees. Examples of probable factors influencing variance include spatial heterogeneity in the distribution of tree mortality, local variation in the spacing of trees, and spatial variation in the rate of downgradient movement for nitrate as influenced by slope or soil characteristics.

An argument could be made for eliminating the zero values from Fig. S2 to satisfy requirements of regression analysis. When this removal is done, the value of r^2 is essentially the same (0.17). Furthermore, a t test for statistical difference between foliar nitrogen in plots with zero mortality as contrasted with plots showing mortality greater than zero shows a statistically significant difference ($P = 0.0001$).

SI Text 3

Defoliation not involving tree mortality (e.g., gypsy moth infestation) causes increased nitrogen export in deciduous forests (7–10), but the increases are one-to-two orders-of-magnitude lower than for harvested forests at similar sites. A study of beetle-induced mortality in a Bavarian forest (10) showed large increases in the nitrate content of soil water, but there are no accompanying data on stream water, which may not reflect groundwater conditions when nitrate is intercepted by residual vegetation along the pathway to an adjacent stream. In addition, the Bavarian study site had high inorganic nitrogen deposition (12–16 kg N ha⁻¹·y⁻¹).

Study of a small (<1 ha) catchment in Japan (11) following mortality of red pine caused by nematodes revealed increases in soil nitrate concentrations caused by nitrification of soil ammonium; increases of nitrate (four to five times) occurred in a headwater stream receiving runoff from the watershed. The site had significant residual vegetation following the nematode attack and atmospheric inorganic nitrogen deposition was below 10 kg ha⁻¹·y⁻¹. The spatial scale of the study may have been important in determining its outcome, however, given that nitrate-enriched groundwater traveling over short distances may be less subject to uptake than groundwater moving over much longer distances. The study also is complicated by a typhoon that uprooted many of the infected trees, causing soil disturbance during the study.

SI Text 4

Partial tree harvests were of several types. The study by Burns and Murdoch (12) involved a watershed that was 80% harvested. The study by Feller and Kimmins (13) similarly involved harvesting portions of watersheds (61% of watershed A and 19% of watershed B) and leaving the residual portion undisturbed. In addition, the sites studied by Löfgren et al. (14) were logged entirely in some areas (30% and 73% for the two watersheds) but other portions of the watersheds were left undisturbed. Harvested areas included a buffer zone of 5–10 m on each side of the stream. The Colorado partial harvest was for one-third of the watershed in multiple patches.

Sources of data for atmospheric deposition of inorganic nitrogen as shown in Fig. 2 are the same as for data on nitrate on stream water chemistry, except for the following: Swedish harvest (15), ice storm eastern United States (16), Colorado partial harvest (17), and Puerto Rico hurricane (18). Watersheds with high N deposition (e.g., >10 kg·ha⁻¹·y⁻¹) would be expected to show notably higher N concentrations in stream water even without watershed disturbance (19–21); no such watersheds are included in Fig. 2.

For Fig. 2, references to Clow et al. (22) and Löfgren et al. (14) (referred to as references 18 and 21 in Fig. 2) appear twice in the bar graph and twice in the regression graph because these two references report results for two different kinds of treatments, as described on the bar graph. The regression analysis for Fig. 2 was conducted first for all points and then for points falling within the 95th percentile boundaries. When all points were included in

the analysis (no exclusions), intercept = 2.11, slope = 1.21, $r^2 = 0.78$, $P < 0.001$. In a second analysis, points outside the 95th percentile boundaries were excluded (4 and 20 on the high side and 18 and beetle kill on the low side). The trend line with the exclusions is highly significant and is very similar to the trend line similar to the slope without exclusions (intercept = 1.36, slope = 0.89, $r^2 = 0.96$). The statistical outliers (outside 95%) are noted here as a means of supporting the discussion of factors that likely cause major deviation from the trend line. Outlier 4 is for a Hubbard Brook Experimental Forest (HBEF) harvest with herbicide treatment (23). Outlier 20 is a whole tree harvest at HBEF (removal of all aboveground tree components) (24). Outlier 21 on the low side is for partial Swedish harvest with buffer strips (14). The outlier beetle kill point on the low side is a composite of the beetle kill information for studies described in this article.

SI Text 5

Modeling was used to compare the nitrate response of watersheds to tree harvesting or other physical disturbance with the nitrate response to beetle induced mortality. The basis for modeling is a hypothetical, spatially segmented watershed consisting of individual blocks connected by a stream drainage network (Fig. S3). For each block, the concentration of nitrate in water entering a stream varies over time in response to: (i) the duration of forest disturbance (e.g., harvesting, beetle induced mortality, or other processes that damage or remove vegetation) and (ii) the final amount of disturbance, as a proportion of the watershed canopy cover. Disturbance can occur simultaneously (e.g., a 1-y harvest) or at different times for different blocks (e.g., staged harvest or beetle-induced mortality). Modeling results are presented for a hypothetical watershed consisting of 24 blocks; modeling for watersheds of 48 and 96 blocks also was tested but gave virtually identical results.

Application of the model is summarized in Fig. S3. Modeling steps leading to final results are separated by vertical arrows on the left side of Fig. S3. The first application of the model is based on a calibration for harvest conditions that produce a nitrate response in the stream water that is intermediate between: (i) the nitrate response documented for the Colorado partial (33%) harvest as described by Stottlemeyer (6), and (ii) the trend line in Fig. 2. The second model run differs from the first in its assumption that tree mortality is spread over 8 y and produces within individually modeled blocks (patches within the watershed) a response that is identical to the response used in the initial calibration for tree harvest. The watershed output for this run differs from the first model run in that mortality is spread through time, thus making it comparable in time sequence to beetle-induced mortality. Duration of infestation varies greatly among watersheds (Fig. S4). As is common for infestations in general, cumulative infestation increases slowly in its initial phases, accelerates in a manner that is generally exponential, decelerates in a similar manner, and nears an asymptote representing final infestation (i.e., similar to a logistic curve). Although this general pattern exists (Fig. S4), it shows irregularities that are influenced by year-to-year climate variability (25). Duration of infestation, which spans the interval between the initial quantifiable degrees of increasing infestation and the approach to the terminal state of infestation, consistently requires multiple years but typically is complete within a decade. If the assumed duration were allowed to vary between 4 and 10 y rather than being fixed at 8 y, the modeling outcomes would be qualitatively similar to those shown in Fig. S3. The rate of mortality reflects the rate of infestation, as infected trees typically die within 1 y.

Although duration of infestation varies, it usually has peaked within 8 y (Fig. S4). Sensitivity analysis involving shorter or longer duration shows that length of mortality sequence is inversely related to height of peak concentrations of nitrate and directly related to the duration of nitrate concentrations exceeding

background. As expected, the peak for nitrate concentrations is lower and the breadth of the increased concentrations is higher in all model runs involving multiple years compared with single year mortality (e.g., a 1-y harvest).

The third model run retains the assumption of mortality over multiple years (8 y in the example of Fig. 3 and Fig. S3), but incorporates the further assumption that 50% of the vegetation remains undamaged. The purpose of this assumption is to approximate observed field conditions for beetle-induced mortality, which causes variable percentage loss of lodgepole (20–90%) (Fig. S4), but not complete mortality, and leaves species other than lodgepole mostly undamaged (26, 27). For this model run, it is assumed that percent reduction in nitrate concentration relative to harvest equals percent of the canopy that experiences mortality. Assumption of other values for percent loss of canopy raise or lower the nitrate curve, but do not change the results qualitatively (Fig. S3).

The final step in modeling is to compare the results for modeling step three with the observed response of nitrate concentration in streamwater to beetle kill. The observed nitrate response of streams to beetle kill is extremely low or nil, as explained in the main text. The difference between the baseline defined empirically in this way and the observed outcome for modeling based on calibration for harvest must be attributed to

a factor other than distribution of mortality through time and failure of beetle kill to remove all canopy. This additional factor is designated as “compensatory response.” The existence of compensatory response, as predicted by the model, is demonstrated empirically by the NA study, which shows increased foliar uptake of nitrogen by vegetation that remains following beetle kill. Increased N uptake likely corresponds to increased growth (26, 28). Compensatory uptake may also include other processes, such as changes in microbial processing of N species that are less well understood.

Compensatory response in watersheds disturbed by timber harvesting could be explained by hydrologic factors as well as biotic factors. Stednick’s (29) data summary shows for United States forests a highly variable hydrologic response (including no response) to timber harvest. Typically there is an increase in water yield but it seldom reaches half of the preharvest stream flows. Fig. 2 provides some evidence that hydrologic response to physical disturbance is not as important for nitrate concentrations as suppression of the biotic components of compensatory response. Specifically, nitrate response to an ice storm, which did not involve soil disturbance, falls on the same trend line as timber harvesting, suggesting that the key processes are biotic rather than hydrologic.

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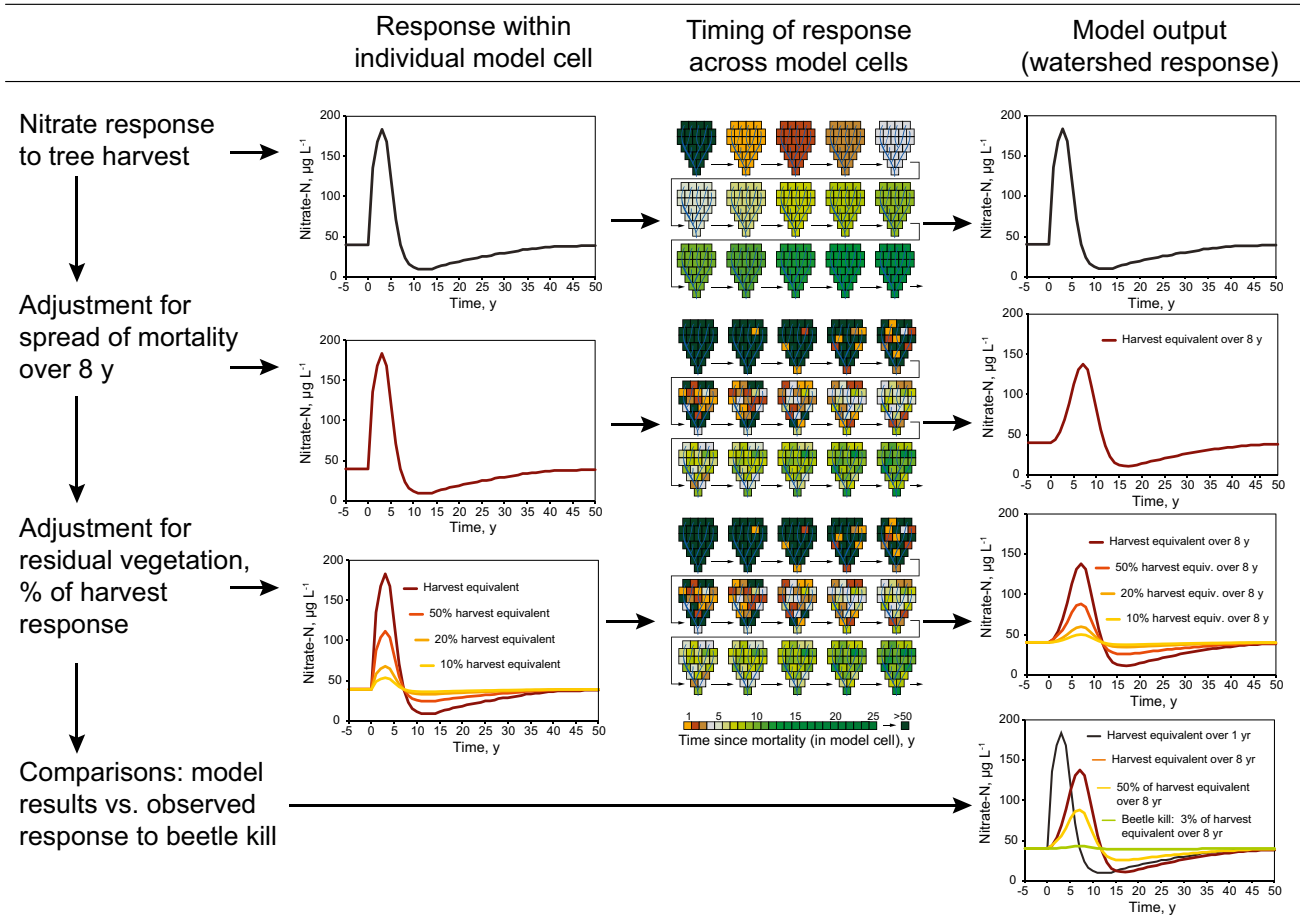


Fig. S3. Illustration of the modeling strategy, which is calibrated to match the effects of harvesting and then modified to reflect differences between harvest and beetle induced mortality.

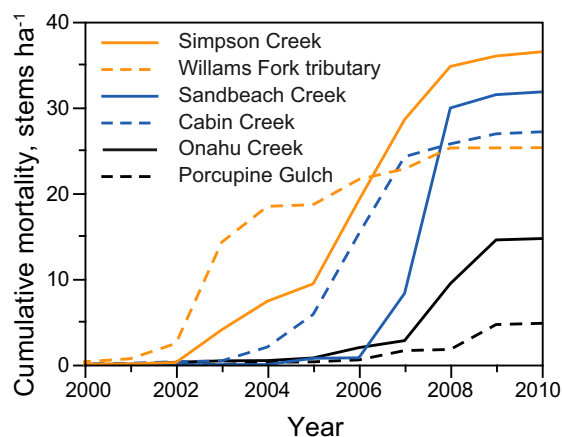


Fig. S4. Examples of the temporal progression of beetle-induced mortality of canopy trees in some of the watersheds included in this study (Source: US Forest Survey aerial surveys).

Table S1. Results of a stepwise regression, SD study, for variance in mean nitrate concentration across 53 plots in 12 watersheds showing various degrees of beetle-induced tree mortality

Variable	Estimate	<i>P</i>	<i>r</i> ²
Intercept	0.447	—	—
Watershed slope (mean) (%)	0.080	0.000	0.54
Log10 Discharge (m ³ ·s ⁻¹)	0.479	0.001	0.70
Northing (km)	0.000	0.001	0.73
Easting (km)	0.000	NS	NS
Elevation (mean) meters above mean sea level	0.000	NS	NS
Aspect (mean)	0.000	NS	NS
Mortality, trees (ha ⁻¹)	0.000	NS	NS

NS = not significant at *P* = 0.05.