

A Framework to Assess Biogeochemical Response to Ecosystem Disturbance Using Nutrient Partitioning Ratios

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ABSTRACT

Disturbances affect almost all terrestrial ecosystems, but it has been difficult to identify general principles regarding these influences. To improve our understanding of the long-term consequences of disturbance on terrestrial ecosystems, we present a conceptual framework that analyzes disturbances by their biogeochemical impacts. We posit that the

ratio of soil and plant nutrient stocks in mature ecosystems represents a characteristic site property. Focusing on nitrogen (N), we hypothesize that this partitioning ratio (soil N: plant N) will undergo a predictable trajectory after disturbance. We investigate the nature of this partitioning ratio with three approaches: (1) nutrient stock data from forested ecosystems in North America, (2) a process-based ecosystem model, and (3) conceptual shifts in site nutrient availability with altered disturbance frequency. Partitioning ratios could be applied to a variety of ecosystems and successional states, allowing for improved temporal scaling of disturbance events. The generally short-term empirical evidence for recovery trajectories of nutrient stocks and partitioning ratios suggests two

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areas for future research. First, we need to recognize and quantify how disturbance effects can be accreting or depleting, depending on whether their net effect is to increase or decrease ecosystem nutrient stocks. Second, we need to test how altered disturbance frequencies from the present state may be constructive or destructive in their effects on biogeochemical cycling and nutrient

availability. Long-term studies, with repeated sampling of soils and vegetation, will be essential in further developing this framework of biogeochemical response to disturbance.

Key words: Disturbance; Fire regime; Succession; Multiple element limitation (MEL) model; Nitrogen stocks; Nutrient ratio.

INTRODUCTION

An ecosystem disturbance is a “relatively discrete event in time that disrupts ecosystem, community or population structure and changes resource, substrate availability, or the physical environment” (Pickett and White 1985), which encompasses both a wide variety of natural disturbance types (fires, storms, landslides, flooding, volcanic eruptions) and terrestrial biomes (forest, grassland, alpine, deserts). The many additional types of anthropogenic influences (pollution, intensive land-use practices, climate change, and invasive species) which interact with and underscore global environmental change highlight the need for a deeper understanding of disturbance ecology (Peters and others 2011). Yet disturbances are complex, individual events. Characterizing a disturbance from a biogeochemical perspective aids in generalizations about its outcomes because of the potential to integrate ecosystem processes over space and time into metrics that ultimately control post-disturbance ecosystem trajectories (Turner 2010). The challenge is building an adequate understanding of processes in key abiotic and biotic parameters which more accurately predict the biogeochemical impacts of single or multiple disturbance events.

Biogeochemical cycles of carbon (C) and nutrients exhibit a range of responses to disturbance over ecologically meaningful time scales (Running 2008). In turn, biogeochemical cycles and their interactions can influence the pattern and pace of ecosystem recovery from disturbance; both disturbance legacies and feedbacks between plant regrowth and soil element stores are particularly influential in shaping recovery (Gough and others 2007; Pearce and others 2015). Feedbacks among C accumulation, nutrient recycling, and other ecosystem processes may interact with whole-ecosystem constraints on element supply and loss (Belyea and Baird 2006). These constraints on the various individual and feedback processes can result in surprisingly consistent patterns in biogeochemical cycling after disturbance across a wide range of ecosystem types (Davidson and others 2007; Rastetter

and others 2013). Yet, key uncertainties remain in both the consequences of disturbance events and their impacts at landscape scales. Thus it has been difficult, for example, to quantify the direction and magnitude of biotic disturbances on forest C cycling in the United States and Canada (that is, Hicke and others 2012). Nonetheless, generalization of disturbance ecology would benefit from a theoretical biogeochemical framework which would apply across single and multiple events, in multiple biomes.

For many terrestrial ecosystems, both the infrequent nature of disturbance events and slow post-disturbance processes complicate efforts to empirically study biogeochemical responses on long time-scales. Although a single disturbance event has the potential to create a significant biogeochemical impact (Paré and others 2002; Foster and others 2003; Romme and others 2011), over the long term a shift in the disturbance regime itself and its associated successional pathways may combine to affect ecosystems more profoundly (for example, directional change, Reiners 1983). Detecting shifts in disturbance regimes necessitates extending the temporal scale of disturbance history beyond the time period of direct or historical observations (Marlon and others 2012). Recent studies have provided increasingly clear characterizations of disturbance regimes (at least for fire and storm regimes) on millennial timescales (Donnelly and Woodruff 2007; Higuera and others 2014), including return intervals, spatial extent, and intensity (Baker 2009). Several lines of evidence indicate incipient or ongoing shifts in disturbance regimes during the past few decades, with larger and more frequent fire events (Dennison and others 2014) and seemingly unprecedented bark beetle outbreaks (Raffa and others 2008). Projecting the future biogeochemical trajectory of disturbed systems requires the ability to identify how profoundly a disturbance regime has departed from the present state (Walker and Wardle 2014).

Here, we introduce a conceptual framework using the ratio of plant and soil nutrient stocks to characterize the relative stasis of mature ecosys-

tems and to hypothesize the consequences of a single disturbance event on nutrient loss and recovery. We suggest this framework will improve ecosystem comparisons of biogeochemical response to multiple disturbances over time. This framework is designed for temporal scaling and it is flexible with regard to disturbance mechanism, ecosystem type, and spatial extent. We develop this framework with three different approaches: (1) nutrient stock data from forested ecosystems in North America, (2) a process-based ecosystem model, and (3) conceptual shifts in site nutrient availability with altered disturbance frequency. We expect that this framework will be sufficiently robust to improve our understanding of biogeochemical outcomes across new disturbance types, regimes, and interactions.

CHARACTERIZING TERRESTRIAL ECOSYSTEMS BY PARTITIONING RATIOS

In a mature terrestrial ecosystem (that is, when aboveground biomass accumulation has plateaued), nutrients are entrained into ecosystem cycles and accumulated predominantly in soils and vegetation. For this accumulation to occur, a balance has to be maintained between soil and plant processes; soil organic matter (SOM) cannot accumulate without the litter produced by vegetation and the vegetation cannot grow and continue to produce organic matter without the nutrients mineralized from the SOM. In addition, the accumulation of nutrients has to be synchronized; nitrogen (N) cannot accumulate in the ecosystem unless P and other vital nutrients also accumulate and vice versa. We posit that the ratio between soil and plant nutrient stocks represents a characteristic property of an ecosystem that can be quantified empirically, both to better allow cross-system comparisons and to provide insight into the fluxes between pools (given that internal cycling fluxes are often much larger than input and output fluxes) (Rastetter and others 2013). We call this value the *partitioning ratio*.

There is empirical support for characteristic differences in the partitioning ratio among ecosystems at the biome scale. For illustrative purposes we focus our discussion on N, the most commonly limiting nutrient in terrestrial ecosystems, although it should be recognized this element has unique characteristics such as significant organic forms, multiple loss pathways, and multiple biotically mediated transformations. As an example, six types of North American forests ranging from boreal

moist in British Columbia to subtropical dry in Texas exhibit wide variability in soil N: vegetation N, spanning 1.3–40.9 across total soil N pools ranging from 724 to 6929 kg ha⁻¹ (Figure 1a) (Ponder and others 2012). However, for the four forest types with sufficient sample size, there are separate, unique values of soil N: vegetation N (Figure 1b). These results suggest that boreal and temperate forested biomes as a whole may

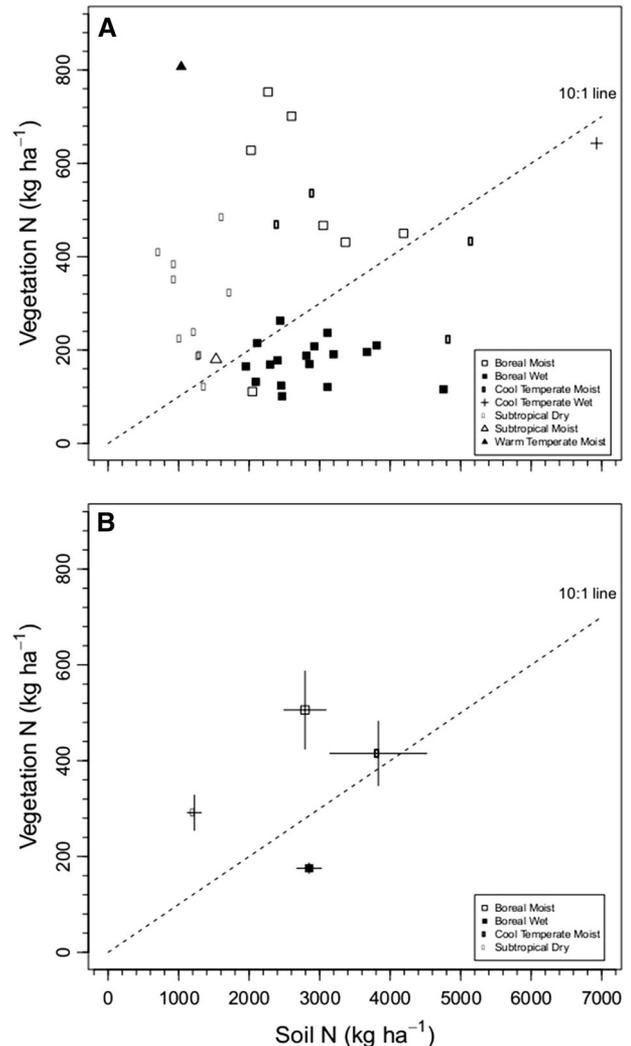


Figure 1. **A** Ratios of soil N and vegetation N pools in 41 forests in North America that are part of the long-term soil productivity network (Ponder and others 2012). **B** Mean values for four Holdridge life zones with one standard error for both soil and vegetation N. Vegetation N includes both tree bole and tree crown N, whereas soil N includes both O horizon and mineral soil N measured to 20 cm depth. Sites represent a variety of successional stages, climate types, and dominant species. Locations: British Columbia, Ontario, Louisiana, Mississippi, Texas, Washington, Missouri, North Carolina, and Idaho.

demonstrate consistent and predictable partitioning ratios, at least in late successional stages.

This partitioning ratio concept may extend to other biomes beyond temperate forests. For example, grasslands contain large belowground N stocks in the soil pool relative to aboveground biomass. A prairie in Oklahoma (U.S.A.) had a partitioning ratio of 232 over a three-year period in the 1970s (Risser and others 1981). Deserts of the southwestern U.S. generally have both low aboveground biomass and low SOM stocks. Their N partitioning ratios range from 4 to 203 depending on the dominant vegetation type [for example, mesquite, sagebrush, creosote, and paloverde (West and Skujins 1978)]. Tropical forests with relatively organic-poor soils have low soil nutrient stocks relative to vegetation nutrient stocks and exhibit partitioning ratios of 1.6 to 4.8 (Jordan 1985). Thus, the quantification of soil and plant nutrient stocks via a partitioning ratio appears to be a useful characteristic descriptor of biomes.

SINGLE DISTURBANCE EVENTS AND RECOVERY OF NUTRIENT STOCKS

Disturbance events can immediately and dramatically alter the ratio of soil and vegetation N stocks, shifting the system away from the partitioning ratio. For example, a wildfire on Alaskan tundra in 2007 changed the N partitioning ratio from 16.8 to nearly infinity due to the complete combustion of aboveground biomass (Mack and others 2011). It is our contention that ecosystems undergo a predictable trajectory in recovery of nutrient stocks and partitioning ratios during a return to the pre-disturbance condition over secondary successional timescales (Jordan and others 1972; Vitousek and Reiners 1975). The ratio between soil and plant nutrient stocks represents a characteristic property of an ecosystem such that over time, the internal and external factors affecting a given ecosystem cause this ratio to be “attracted” (*sensu* Haeussler 2011) to a characteristic value.

To illustrate, after a disturbance event we postulate a redistribution phase where there is a net release of nutrients from soil and net accumulation by plants (Figure 2). If the nutrient is limiting to growth during the recovery, the recovery trajectory will parallel the isopleths of total ecosystem nutrient or be slightly above and to the right of those isopleths if nutrient is also accumulated in the ecosystem as a whole. If the nutrient is not limiting during recovery, there will tend to be a net loss from the ecosystem and the recovery trajectory will

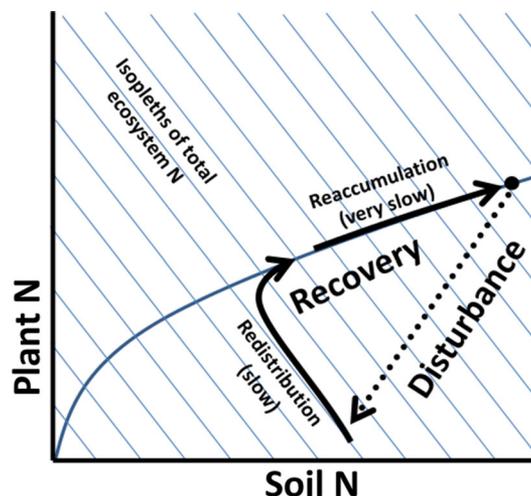


Figure 2. Plant nitrogen (N) and soil N plot illustrating theoretical trajectories of nutrient recovery after disturbance to re-establish characteristic partitioning ratios of an ecosystem. The trajectory of succession in the plot proceeds up and toward the right as the ecosystem accumulates nutrient. The exact trajectory will depend on the local environmental conditions (climate, parent material, topography, potential biota), but because of the slow rate of nutrient accumulation, the plant and soil process will remain in balance. Isopleths of total nutrient in the ecosystem (vegetation and soil, assuming negligible nutrient content in other ecosystem components) are diagonal lines in this plot.

be below and to the left of the isopleths of total ecosystem nutrient. This redistribution trajectory should approach the pre-disturbance baseline as plant and soil processes come back into balance. Once the balance is re-established, the ecosystem will be more effective at entraining and retaining nutrients in the ecosystem cycle and from that point on, the recovery trajectory should coincide with characteristic partitioning ratio of the ecosystem. DeAngelis (1980) hypothesized that this recovery time reflected system energetics, in particular the mean transit time of essential and nonessential nutrients recycled between soils and vegetation during succession.

Several post-disturbance sampling sequences indicate some degree of predictable temporal change in soil N: vegetation N over time (Johnson and Turner 2014). In lodgepole pine forests of the Greater Yellowstone ecosystem, soil N and vegetation N stocks recovered at different rates during 331 years after stand-replacing fires, converging on a characteristic partitioning ratio over time (Smithwick and others 2009). In tropical rainforests of the Andean foothills in western Amazonia, the partitioning ratio changed from 39 at three

years post-disturbance, to 7.25 at 25–30 years post-disturbance, relative to a ratio of 2.2 in primary forest (Scott 1978). Although we emphasize ratios because of the balance struck between plant:soil nutrient cycles in the conceptual model, the absolute amounts of ecosystem nutrient capital (isopleths in Figure 2) could also be a vital measure of biogeochemical recovery under many applications.

The initial effect of a disturbance on the partitioning ratio and nutrient stocks depends on the specific mechanism because the biogeochemical consequences of disturbance events are not simply loss of nutrients. Disturbances can also increase ecosystem nutrient stocks or change their distributions among pools. This argues for the need to expand current definitions of disturbance. Examples of disturbance increasing nutrient stocks (either concurrent with the disturbance event or displaced over time) include deposition of calcium-rich volcanic ash (Ayris and Delmelle 2012), post-fire N fixation by early successional plants such as alder (Perakis and others 2011), sediment deposition during floodplain disturbances (Appling 2012), thermokarst delivery of phosphorus (P) to tundra, or anthropogenic N additions (Block and others 2012). These types of accreting disturbance events are an important counterexample to the traditional view of disturbance as reducing terrestrial ecosystem nutrient stocks.

MODELING NUTRIENT STOCK RECOVERY TO A DISTURBANCE EVENT ACROSS CONTRASTING ECOSYSTEMS

To illustrate how ecosystems with differing partitioning ratios may recover N stocks following a

disturbance event, we used the multiple element limitation (MEL) model with parameters as described by Rastetter and others (2013) (Figure 3). The MEL model was used to simulate three broadly contrasting ecosystems in the U.S.A.: (1) the mixed deciduous and coniferous forest of Hubbard Brook Experimental Forest, located in New Hampshire (Bormann and Likens 1979), (2) temperate wet coniferous forest of the H. J. Andrews Experimental Forest in Oregon (Harmon 1992), and (3) Arctic tundra at the Toolik Lake Long Term Ecological Research site in Alaska (Hobbie and Kling 2014). We calculated the partitioning ratio for N (soil N:vegetation N) at steady state for each ecosystem. The partitioning ratios at Hubbard Brook, H. J. Andrews, and Toolik Lake were 10.1, 5.5, and 52.7, respectively. A disturbance was simulated in the model by removing 90% of the aboveground biomass. To simulate a range of successional pathways, 80 or 100% of the predisturbance biomass was added to the soil and coarse woody debris pools following the disturbance event.

In all three modeled ecosystems there was a temporal trajectory of return to the original partitioning ratio after the disturbance event but at greatly different rates because the mechanisms of recovery differed among the three ecosystems (Figure 3). The quantity of biomass returned to the system has a slight effect on the rate of recovery, but recovery pathways are quite similar. Symbiotic N fixation is not thought to be a major component of the recovery at Hubbard Brook or Toolik Lake, but it is a major contributor to the N budget during the recovery at H.J. Andrews. Hence, the N trajectory for H.J. Andrews indicates a net gain of N by the ecosystem soon after the disturbance, which is

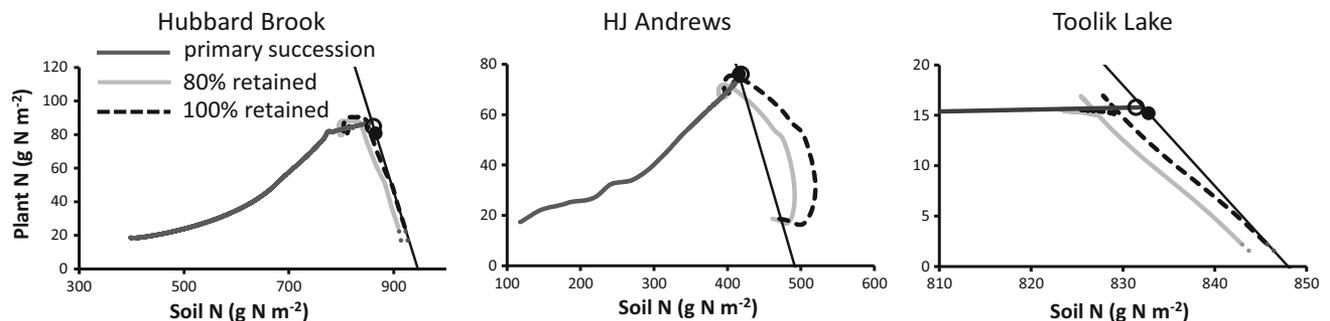


Figure 3. Trajectory of N recovery in vegetation versus soil following disturbance at the Hubbard Brook, H.J. Andrews, and Toolik Lake LTER sites as predicted by the multiple element limitation (MEL) model. The *filled circles* are the assumed steady state values for each ecosystem (to which the model was calibrated). The thin black lines are isopleths of constant total ecosystem N (soil + plant N). The solid lines represent the trajectory of recovery following a 90% removal of vegetation biomass with either 80% or 100% of that removed biomass added to the soil and coarse woody debris pools. Points above and to the right of the line have more N than the steady state and points below and to the left have less.

then lost during later stages of succession. Note that the recovery trajectories following disturbance converge at a lower point in succession rather than returning directly to predisturbance levels. This convergence results from the loss of nutrients in the disturbance and in the early recovery phase. These nutrients need to be recovered before the relative stasis of a mature ecosystem can be reached. There is potentially a high capacity for predicting post-disturbance trajectories with this framework. In addition to measuring the immediate effects of a disturbance (accreting or depleting in terms of any given soil nutrient stock, such as a reduction in soil N), the relative ratio change through time could be predicted based on known successional ratio development.

ASSESSING BIOGEOCHEMICAL VULNERABILITY TO DISTURBANCES

The partitioning ratio could theoretically be used to predict biogeochemical vulnerability to disturbances. Forest scientists have proposed analogous “stability ratios” for ranking the sensitivity of sites to nutrient loss through disturbance and corresponding vegetation removal (Himes and others 2014). Conceptually, sites with proportionally greater allocation of nutrients in vegetation are at risk of diminished productivity due to direct losses through disturbance. Himes and others (2014) postulated that forested sites with stability ratios less than 0.1 have low risk, those with 0.1–0.3 have minor risk, those with 0.3–0.5 have significant risk, and those with greater than 0.5 have an immediate and high risk of productivity declines. In their analysis of forests in the Pacific Northwest, the areas with the highest concentrations of at-risk sites were those with young, glacially derived soils.

Stability ratios have in many cases not been empirically confirmed, but this is an area of active research through programs such as the Long-term soil productivity study (LTSP) (Powers 2006) and the Centre for International Forestry Research (Saint-André and others 2008). Over the first 10 years of the LTSP study, the complete site-level organic matter removal treatment has not yet resulted in significant overall declines in regenerating stand productivity (Ponder and others 2012), but early trends indicate some differing sensitivities to nutrient loss by forest soil type (for example, deeply weathered subtropical soils versus less developed glacial soils) that may corroborate the partitioning ratio concept. More significant effects of nutrient removal may appear after canopy closure,

when regenerating forests place greater demands on soil nutrients (Thiffault and others 2011), but it is also possible that losses in nutrient stocks will result in only temporary, rather than permanent, reductions in growth capacity as soil processes recover (Egnell 2011). For example, recent studies in the Brazilian Cerrado forest/savanna ecotone suggest that less fertile sites are more sensitive to changes in fire frequency, likely because fire-induced losses of nutrients greatly exceed the supply of nutrients (de Dantas and others 2013; Pellegrini and others 2014). Alternatively, there is evidence that tropical savannas are well adapted to fire (Bond 2008; Staver and others 2011), and the long-term nutrient balance of these biomes seems to not be altered, as N supply can keep pace with losses from periodic, low intensity disturbance.

STABILITY OF NUTRIENT STOCKS UNDER SHIFTING DISTURBANCE FREQUENCIES

It might be argued that, as illustrated by the modeling exercise, a single disturbance event may be less a question of ‘if’ nutrient stocks recover but rather a question of ‘when’. We suggest more fundamental alterations in nutrient stocks and partitioning ratios may require changes in disturbance frequency or intensity over multiple generations of a plant community (for example, many decades for grasslands, many centuries for forests). A number of mechanisms have been identified or hypothesized as drivers in the biogeochemical response of ecosystems to disturbance frequency and intensity (Gorham and others 1979), such as bryophyte- and lichen-associated N fixation, water table fluctuations, mineral weathering rates, forest floor accumulations, and inputs of ericaceous plant roots (Antoine 2004; Zackrisson and others 2004; Simard and others 2007; Hazlett and others 2011; Clemmensen and others 2013). Quantification of these processes further develops the concept of accreting or depleting disturbances by identifying mechanisms of biogeochemical change. Both processes might even occur simultaneously, as in the positive and negative aspects of forest floor accumulation and loss (Prescott and others 2000). The strength of these constructive and destructive processes may mean that shifts in disturbance frequency could push biogeochemical cycles to support either an altered productive capacity of the ecosystem, or perhaps an entirely new, alternative stable state (Reiners 1983).

We have conceptually portrayed these possible interactions of site properties with disturbance

frequency to illustrate how ecosystems may respond with increased, decreased, or no change in long-term nutrient supply rates (Figure 4). Ecosystems exhibiting low sensitivity to excessive disturbance (that is, showing small changes in total nutrient capital, point A in Figure 4) would theoretically have rapid vegetation recovery with a significant component of N-fixing plants, soils with high buffering capacity, weatherable minerals for P and base cation replenishment, and a high allocation of site nutrients in belowground pools. Ecosystems exhibiting high sensitivity to excessive disturbance (point B) would be relatively slow to revegetate, highly prone to nutrient leaching (high precipitation regime, low retention capacity of the soil) and nutrient volatilization (deep, dry surface

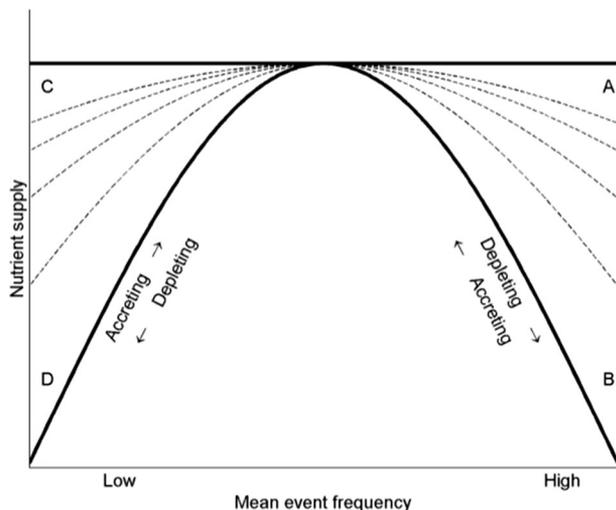


Figure 4. Conceptual figure of how disturbance frequency can balance the potentially accreting and depleting processes affecting ecosystem nutrient capital. Projected response ranges from complete loss (*lower portion* of the *converse black curve*) to no effect (*top, flat black line*) of disturbance frequency on nutrient supply. Points A through D represent four contrasting ecosystem responses as described in the text; for example, a coniferous forest that requires a sufficient return interval of fire to sustain productivity because nutrients immobilized in stand biomass and forest floors of old-growth are released for a new cycle of growth (*left side* of the *black curve* moving toward the center, marked D). Higher fire frequency, however, could be destructive (moving from center to the *right side* of the *black curve*, marked B) because nutrients are depleted faster than they can be replaced, thereby lowering ecosystem productivity. Every ecosystem and site type could occupy a unique spot in the conceptual figure, helping researchers formulate specific hypotheses on how disturbance frequency may be constructive, destructive, or of no consequence to nutrient supply and ecosystem productivity.

organic accumulations), low rates of symbiotic and asymbiotic N fixation, highly weathered soils, and a high allocation of site nutrients in aboveground pools. Ecosystems with low sensitivity to reduced disturbance frequency (point C) would have efficient and sustainable nutrient cycling between soils and vegetation (low loss rates), adequate ongoing replenishment of sequestered nutrients (via mineral weathering and N fixation), and balanced organic matter inputs (for example, wood, litter, roots, bryophytes) and outputs (decomposition). Mechanisms leading to a high sensitivity to infrequent disturbances (point D) would be excessive nutrient immobilization through biomass sequestration, detrimental changes over time in soil thermal properties or drainage (cooling via forest floor accumulations, paludification), reduced rhizodeposition, and high inputs of low-quality litter such as peat or ericaceous plants. These characterizations of ecosystem properties and responses to multiple disturbances should generate several testable hypotheses suitable for cross-biome synthesis.

CONCLUSIONS

- The partitioning ratio (soil N: vegetation N) could be a useful and fundamental characterization of terrestrial ecosystems, as well as a simple predictor of ecosystem resilience to disturbance. More experimental evidence to identify ecosystems that may be sensitive or insensitive to nutrient losses from aboveground disturbance should be collected from a variety of ecosystems and successional states.
- We suggest that classifying disturbances by their biogeochemical impacts may improve understanding of their long-term consequences on ecosystems. Particularly, disturbances can be considered accreting or depleting depending on whether they increase or decrease nutrient stocks. Standardization of accretion or depletion will, in some cases, require consideration of return intervals, establishment of common timeframes for disturbance events, and assessment of typical spatial patterns to facilitate cross-biome comparisons.
- Sustainable management of forest, grassland, and other terrestrial ecosystems over long time periods can be conceptualized and tested by considering how changes in disturbance frequency (for example, livestock grazing intensity, forest plantation rotation age) might balance the

accreting and depleting processes influencing soil nutrient availability.

- Further development of this framework could focus on multiple elements in state space. Our modeling results indicate that the post-disturbance ecosystem trajectories reflect cycling rates and stoichiometry in plant and soil pools. Stoichiometry is also likely to be important in post-disturbance trajectories of the empirical partitioning ratio.

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REFERENCES

- Antoine ME. 2004. An ecophysiological approach to quantifying nitrogen fixation by *Lobaria oregana*. *Bryologist* 107:82–7.
- Appling AP. 2012. Connectivity drives function: carbon and nitrogen dynamics in a floodplain-aquifer ecosystem. Durham: Duke University.
- Ayris PM, Delmelle P. 2012. The immediate environmental effects of tephra emission. *Bull Volcanol* 74:1905–36.
- Baker WL. 2009. Fire ecology in rocky mountain landscapes. Washington DC: Island Press.
- Belyea LR, Baird AJ. 2006. Beyond ‘the limits to peat bog growth’: cross-scale feedback in peatland development. *Ecol Monogr* 76:299–322.
- Block CE, Knoepp JD, Elliott KJ, Fraterrigo JM. 2012. Impacts of hemlock loss on nitrogen retention vary with soil nitrogen availability in the southern Appalachian mountains. *Ecosystems* 15:1108–20.
- Bond WJ. 2008. What limits trees in C-4 grasslands and savannas? *Annu Rev Ecol Evol Syst* 39:641–59.
- Bormann FH, Likens GE. 1979. Pattern and process in a forested ecosystem. New York: Springer.
- Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339:1615–18.
- de Dantas VL, Batalha MA, Pausas JG. 2013. Fire drives functional thresholds on the savanna–forest transition. *Ecology* 94:2454–63.
- DeAngelis DL. 1980. Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* 61:764–71.
- Davidson EA, de Carvalho CJR, Figueira AM, Ishida FY, Ometto JP, Nardoto GB, Saba RT, Hayashi SN, Leal EC, Vieira IC, Martinelli L. 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447:995–8.
- Dennison PE, Brewer SC, Arnold JD, Moritz MA. 2014. Large wildfire trends in the western United States, 1984–2011. *Geophys Res Lett* 41:2928–33.
- Donnelly JP, Woodruff JD. 2007. Intense hurricane activity over the past 5,000 years controlled by El Niño and the West African monsoon. *Nature* 447:465–8.
- Egnell G. 2011. Is the productivity decline in Norway spruce following whole-tree harvesting in the final felling in boreal Sweden permanent or temporary? *Forest Ecol Manag* 261:148–53.
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A. 2003. The importance of land-use legacies to ecology and conservation. *Bioscience* 53:77–88.
- Gorham E, Vitousek PM, Reiners WA. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annu Rev Ecol Syst* 10:53–84.
- Gough C, Vogel C, Harrold K, George K, Curtis P. 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Global Change Biol* 13:1935–49.
- Harmon ME. 1992. Long-term experiments on log decomposition at the H.J. Andrews Experimental Forest. PNW-GTR-280, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Haeussler S. 2011. Rethinking biogeoclimatic ecosystem classification for a changing world. *Environ Rev* 19:254–77.
- Hazlett PW, Curry JM, Weldon TP. 2011. Assessing decadal change in mineral soil cation chemistry at the Turkey Lakes watershed. *Soil Sci Soc Am J* 75:287–305.
- Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN, Vogelmann J. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biol* 18:7–34.
- Higuera PE, Briles CE, Whitlock C. 2014. Fire-regime complacency and sensitivity to centennial-through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA. *J Ecol* 102:1429–41.
- Himes AJ, Turnblom EC, Harrison RB, Littke KM, Devine WD, Zabowski D, Briggs DG. 2014. Predicting risk of long-term nitrogen depletion under whole-tree harvesting in the Coastal Pacific Northwest. *Forest Sci* 60:382–90.
- Hobbie JE, Kling GW. 2014. Alaska’s changing arctic: ecological consequences for tundra, streams, and lakes. Oxford: Oxford University Press.
- Johnson DW, Turner J. 2014. Nitrogen budgets of forest ecosystems: a review. *Forest Ecol Manag* 318:370–9.
- Jordan CF. 1985. Nutrient cycling in tropical forest ecosystems. Chichester: Wiley.
- Jordan CF, Cline JR, Sasscer DS. 1972. Relative stability of mineral cycles in forest ecosystems. *Am Nat* 106:237–53.
- Mack MC, Bret-Harte MS, Hollingsworth TN, Jandt RR, Schuur EAG, Shaver GR, Verbyla DL. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* 475:489–92.
- Marlon JR, Bartlein PJ, Gavin DG, Long CJ, Anderson RS, Briles CE, Brown KJ, Colombaroli D, Hallett DJ, Power MJ, Scharf

- EA, Walsh MK. 2012. Long-term perspective on wildfires in the western USA. *Proc Natl Acad Sci USA* 109:E535–43.
- Paré D, Rochon P, Brais S. 2002. Assessing the geochemical balance of managed boreal forests. *Ecol Indic* 1:293–311.
- Pearce AR, Rastetter EB, Kwiatkowski BL, Bowden WB, Mack MC, Jiang Y. 2015. Recovery of Arctic tundra from thermal erosion disturbance is constrained by nutrient accumulation: a modeling analysis. *Ecol Appl*, in press. <http://dx.doi.org/10.1890/14-1323.1>
- Pellegrini AFA, Hoffmann WA, Franco AC. 2014. Carbon accumulation and nitrogen pool recovery during transitions from savanna to forest in central Brazil. *Ecology* 95:342–52.
- Perakis SS, Sinkhorn ER, Compton JE. 2011. Delta(15)N constraints on long-term nitrogen balances in temperate forests. *Oecologia* 167:793–807.
- Peters DPC, Lugo AE, Chapin III FS, Pickett STA, Duniway M, Rocha AV, Swanson FJ, Laney C, Jones J. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2:art81.
- Pickett STA, White PS. 1985. *The ecology of natural disturbance and patch dynamics*. NY: Academic Press.
- Ponder F Jr, Fleming RL, Berch S, Busse MD, Elioff JD, Hazlett PW, Kabzems RD, Kranabetter JM, Morris DM, Page-Dumroese D, Palik BJ, Powers RF, Sanchez FG, Scott DA, Stagg RH, Stone DM, Young DH, Zhang J, Ludovici KH, McKenney DW, Mossa DS, Sanborn PT, Voldseth RA. 2012. Effects of organic matter removal, soil compaction and vegetation control on 10th year biomass and foliar nutrition: LTSP continent-wide comparisons. *Forest Ecol Manag* 278:35–54.
- Powers RF. 2006. Long-Term Soil Productivity: genesis of the concept and principles behind the program. *Can J Forest Res* 36:519–28.
- Prescott CE, Maynard DG, Laiho R. 2000. Humus in northern forests: friend or foe? *Forest Ecol Manag* 133:23–36.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58:501–17.
- Rastetter EB, Yanai RD, Thomas RQ, Vadeboncoeur MA, Fahey TJ, Fisk MC, Kwiatkowski BL, Hamburg SP. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. *Ecol Appl* 23:621–42.
- Reiners WA. 1983. Disturbance and basic properties of ecosystem energetics. In: Mooney HM, Gordon M, Eds. *Disturbance and ecosystems: components of response*. Ecological Studies, vol 44, New York: Springer, pp 83–98.
- Risser PG, Birney EC, Blocker HD, May SW, Parton WJ, Wiens JA. 1981. *The true prairie ecosystem*. Stroudsburg: Academic Press.
- Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems* 14:1196–215.
- Running SW. 2008. Ecosystem disturbance, carbon, and climate. *Science* 321:652–3.
- Saint-André L, Laclau J-P, Deleporte P, Gava JL, Gonçalves JL, Mendham D, Nzila JD, Smith C, duToit B, Xu DP, Sankaran KV, Marien JN, Nouvellon Y, Bouillet J-P, Ranger J. 2008. Slash and litter management effects on Eucalyptus productivity: a synthesis using a growth and yield modelling approach. Nambiar EKS, editor. *Site management and productivity in tropical plantation forests: workshop proceedings, 22–26 November 2004, Piracicaba, Brazil and 6–9 November, Bogor, Indonesia*. Center for International Forestry Research, Bogor, Indonesia. pp 173–189.
- Scott GAJ. 1978. *Grassland development in the Gran Pajonal of eastern Peru*. Honolulu: University of Hawaii.
- Simard M, Lecomte N, Bergeron Y, Bernier PY, Paré D. 2007. Forest productivity decline caused by successional paludification of boreal soils. *Ecol Appl* 17:1619–37.
- Smithwick EAH, Kashian DM, Ryan MG, Turner MG. 2009. Long-term nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. *Ecosystems* 12:792–806.
- Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–2.
- Thiffault E, Hannam KD, Paré D, Titus BD, Hazlett PW, Maynard DG, Brais S. 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests—a review. *Environ Rev* 19:278–309.
- Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–49.
- Vitousek PM, Reiners WA. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25:376–81.
- Walker LR, Wardle DA. 2014. Plant succession as an integrator of contrasting ecological time scales. *Trends Ecol Evol* 29:504–10.
- West NE, Skujins JJ. 1978. *Nitrogen in desert ecosystems*. Stroudsburg: Academic Press.
- Zackrisson O, DeLuca TH, Nilsson M-C, Sellstedt A, Berglund LM. 2004. Nitrogen fixation increases with successional age in boreal forests. *Ecology* 85:3327–34.