Ecosystem Recovery from Disturbance Is Constrained by N Cycle Openness, Vegetation-Soil N Distribution, Form of N Losses, and the Balance between Vegetation and Soil-Microbial Processes

Short title: Biogeochemical Recovery from Disturbance

Edward B. Rastetter[1*], George W. Kling[2], Gaius R. Shaver[1], Byron C. Crump[3], Laura Gough[4], and Kevin L. Griffin[5]

* Corresponding Author, erastetter@mbl.edu, 508 289 7483
1 The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543
2 Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109
3 College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331
4 Department of Biological Sciences, Towson University, Towson, MD 21252
5 Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964

This work derived from the conceptual framework used to guide the Arctic Long-Term Ecological Research (ARC LTER) Project titled “LTER: The Role of Biogeochemical and Community Openness in Governing Arctic Ecosystem Response to Climate Change and Disturbance.” All authors contributed to this conceptual framework, helped interpret the simulations, and helped write the paper.

Ecosystems In press.

Abstract

We present a framework for assessing biogeochemical recovery of terrestrial ecosystems from disturbance. We identify three recovery phases. In Phase 1, nitrogen is redistributed from soil organic matter to vegetation, but the ecosystem continues to lose nitrogen because the recovering vegetation cannot take up nitrogen as fast as it is released from soil. In Phase 2, the ecosystem begins re-accumulating nitrogen and converges on a quasi-steady state in which vegetation and soil-microbial processes are in balance. In Phase 3, vegetation and soil-microbial processes remain in balance and the ecosystem slowly re-accumulates the remaining nitrogen. Phase 3 follows a balanced-accumulation trajectory along a continuum of quasi-steady states that approaches the true steady state asymptotically. We examine the effects of three ecosystem properties on recovery: openness of the nitrogen cycle, nitrogen distribution in and turnover between vegetation and soils, and the proportion of nitrogen losses that are in a refractory form. Openness exacerbates Phase 1 nitrogen losses but speeds recovery in Phases 2 and 3. A high fraction of ecosystem nitrogen in vegetation, resulting from nitrogen turnover that is slow in vegetation but fast in soil, exacerbates Phase 1 nitrogen losses but speeds recovery in Phases 2 and 3. A high proportion of nitrogen loss in refractory form mitigates Phase 1 nitrogen losses and speeds recovery in Phases 2 and 3. Application of our conceptual framework requires empirical recognition of the continuum of quasi-steady states constituting the balanced-accumulation trajectory and a distinction between the balanced-accumulation trajectory and the true steady state.

Key words

Element cycles, disturbance, biogeochemistry of succession, plant-soil interactions, ecosystem development, nutrient accumulation, organic matter accumulation

Highlights

Ecosystem development entails biogeochemical balance between plant and soil processes
Recovery first reestablishes this balance before elements can re-accumulate
Recovery is constrained by element cycle openness, distribution, and chemical form of losses

Introduction

How ecosystems develop through time and the effects of disturbance on development are long-standing questions in ecology (e.g., Odum 1969, Odum and others 1995). Recent syntheses have advanced the theory and conceptual framework of development and disturbance by suggesting roles for legacy effects (Gaiser and others 2020) and the effects of pulsed dynamics and disturbance on recovery (Kominoski and others 2018, Jentsch and White 2019). Ecosystems can lose a substantial fraction of their biomass and nutrient capital as a result of disturbance. In the long term, the ecosystem must re-accumulate these nutrients to rebuild biomass and fully recover. In the short term, however, the need to re-accumulate nutrients can be mitigated if residual nutrient stocks can be retained within the ecosystem and the initial recovery of vegetation can be supported, at least in part, by tapping into these residual nutrient stocks (Yanai and others 2013, Lovett and others 2018). Here we argue that these recovery processes are subject to (1) the relative dependence of the ecosystem on external versus internal nutrient sources (nutrient cycle openness), (2) the pre-disturbance distribution of nutrients between vegetation and soils, and (3) how readily further nutrient losses can be curtailed by vegetation and soil microbes (the form of nutrient loss). We further argue that the recovery from such disturbances requires that vegetation and soil-microbial processes first come into balance before the ecosystem can re-accumulate its lost nutrient capital. Perspectives on these factors affecting recovery from disturbance have evolved substantially in the literature.

Based on extensive observations of Northern Hardwood forests and building on ideas put forth by Odum (1969) and Vitousek and Reiners (1975), Bormann and Likens (1979, 1994) present a conceptual model of forest recovery from the removal of vegetation. They make two assumptions about nutrient sources, both of which could have significant effects on the dynamics of ecosystem recovery from disturbance. First, although they acknowledge that following disturbance "the ecosystem 'digs deeply' into its nutrient capital to effect repair" (Bormann and Likens 1994), they assume that the very large stocks of soil organic matter in mineral soil "have only minor influence on the overall biomass balance of the ecosystem." Second, because the observed rate of nitrogen (N) accumulation exceeds the amount that can be accounted for in measured input-output budgets, they assume non-symbiotic N fixation rates that are over twice the annual inputs in precipitation and about ten times larger than non-symbiotic N fixation rates estimated by Roskoski (1980).

Yanai and others (2013) reevaluated the N cycle in Northern Hardwood forests. They found that mineral soil holds over 70% of the total ecosystem N stock. However, the uncertainty in this estimate is too large to assess temporal changes in mineral soil N from their data. Nevertheless, they speculate that the N accumulating in vegetation and forest floor following disturbance could come from the slow turnover of this very large N stock in mineral soil rather than from non-symbiotic N fixation; just the uncertainty in their estimate of mineral soil N is comparable to the total amount of N in the mature vegetation and could account for over 50 years of N at the fixation rate assumed by Bormann and Likens (1994). Hooker and Compton (2003) and Compton and others (2007) found that the total ecosystem N remained constant in abandoned agricultural fields for 100 years, but the regrowth of vegetation and buildup of forests floor was supported by a redistribution of N from mineral soil to vegetation. Lovett and others (2018) revised the Bormann and Likens (1994) conceptual model to include mineral-soil N as both a means to retain N within the ecosystem following the disturbance and as a source of N for recovering vegetation and accumulating forest floor. Rastetter and others (2013) report the same role for mineral soil N in a modeling study. This redistribution pattern is consistent with data from Mayes and others (2019) on African woodland and with the conceptual model of Figueiredo and others (2019) for Amazonian rainforest. Based on data from a wide variety of tropical and temperate forests, Jordan (1985) makes similar inferences about both the large fraction of ecosystem N stocks in soils and the role soil N might play in the recovery of vegetation after disturbance. However, he also acknowledges the vital role of N fixation in both ecosystem development and recovery from disturbance.

The differences in perspective between Bormann and Likens (1994) and those of Yanai and others (2013) and Lovett and others (2018) amount to a difference in the presumed openness of the N cycle in these forests. In many terrestrial ecosystems, essential elements like N and phosphorus (P) are tightly cycled, at least when the ecosystems are mature (Vitousek and Reiners 1975). The dependence on recycled N and P in most mature terrestrial ecosystems is possible because of the entrainment of external elements into the internal ecosystem cycle and their slow accumulation over thousands of years of soil and vegetation development (Jenny 1941, Walker and Syers 1976, Post and others 1985, Kranabetter and others 2016).

The long-term entrainment and retention of elements in terrestrial ecosystems depends on balanced interactions between vegetation and soil-microbial processes. Without the elements released from soil organic matter and made available to plants by microbial activity (Lambers and others 2008), plants would fix much less carbon (C) into new organic matter, and organic matter accumulation in vegetation would slow substantially. Without the C-rich litter from plants, organic matter could not accumulate in soils, and soil microbes would neither accumulate mineral elements into microbial biomass and soil organic matter nor re-release those elements in a labile form available to plants to support their further growth and accumulation of organic matter in vegetation (organic C, N, P, etc.). If plants and soil microbes did not take up the elements entering the ecosystem or released from soils, the elements would be more susceptible to being washed out of or otherwise lost from the ecosystem and could not accumulate (Jordan 1985). Thus, there is a codependence between vegetation and soil-microbial processes that must remain in balance for C and other elements to accumulate in an ecosystem.

This codependence between vegetation and soil-microbial processes should strengthen as an ecosystem develops. As elements like N and P accumulate, the vegetation and soil microbes become more reliant on the recycling of these elements within the ecosystem and less reliant on external element sources. At maturity, recycled N and P accounts for over 90% of plant requirements in forests (Whittaker and others 1979, Sollins and others 1980, Yanai 1992), over 80% in grassland and prairies (Blair and others 1998, Knapp and others 1998), and over 95% in arctic tundra (Shaver and others 1992).

This high rate of internal cycling is the basis for the major biogeochemical feedback between vegetation and soil-microbial processes. This feedback, acting on a time scale of years to decades, is fast relative to the slow accumulation of nutrients from external sources, which can take centuries to millennia in primary succession. Following perturbation, any system with processes acting on such different time scales is likely to undergo a fast initial response toward a quasi-steady state (the proximate attractor; Birkhoff 1927) followed by a slower, asymptotic response toward the true steady state (the ultimate attractor; Segel and Slemrod 1989). For terrestrial ecosystems, we hypothesize that, after a disturbance that removes vegetation, the initial, fast response to the disturbance is a redistribution of elements like N and P from soil to vegetation. This redistribution will move the ecosystem toward a quasi-steady state in which vegetation and soil-microbial processes come into relative balance in terms of the cycling of nutrients like N and P. This quasi-steady state should be determined by the amount of nutrient the ecosystem is able to retain following the disturbance. At the quasi-steady state, the ecosystem should be more effective at retaining and re-accumulating nutrients. As these nutrients are slowly re-accumulated from external sources, the quasi-steady state will move toward the ultimate steady state. We define this trajectory traced by the quasi-steady state, in which the ecosystem accumulates nutrients, and vegetation and soil-microbial processes remain in relative balance, as the *balanced-accumulation trajectory*. The balanced-accumulation trajectory should be uniquely determined by the local climate, underlying parent material, topography, and biota (Jenny 1941, Brady 1974, Vitousek and Reiners 1975, van Cleve and others 1983, Chapin and others 1994, Vitousek 2004, Vitousek and others 2010).

In this paper we use a simple model of coupled C and N fluxes in terrestrial ecosystems as an example to examine biogeochemical aspects of ecosystem recovery from disturbances that redistribute C and N from vegetation to soils, remove vegetation, or remove both vegetation and soil. We focus our analysis on three properties of the ecosystem N cycle:

(A) **Openness:** the rate of external N inputs to the ecosystem divided by the steady-state rate of N uptake by vegetation as an indicator of the ratio of ecosystem N throughput to internal N cycling. Because openness is a measure of both N inputs and outputs relative to internal cycling, it determines both the potential rate of N accumulation in the ecosystem and the potential for N losses following a disturbance.

(B) **Vegetation-soil N distribution:** the percent of total ecosystem N stocks in the vegetation versus soil at steady state, which with a tight (nearly closed) N cycle is an indicator of the relative rates of N turnover in vegetation versus soils. Because most disturbances in terrestrial ecosystems involve a disproportionate loss of vegetation biomass relative to soil organic matter, the vegetation-soil N distribution determines the potential for vegetation recovery based on an internal redistribution of N from soil to vegetation.

(C) **Refractory N loss:** the fraction of total N losses from the ecosystem at steady state that cannot be curtailed by increased uptake by either vegetation or soil microbes (e.g., loss of recalcitrant dissolved organic N). Because refractory N must first accumulate in the ecosystem before it can contribute to N losses, a high fraction of total N losses in refractory form can slow total N losses and thereby increase the rate of N accumulation following a disturbance that resulted in a loss of N capital.

Methods

Model: We simplify the representation of ecosystem C and N budgets as much as possible to optimize the heuristic value of our model (Rastetter 2017). The model is complex enough to represent the interactions between C and N and between vegetation and soil-microbial processes that are important to the questions we address, but still simple enough to be broadly illustrative of terrestrial ecosystems and easily implemented and analyzed. We develop the model based on five mass-balance equations (Fig. 1, Table 1 Eqs. 1-5, Table 2) representing changes in C and N in vegetation biomass (B_C & B_N), C and N in soil organic matter and associated microbes and fauna (D_C & D_N), and inorganic N (N). We assume a constant CO_2 concentration available in the atmosphere, which makes the CO_2 supply effectively infinite. In contrast, available inorganic N in the soil is "depletable" (*sensu* Rastetter and Shaver 1992) and must therefore be replenished from sources outside the ecosystem or through recycling from soil organic matter. Photosynthesis (P_s, Eq. 6) and N uptake by vegetation (U_N, Eq. 7) are each Michaelis-Menten functions of, respectively, atmospheric CO_2 (C_a) and inorganic N (N). However, these rates are modified first by an allometric constraint (S, Eq. 8) that results in an asymptotic increase in uptake as biomass increases (e.g., canopy closure, full exploitation of soil volume by roots; Rastetter and Ågren 2002) and second by a vegetation stoichiometric constraint (Ψ, Eq. 11) that compensates for any element imbalance by decreasing photosynthesis and increasing N uptake as the C:N ratio of biomass increases. The rate of C loss from vegetation in litter fall (L_{itC}, Eq. 9) is simply proportional to vegetation C. The rate of N loss from vegetation in litter fall (L_{itN}, Eq. 10) is proportional to vegetation N, but modified by the vegetation stoichiometric constraint (Ψ) to decrease N losses as the vegetation C:N ratio increases. Carbon loss through autotrophic respiration (R_a, Eq. 12) increases in proportion to vegetation C, but is modified by the vegetation stoichiometric constraint (Ψ) to increase respiration as the C:N ratio of vegetation increases. Immobilization of inorganic N into soil organic matter by soil microbes (U_{Nm}, Eq. 13) is a Michaelis-Menten function of inorganic N (N), is proportional to soil organic C (D_C), and is modified by the soil stoichiometric constraint (Φ, Eq. 14) to increase as the soil C:N ratio increases. Heterotrophic respiration (R_h, Eq. 15) is proportional to soil C (D_C) and increases with the soil stoichiometric constraint (Φ) as the soil C:N ratio increases. Mineralization of N from soil organic matter (N_{min}, Eq. 16) is proportional to soil organic N (D_N) but is modified by the soil stoichiometric constraint (Φ) to decrease as the soil C:N ratio increases. We assume refractory N losses (Q_{NR}, Eq. 18) are directly from the soil organic matter and are proportional to soil organic N (D_N). Because refractory N losses are assumed to be organic, we include an organic C loss (Q_{CR}, Eq. 17) that is proportional to the loss of refractory N (Q_{NR}). We recognize that labile organic N also cycles and is lost from the ecosystem. We assume that most of this labile organic N is rapidly taken up into soil organic matter by soil microbes and is therefore retained within the soil organic matter and that any uptake by plants or losses from the ecosystem can be lumped in with the dynamics of inorganic N. Losses of inorganic N (Q_{DIN}, Eq. 19) from the ecosystem are proportional to inorganic N (N). We assume atmospheric CO_2 concentration (C_a) is constant and the same in all simulations (400 μmol mol^{-1}). The input of N from outside the ecosystem into the inorganic N pool (N_{in}) is also constant for any simulation but varies among simulations (see appendix Table A1).

The differential equations are solved numerically with a 4th/5th order Runge-Kutta integrator with adapting time steps to optimize precision and computation time (Press and others 1986). The model is coded in Lazarus 2.0.4 (2019) Free Pascal. Inputs to the model are all parameter values, initial values for all state variables, and values for all driver variables for all time steps (see appendix Table A1). Outputs from the model are all state and process variables for each time step.

Parameterization: We run simulations for a 2 × 2 × 2 factorial experiment on (A) openness, (B) vegetation-soil N distribution, and (C) refractory N loss. This experimental design results in parameterization of the model for eight hypothetical ecosystems that differ in these three properties but are otherwise the same (see appendix Table A1). At steady state, all eight ecosystems have the same total amount of organic N in soils plus vegetation (700 g N m^{-2}), the same amount of inorganic N (1 g N m^{-2}), and the same parameter values for all the processes except the rate parameters for litter-fall losses of C and N (m_{CB} & m_{NB}), heterotrophic respiration (r_D), N mineralization (m_{Nm}), and the losses of inorganic and refractory N (β_N and β_{NR}). We adjust these six parameters and the N input rate (N_{in}) to set (1) the steady-state inputs and losses of N relative to internal N cycling (openness), (2) the steady-state amounts of N in soils and vegetation (vegetation-soil N distribution), and (3) the steady-state rates of ecosystem N losses from the inorganic N pool and from soil organic matter (refractory N loss). We chose characteristics that are intermediate among several types of terrestrial ecosystems in terms of the range of reported values of openness and N distribution between vegetation and soils (Nagy and others 2017, Rastetter 2011, Rastetter and others 2013, Pearce and others 2015, Woodmansee and Dugan 1980, Blair and others 1998, and Risser and Parton 1982; see Appendix Fig. A1).

To set the **openness** of the N cycles, we adjust the N input to the ecosystem (N_{in}) to either 3% (Ecosystems 1, 3, 5, & 7) or 20% (Ecosystems 2, 4, 6, & 8) of the steady-state N uptake by vegetation (U_N at steady state). Thus, the less-open ecosystem has 97% of the plant-required N supplied internally at steady state, whereas the more-open ecosystem has only 80% of the plant-required N supplied internally. We then adjust the N loss rate parameters (β_N & β_{NR}) so that the steady-state concentration of inorganic N (N) equals 1 g N m^{-2} and inorganic plus refractory N losses equal the N inputs. In the ecosystems with refractory N losses, we compensate for the extra losses of soil organic C and N by adjusting soil respiration and N mineralization parameters (r_D & m_{Nm}) so that at steady state the soil C:N ratio is 20 and the soil has either 90 or 95% of the organic N in the ecosystem (depending on the vegetation-soil N distribution for that ecosystem).

To set the **vegetation-soil N distribution**, we adjust vegetation and soil N turnover rates (m_{NB} and m_{Nm}) until the total organic N in the ecosystem is 700 g N m^{-2} and either 5% (fast-vegetation turnover, slow-soil turnover; Ecosystems 3, 4, 7, & 8) or 10% (slow-vegetation turnover, fast-soil turnover; Ecosystems 1, 2, 5, & 6) of the organic N in the ecosystems is in vegetation at steady state. We then adjust vegetation C turnover in litter and soil respiration (m_{CB} snd r_D) so that the steady-state C:N ratios of the vegetation and soils are, respectively, 100 and 20 g C g^{-1} N (i.e., $B_C/B_N = q_B$ and $D_C/D_N = q_D$).

To set the **refractory N losses**, we adjust the two N loss rate parameters (β_N & β_{NR}) until steady-state refractory losses are either 0% (Ecosystems 1 - 4) or 95% (Ecosystems 5 - 8) of the total N losses. To compensate for the extra organic losses of N and C from the soil organic matter, we also adjust the parameters for N mineralization (m_{Nm}) and heterotrophic respiration (r_D) to maintain 90% or 95% of the total ecosystem N at steady state in soils and to maintain the soil C:N ratio of 20. The magnitude of refractory N losses was found to influence C sequestration in response to climate change in an earlier modeling study (Rastetter and others 2005). A wide range of dissolved organic N losses have been reported based on stream chemistry (<20% to > 80% of total N losses; Goodale and others 2000, McHale and others 2000, Buffam and others 2001, Perakis and Hedin 2002, Qualls and others 2002). However, this N has likely been processed several times along the flow path from leaving the rooting zone to the location of measurement in the stream (Newbold and others 1982, Hedin and others 1998, Kroeger 2003). Therefore, in the ecosystems with refractory N losses we assume 95% of the N losses are refractory in our simulations based on the dissolved organic N reported by Currie and others (1996) for the deep root zone of a Northern Hardwood forest.

Analyses: For each of these eight ecosystems we generate a balanced-accumulation trajectory by approximating the quasi-steady state for specified total ecosystem N stocks. To make this approximation, we first set $N_{in} = Q_{NR} + Q_{DIN}$ so that N losses are instantly returned to the ecosystem and there is no net loss or gain of N. For the ecosystems with only inorganic N losses, this constraint is equivalent to setting the inputs and losses of N to zero. For the ecosystems with organic N losses, the constraint effectively augments heterotrophic respiration and N mineralization by the amounts of C and N that would have been lost as dissolved organic matter, but does not alter the turnover rate of soil organic matter. We then set the amounts of N in vegetation, soil organic matter, and inorganic N to 0.4, 0.4, and 0.2 (total of 1 g N m^{-2}) and run the model to a near steady state until the derivatives for all five state variables are less than 0.01% to the standing stock ($dX/dt < 0.0001\ X$, for all $X = B_C, B_N, D_C, D_N$, and N). We then increment D_N by 1 g N m^{-2} and again allow the system to come to a near steady state and repeat the incremental increase in N until the total ecosystem N equals the 701 g N m^{-2} to which the model is parameterized at steady state. Our argument for the quasi-steady state above is based on the fast rate of internal N cycling relative to the slow rate of N inputs from outside the ecosystem. This condition is clearly violated at low biomass when the rate of internal cycling is much smaller. We nevertheless extend our estimates of the balanced-accumulation trajectory to low biomass to serve as a means to compare dynamics among ecosystems, but acknowledge that at low biomass it is the external supply of N that dominates dynamics and there is therefore no quasi-steady state.

For each of the eight ecosystems we present four simulations. To represent ecosystem development from bare ground, we run one simulation starting with no soil organic matter and only 1 g C m^{-2} and 0.01 g N m^{-2} in vegetation biomass (some finite amount of vegetation biomass is required to initiate growth). We also run three disturbance-recovery simulations starting with 1 g C m^{-2} and 0.01 g N m^{-2} in vegetation biomass. In one of these disturbance simulations we simulate a blow down by adding the C and N removed from the mature vegetation to the soil organic matter (i.e., transfer C and N from vegetation to soil, but leave the total ecosystem C and N unchanged from the steady state). In the other two disturbance simulations, we simulate a removal of vegetation (e.g., harvest) and a removal of vegetation and part of the soil (e.g., as might result from fire) by removing all but the 1 g C m^{-2} and 0.01 g N m^{-2} from the vegetation and removing either 0% (harvest) or 30% (fire) of the steady-state soil organic matter. We acknowledge the caveat that with the constant parameters in our simple heuristic model we cannot capture dynamics associated with the changes in species composition that occur during both primary and secondary succession.

Results

Because our analysis is based on the accumulation and distribution of N in ecosystems, we present our primary results on phase-plane plots of vegetation N versus total soil N (inorganic plus organic: Figs. 2 & 3). Changes in total ecosystem N and in the distribution of N can thereby be represented by a single trajectory on these phase-plane plots (Kranabetter and others 2016).

Effects of ecosystem properties on the balanced-accumulation trajectory: Along the continuum of quasi-steady states represented by the balanced-accumulation trajectory, vegetation N increases monotonically as soil N increases for all eight of the simulated ecosystems and terminates at the true steady state (thick long-dash lines in Figs. 2 & 3). Because this terminus is anchored by the steady state, the *vegetation-soil N distribution* at steady state (property B above) has a major effect on the balanced-accumulation trajectory. *Openness* (property A) has no effect on the balanced-accumulation trajectory in ecosystems with only inorganic N losses because we effectively close the N cycle to estimate each quasi-steady state along the continuum. In ecosystems with refractory N losses the effect of openness is very small. *Refractory N loss* (property C) has only a small effect on the balanced-accumulation trajectory, shifting the N distribution very slightly toward the soil because the organic N loss is returned to the inorganic N pool in our estimation of the quasi-steady state.

Effects of ecosystem properties on ecosystem development from bare ground: When developing from bare ground, vegetation in all eight ecosystems initially accumulates N from sources external to the ecosystem. This reliance on external N sources places the developing ecosystem above the balanced-accumulation trajectory in the phase-plane plots (solid lines in

Figs. 2 & 3). The developing ecosystem then converges on the balanced-accumulation trajectory as it depends more and more on internally recycled N. Because the approach to the steady state is asymptotic, the rate of N accumulation in the ecosystem decreases exponentially through time.

OPENNESS: The magnitude of the initial displacement above the balanced-accumulation trajectory is larger with a faster external N supply (displacement larger for more-open ecosystems in right panels than less-open ecosystems in left panels in Figs. 2 & 3). As the soil develops, N mineralization increases until it becomes the major source of N to the vegetation. Thus, after the initially rapid growth, the vegetation becomes more dependent on N recycled within the ecosystem, vegetation and soil N accumulate in tandem, and the ecosystem converges on the balanced-accumulation trajectory. Nevertheless, the more-open ecosystems continue to accumulate N about six times faster than the less-open ecosystems (bottom of Table 3).

VEGETATION-SOIL N DISTRIBUTION: Because vegetation in the driver of biomass and organic matter accumulation and N accumulation is into that biomass and organic matter, ecosystems with 10% of their N in vegetation at steady state accumulate N 30-80% faster than ecosystems with only 5% of the N in vegetation (bottom of Table 3). Because the ecosystem converges on the balanced-accumulation trajectory as it develops, the vegetation-soil N distribution at steady state has a major effect on the development trajectory. As a result, N accumulates about ten times faster in soils than vegetation in ecosystems with 10% of the N in vegetation at steady state and about twenty times faster in ecosystems with only 5% of the N in vegetation at steady state (Table 3).

REFRACTORY N LOSS: Refractory N losses are proportional to the amount of soil organic N that has been accumulated. Thus, because of the initially low soil organic matter, ecosystems with refractory N losses accumulate N faster than ecosystems with only inorganic N losses (bottom of Table 3). In ecosystems with 10% of the N in vegetation at steady state, the accumulation is about 40-50% faster with refractory N losses. In ecosystems with 5% of the N in vegetation at steady state, the accumulation is only about 5-20% faster.

Recovery trajectories: Recovery from disturbance in our simulations proceeds in three Phases (Fig. 4). In Phase 1, if the residual soil releases N faster than the now smaller amount of vegetation can take it up, the ecosystem continues to lose N. The N accumulated in vegetation during Phase 1 is derived predominantly from a redistribution of N from soils to vegetation (Figs. 2 & 3). The duration and amount of N lost in Phase 1 depends on the amount of soil left after the disturbance, the recovery rate of the vegetation, and the supply rate of N from outside the ecosystem.

In Phase 2, the vegetation has recovered enough that it accumulates N at least as fast as it is released from soils. Nevertheless, most of the N accumulated in vegetation is still derived from residual soil N stocks and the net accumulation by the whole ecosystem during Phase 2 is small. By the end of Phase 2, the recovery trajectory converges on the balanced-accumulation trajectory (with some damped oscillations, Figs. 2 & 3).

Most of the N lost in the disturbance and during Phase 1 of recovery is re-accumulated in Phase 3 once vegetation and soil-microbial processes have come back into balance (Fig. 4). This Phase-3 re-accumulation of N in our simulations closely follows the balanced-accumulation trajectory and is constrained in the same way as ecosystem development from bare ground. Progress toward the steady state during Phase 3 is very slow (Table 3).

Phase 1 recovery: All but two of the recovery trajectories crossed or nearly reached the balanced-accumulation trajectories during Phase 1 of recovery (Figs. 2 & 3; exceptions discussed below). Thus, in Phase 1 although the soil is losing N faster than the vegetation takes it up, and overall the ecosystem is therefore losing N, in most cases the vegetation is able to sequester enough N to return to the balanced-accumulation trajectory before the ecosystem as a whole starts to gain N. In half the ecosystems, the Phase 1 recovery trajectories are very close to the total ecosystem N isopleths (Figs 2 & 3), indicating that these ecosystems conserve their N stocks tightly. This tight N retention is especially true of ecosystems that are less open (slower throughput) and ecosystems with refractory N losses.

Accumulation of N in vegetation is much faster during Phase 1 of recovery than during the development of vegetation from bare ground (Table 3). This fast recovery of vegetation is possible because it is fueled predominantly by microbial release of soil organic N and the consequent redistribution of residual organic N from soils to vegetation. During Phase 1, the rate of N loss from soils in the less-open ecosystems is 4.7 to 13.2 times faster than the supply of N from outside the ecosystem. In the more-open systems, the rate of N loss from soils is only 0.8 to 2.7 times the supply of N. Except in the case of the blow-down disturbance where no C is removed from the ecosystem in the disturbance, following an initial loss of total ecosystem C, the transfer of N from soil (C:N = 20) to vegetation (C:N = 100) results in a net accumulation of C in the ecosystem by the end of Phase 1.

The two simulations in which the recovery trajectory did not approach the balanced-accumulation trajectory during Phase 1 are the recoveries of ecosystems 7 and 8 from vegetation removal and 30% loss of soil organic matter. In these two simulations, the ecosystems began accumulating N immediately and therefore began Phase-2 recovery without Phase 1 (Figs. 3, A2, & A3). In addition to the 30% loss of soil organic N, the other two factors both of these ecosystems have in common are that 95% of their N is in soils and 95% of their total N losses at steady state are as refractory N. Each of these three factors contributes to low Phase-1 N loss, as discussed below.

In the blow-down simulations, C-rich organic matter from vegetation is added to the soil, which favors immobilization of N into soil organic matter (Vitousek and Matson 1984). There is therefore a smaller loss of N from the ecosystem following the blow down than if organic matter is left untouched (Fig. 5). Also, the high immobilization of N following a blowdown makes less N available for plant growth, and it makes the recovery of vegetation N slower than if soil organic matter is left untouched (Table 3).

OPENNESS: The reliance on large internal N stocks even in the more open ecosystems means that the initial recovery of vegetation is not strongly affected by the external N supply. However, during Phase 1 of recovery as microbes continue to mineralize soil N in excess of plant requirements, inorganic N accumulates and is subject to faster loss. Because openness increases throughput and therefore increases losses as much as inputs, the Phase 1 losses are faster and larger in more-open ecosystems (Fig. 5). Nevertheless, the nearly 7-fold increase in N inputs in the more open ecosystems is not enough to compensate for the N-immobilization effect of C-rich organic matter from the blow down on vegetation recovery (Table 3).

VEGETATION-SOIL N DISTRIBUTION: Ecosystems with less vegetation N and more soil N at steady state have slower rates of soil N turnover. Thus, Phase 1 N accumulation in vegetation is substantially slower in ecosystems that have less N in vegetation at steady state (Table 3). Nevertheless, because there is less vegetation biomass to recover in these ecosystems, the recovery trajectories cross the balanced-accumulation trajectory in roughly the same amount of time in both ecosystems with high and low vegetation N at steady state. The ecosystems with more vegetation N and less soil N at steady state have faster rates of soil N turnover. This fast N turnover enhances the buildup of inorganic N during Phase 1 recovery, resulting in higher Phase-

1 N losses from ecosystems with more N in vegetation (Fig. 5; curves slant more to the left in upper panels than in lower panels in Figs. 2 & 3).

REFRACTORY N LOSS: In the ecosystems where most of the steady-state N loss is refractory N, inorganic N losses are small relative to the stock of inorganic N (small β_N). Thus, with high refractory N losses, the inorganic N that accumulates during Phase 1 is less susceptible to loss. Therefore, high refractory N losses and commensurately low inorganic N losses mitigate Phase-1 total N losses, especially in ecosystems with more-open N cycles (Fig. 5; recovery curves slant further to the left in Fig. 2 than in Fig. 3, especially in panels on the right). In addition, losses of N are lower in simulations where soil organic matter is removed in the disturbance because there is less organic N in these ecosystems to be mineralized and become susceptible to loss (Fig. 5). This effect of organic matter removal is particularly evident in Ecosystems 7 and 8 in the simulations with 30% soil-organic-matter removal; as discussed previously, in these simulations the ecosystems began accumulating N immediately so there was no Phase 1 and therefore no Phase-1 N loss. The effect is also evident in Ecosystems 3 and 5, which lose very little N during Phase 1 of recovery from vegetation removal and a 30% soil-organic-matter removal.

Phase 2 recovery: During Phase 2 of recovery, the ecosystems begin to re-accumulate N lost in the disturbance and during Phase 1 of the recovery. As in ecosystem development from bare ground, this accumulation of N is constrained by the supply rate of external sources of N. Therefore, although Phase 2 has a long duration in all the simulations, the amount of N gained is small relative to the initial losses in the disturbance (see appendix Table A2). In addition, because most of the simulations approached the balanced-accumulation trajectory in Phase 1 of recovery, there is very little redistribution of N from the residual soil to the vegetation during Phase 2. In the two simulations where the recovery *did not* approach the balanced-accumulation trajectory by the end of Phase 1 (ecosystems 7 & 8 with 30% soil removed), the initial Phase-2 trajectory is almost exclusively a redistribution of N from soils to vegetation (Figs. 3, A2, & A3). The small amount of N that is accumulated in Phase 2 is mostly toward the end of Phase 2 as the recovery trajectory converges on the balanced-accumulation trajectory in a damped oscillation. The amount of N accumulated during Phase 2 increases with the amount of N lost in the initial disturbance (Fig. 5; largest accumulation in disturbance with 30% soil loss and smallest accumulation in blowdown disturbance).

OPENNESS: Because the N accumulation rate is constrained by the supply rate of external N, the rates of Phase-2 N re-accumulation are roughly comparable in magnitude to the rates of N accumulation during development from bare ground in ecosystems with comparable total N stocks. In all cases the ecosystems with more-open N cycles accumulated N faster than those with less-open N cycles (Fig. 5).

VEGETATION-SOIL N DISTRIBUTION: Ecosystems with 10% of their N in vegetation at steady state had faster Phase-2 N accumulation rates than ecosystems with less N in the steady-state vegetation (Fig. 5). As with ecosystem development from bare ground, more vegetation biomass results in faster uptake of inorganic N, both directly by the vegetation and indirectly by the increased immobilization potential associated with more litter inputs to soil. The higher N uptake in turn leaves less inorganic N available to be lost. Hence the faster rate of Phase-2 N accumulation in ecosystems with more vegetation.

REFRACTORY N LOSS: The effects of refractory N losses on Phase-2 N accumulation are like those in the development from bare ground (discussed above); because refractory N loses are proportional to the amount of N that has accumulated in soil organic matter, in most simulations N accumulates in the ecosystem faster if most of the total N losses are in refractory form rather than as inorganic N. However, this effect is so weak that it is overridden by the effects of openness and vegetation-soil N distribution except when the N losses during the disturbance and during Phase 1 are large (e.g., when 30% of soil is removed).

Phase 3 recovery: As with the development from bare ground, the recovery trajectories converge on the balanced-accumulation trajectory during Phase 3. Except for the very small residual oscillations (<0.01% of vegetation N in recovery relative to development from bare ground), by Phase 3 the recovery trajectories are essentially the same as the trajectory of ecosystem development from bare ground. The effects of openness, vegetation-soil N distribution, and refractory N losses are therefore identical to those in the later stages of ecosystem development from bare ground. Most of the N re-accumulated in the recovery is accumulated during Phase 3 (see appendix Table A2).

Discussion

The balanced accumulation of elements in ecosystems is analogous to the concept of stoichiometrically balanced plant growth used by Ingestad and Ågren (1988) to analyze element limitation, uptake, and allocation in plants. The stoichiometric approach provides an idealized framework to assess the biogeochemical constraints and stimuli that regulate ecosystem recovery from disturbance. The most important result of our simulations is the three-phase trajectory of the recovery from disturbances that remove vegetation. In Phase 1, the ecosystem trends toward a quasi-steady state along the balanced-accumulation trajectory, not toward the true steady state. During this phase, N is redistributed from soils to vegetation but with some additional net loss of N from the ecosystem. Recovery of vegetation is fast during Phase 1 relative to later phases of recovery. In Phase 2, the ecosystem begins re-accumulating N as it converges on the balanced-accumulation trajectory. In Phase 3, most of the N lost in the disturbance and during Phase 1 is slowly re-accumulated along the balanced-accumulation trajectory. Our perspective on ecosystem recovery from disturbance suggests that the recovery dynamics identified by Jentsch and White (2019) should be partitioned into two phases, a fast initial approach to the quasi-steady state followed by a slow approach to the true steady state along the balanced-accumulation trajectory.

Bormann and Likens (1979, 1994) proposed an analogous conceptual model of forest recovery from disturbance in four phases: (1) a Reorganization phase "during which the ecosystem loses total biomass despite the accumulation of living biomass;" (2) an Aggradation phase in which total biomass, both living and dead, accumulates; (3) a Transition phase "during which total biomass declines"; and (4) a Steady State phase in which the "total biomass fluctuates about a mean." Our results suggest a conceptual model that differs from the one proposed by Bormann and Likens (1994) in several ways and extends the conceptual model proposed by Lovett and others (2018). First, rather than biomass, our conceptual model, like the Lovett and others (2018) model, is based on nutrients that are most often limiting to growth in terrestrial ecosystems (N or P) and are tightly cycled within ecosystems. Second, rather than a large increase in nutrient inputs through processes like N fixation, recovery from disturbance in our conceptual model is supported largely by a redistribution of residual nutrients from the soil to the vegetation (Figs. 2 & 3), as suggested by Yanai and others (2013) and Lovett and others (2018). This redistribution dynamic is also obvious with other models in which there is a more complex representation with multiple time scales in the soil dynamics (e.g., Rastetter and others 2013, Pearce and others 2015, Jiang and others 2015, Nagy and others 2017). Finally, if a large amount of nutrient is lost from the ecosystem as a result of the disturbance, our results suggest that the steady state in both the Bormann and Likens (1994) and Lovett and others (2018) conceptual models are most likely quasi-steady states and that the true steady state would only be approached very slowly, but could have the potential to sequester substantially more organic matter and nutrients.

In addition, the three phases in our recovery trajectories do not align well with the phases in the Bormann and Likens (1979, 1994) model (Fig. 4). In our Phase 1, the ecosystem loses N. However, this loss is not coincident with the biomass loss in the Reorganization phase of the Bormann and Likens (1994) model. During our Phase 1, the soil loses both C and N. Some of that N is accumulated in vegetation. Because the C:N ratio is so much higher in vegetation than soil, the ecosystem gains a substantial amount of C in the latter part of Phase 1. Thus, our Phase 1 includes both the Reorganization and at least part of the Aggradation phases in the Bormann and Likens (1994) model. Our Phase 2 likely includes the remainder of the Aggradation phase plus the Transition phase in the Bormann and Likens model. Our Phase 3 is a transition along a continuum of quasi-steady states in which most of the N lost as a result of the disturbance is re-accumulated and is therefore not analogous to the steady state phase in the Bormann and Likens (1994) model.

The empirical challenge in applying our conceptual model following a disturbance is to recognize the reestablishment of balance between vegetation and soil-microbial processes and to distinguish between the continuum of quasi-steady states along our balanced-accumulation trajectory and the true steady state. The very slow progress during Phase 3 of the recovery trajectories and the spatial variability among ecosystems within the same biome will likely make this challenge difficult to address. Having comprehensive data on ecosystem characteristics before the disturbance will of course help in evaluating recovery back to the pre-disturbance state, but it will still be difficult to assess how close the ecosystem was to steady state before it was disturbed.

The simple structure and fixed parameters we use in our model enhances its heuristic value, but at the expense of the specifics that distinguish individual ecosystems. For example, our simple model does not allow us to capture changes in biogeochemical characteristics of the ecosystem associated with long-term successional changes in the vegetation and soil communities (e.g., Jordan 1985, Lambers and others 2008). However, our simulations encompass a wide range of vegetation and soil characteristics (appendix Fig. A1). For example, the transition from fast-turnover to slow-turnover vegetation can be viewed as a transition in the vegetation-soil N distribution (transition from lower to upper panels in Figs. 2 & 3). Similarly, changes in the community, like the exclusion of symbiotic N fixers (discussed below), might change the openness of an ecosystem during succession (transition from right to left panels in Figs. 2 & 3).

We examine the effects of three factors on ecosystem recovery from disturbance. The first is openness of cycles for elements like N. More-open ecosystems have both faster inputs and faster losses. Thus, they accumulate N faster during the later stages of recovery, but also lose more N early in recovery when vegetation uptake cannot keep up with N release from soils by microbes. The second factor we examine is the distribution of N between soil and vegetation at steady state. Ecosystems with low soil and high vegetation N stocks have fast soil N turnover and slow vegetation N turnover rates. The fast soil N turnover exacerbates the inability of plants to keep up with N release by soil microbes following disturbance and therefore results in higher N losses in Phase 1 of recovery, especially if most of the N loss from the ecosystem is as inorganic N rather than as refractory organic N. The third factor we examine is the proportion of total ecosystem N losses that are as refractory organic N versus inorganic N. Refractory stocks of N must first accumulate in soil before they can be lost from the ecosystem. In addition, with high refractory organic N losses and low inorganic N losses, inorganic N can accumulate and be taken up by vegetation and microbes before it is lost. Thus, ecosystem N losses during Phase 1 of recovery are mitigated if most of the losses are as refractory organic N because the accumulation of refractory N is slow and the accumulation of inorganic N is less susceptible to loss. This result is seemingly contrary to the results of Rastetter and others (2005) who found that high organic N losses resulted in lower C sequestration under elevated CO_2 and elevated CO_2 plus warming. However, elevated CO_2 and warming increase N demand by vegetation and microbes (through faster growth) whereas in our manipulations N demand decreases (through removal of plant biomass and less litter following disturbance).

The intensity of the disturbance also affects the pattern of recovery. In all our simulations we removed virtually all of the vegetation but either left the soil untouched or added or removed soil organic matter. Leaving high C:N-ratio slash after the disturbance, like we did in our blow-down simulations, has two major effects. First, because less N is removed from the ecosystem, less N needs to be re-accumulated in the recovery. Second, the slash enhances microbial immobilization of N and thereby keeps N in the ecosystem. This N immobilization can inhibit N uptake by vegetation and can slow vegetation growth early in recovery relative to an ecosystem where the soil is left untouched (Table 3). However, in the long term the retention of N in the ecosystem means less N needs to be re-accumulated in Phase 3 and thereby substantially accelerates full recovery (Figs. 2 & 3; see also Rastetter and others 2013). Removal of soil organic matter in the disturbance slows both initial and long-term recovery. Early in recovery, the loss of soil organic matter means there is less soil N that can be transferred to the recovering vegetation relative to ecosystems where the soil is untouched (Table 3). In the long term, removal of soil organic matter means that there is more N that needs to be re-accumulated in Phase 3 and thereby slows full recovery (Figs. 2 & 3).

Because the accumulation of elements like N is asymptotic, most terrestrial ecosystems would be recognized as "mature" well before the steady state. Disturbance often leaves legacy effects on ecosystems (Gaiser and others 2020); the delay in recovery along the balanced-accumulation trajectory is one such legacy. Indeed, many ecosystems are likely in a quasi-steady state and will not approach the true steady state before they are again harvested or disturbed. This disturbance cycle is easily incorporated into our conceptual framework. If an ecosystem is disturbed again before it can re-accumulate lost N, then its N stocks will ratchet back, and the new recovery trajectory will start with even less N than the previous recovery (Bormann and Likens 1979, Jordan 1985). The newest recovery will still approach the original balanced-accumulation trajectory, which is set by climate, biota, and edaphic factors. However, because of the asymptotic, concave downward nature of the N accumulation trajectories, lower total N stocks are accompanied by a faster N accumulation rate. Thus, with the ratcheting back of N stocks, there will be both less N to re-accumulate and a faster rate of accumulation. Phase 1 will be shorter and post-disturbance losses during Phase 1 will be smaller (compare duration and N loss in Phase 1 with 30% soil removal to other recoveries in appendix Table A2). Eventually the N stocks should ratchet down sufficiently to result in a stable limit cycle of disturbance and recovery on an average disturbance-return interval (see Appendix Fig. A4; Bormann and Likens 1979, Jordan 1985).

Our analysis also suggests strategies for fertilization schedules for harvested ecosystems. Adding fertilizer during Phase 1 of recovery might stimulate vegetation growth if losses from the ecosystem maintain nutrient concentrations below that needed to saturate plant uptake capacity. Thus, even though the vegetation is unable to take up the full amount of nutrient being released by the soil during Phase 1, as long as the uptake capacity is not saturated, that rate of uptake will still increase if the available concentration of the nutrient increases with fertilization. Nevertheless, our simulations, in agreement with Matson and others (1998), suggest that adding fertilizer during Phase 1 would be inefficient even if growth were stimulated because a large fraction of the added fertilizer would also be lost from the ecosystem. A more effective use of fertilizer would be to add it during Phases 2 or 3. Indeed the addition of fertilizer would substantially increase the rate of Phase 3 recovery because that rate is directly limited by nutrient supply from outside the ecosystem.

Like fertilization, symbiotic N fixation would accelerate N accumulation in the ecosystem during recovery. Conditions might be favorable for plant species with N-fixing symbionts early in recovery if the N release by soils is low enough while the canopy is still open (Rastetter and others 2001, Vitousek and others 2002). If so, then the ecosystem should initially behave like a more-open system and then transition to a less-open system as the plant species with N-fixing symbionts get excluded by later successional species (see appendix Fig. A5). In addition, N fixing species generally turn over N more rapidly (Vitousek and others 2002, Perakis and others 2012), which could shift the distribution of N from vegetation to soil. These issues are interesting topics for a future analysis.

Another direction for future analysis is the role of multiple-limiting resources. If, for example, the initial recovery was limited by P, how would the Phase 1 trajectory of N change? The expectation would be that the P limitation would slow vegetation recovery and therefore slow N uptake by vegetation. Inorganic N would therefore build up in the soil and be more readily lost, resulting in a higher loss of soil N relative to N accumulated by vegetation (tilting Phase 1 curves to the left in Figs. 2 & 3). But would the addition of P limitation also shift the position of the balanced-accumulation trajectory for N and thereby alter Phases 2 and 3 of the recovery? Eventually the N and P cycles would synchronize (Rastetter and others 2013), but what effect does this synchronization have on the shapes of the balanced-accumulation and recovery trajectories for both N and P?

In summary, we use a simple model to optimize the heuristic value of the analysis, allowing us to use a single model to compare dynamics among ecosystems with very different characteristics and responses to very different disturbances. This choice, of course, results in a degree of abstraction that would not be necessary in more-complex, more-realistic models. Nevertheless, our analysis should serve as a template against which the results of more complex models can be evaluated. The importance of internally recycled N on ecosystem responses to climate change is now well recognized (Schimel and others 1996, Thornton and others 2007, Compton and others 2007, Running 2008, Figueiredo and others 2019) and is being incorporated in more complex models (Comins and McMurtrie 1993, Comins 1997, Thornton and others 2009). In broad strokes, the more-complex models predict similar post-disturbance, three-phase recovery (e.g., Comins and McMurtrie 1993, Thornton and others 2002, Rastetter and others 2013). As long as recycling of nutrients within the ecosystem is fast relative to the rate of nutrient supply from outside the ecosystem, recovery from disturbance is likely to first approach a quasi-steady state in which vegetation and soil-microbial processes come into relative balance. The ecosystem should then follow a balanced-accumulation trajectory defined by a continuum of these quasi-steady states as the ecosystem continues to accumulate nutrients lost in the disturbance and approaches the true steady state. Our simulation results support the importance of three characteristics of ecosystems that all require further study in relation to ecosystem response to disturbance: (1) openness of element cycles, (2) distribution and turnover of elements in vegetation versus soils, and (3) refractory versus labile losses of vital elements.

Acknowledgements

This work was supported by the National Science Foundation through grants DEB-1651722, DEB-1556772, PLR-1603560, DEB-1754835, OPP-1841608, ARC-1603302, and especially the Arctic LTER DEB-1637459. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect those of the National Science Foundation. We would also like to thank the subject editor, Donald DeAngelis, as well as John Pastor and Pierre Quévreux for their helpful comments on the manuscript.

References:

Birkhoff, GD. 1927. Dynamical Systems. American Mathematical Society Colloquium Publications volume IX. DOI: http://dx.doi.org/10.1090/coll/009

Blair JM, Seastedt TR, Rice CW, Ramundo RA. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pp222-243 in Knapp, A, JM Briggs, DC Hartnett, and SL Collins (eds). Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York.

Bormann, FH, Likens, GE. 1979. Catastrophic Disturbance and the Steady State in Northern Hardwood Forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. American Scientist **67**: 660-669.

Bormann, FH, Likens, GE. 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Brady, NC. 1974. The Nature and Properties of Soils, 8th edition. MacMillan Publishing, New York.

Buffam, ID, Galloway JN, McGlathery KJ, Blum LK. 2001. Dissolved organic matter concentrations and bioavailability in an Appalachian stream during storms. Biogeochemistry **53**:269–306.

Chapin FS, III, Walker LR, Fastie CL, Sharman LC. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64: 149-175.

Comins, HN. 1997. Analysis of nutrient-cycling dynamics, for predicting sustainability and CO_2-response of nutrient-limited forest ecosystems. Ecol. Mod. 99:51-69.

Comins, HN, McMurtrie, RE. 1993. Long-term response of nutrient-limited forest to CO_2 enrichment: Equilibrium behavior of plant-soil models. Ecol. Appl. 3:666-681.

Compton, JE, Hooker, TD, Perakis, SS. 2007. Ecosystem N distribution and δ^{15} N during a century of forest regrowth after agricultural abandonment. Ecosystems 10: 1197-1208.

Currie WS, Aber JD, McDowell WH, Boone RD, Magill AH. 1996. Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. Biogeochemistry **35**:471–505.

Figueiredo, V, Enrich-Prast, A,Rutting, T. 2019. Evolution of nitrogen cycling in regrowing Amazonian rainforest. Nature Scientific Reports 9:8538. doi.org/10.1038/s41598-019-43963-4

Gaiser EE, Bell DM, Castorani MCN, Childers DL, Groffman PM, Jackson CR, Kominoski JS, Peters DPC, Pickett STA, Ripplinger J, Zinnert JC. 2020. Long-term ecological research and evolving frameworks of disturbance ecology. BioScience 70:141-156.

Goodale, CL, Aber JD, McDowell WH. 2000. The long-term effects of disturbance on organic and inorganic nitrogen export in the White Mountains, New Hampshire. Ecosystems 3:433–450.

Hedin, LO, von Fischer JC, Ostrom NE, Kennedy BP, Brown MG, Robertson GP. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil–stream interfaces. Ecology **79**: 684–703.

Hooker, TD, Compton, JE. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecol Appl 13:299-313.

Ingestad, T, Ågren GI. 1988. Nutrient uptake and allocation at steady-state nutrition. Physiol. Plant. 72:450-459.

Jenny, H. 1941. Factors of Soil Formation: A System of Quantitative Pedology. McGraw-Hill, New York, NY

Jentsch A, White P. 2019. A theory of pulse dynamics and disturbance in ecology. Ecology 100(7):e02734. 10.1002/ecy.2734

Jiang, Y, Rastetter, EB, Rocha, AV, Pearce, AR, Kwiatkowski, BL, Shaver, GR. 2015. Modeling Carbon-Nutrient interactions during the early recovery of tundra after fire. Ecol. Appl. 25:1640-1652.

Jordan CF. 1985. Nutrient Cycling in tropical forest ecosystems. Chichester: John Wiley and Sons.

Kominoski JS, Gaiser EE, Baer SG. 2018. Advancing theories of ecosystem development through long-term ecological research. BioScience 68:554-562.

Kranabetter, J, K McLauchlan K, S Enders S, J Fraterrigo J, P Higuera P, J Morris J, E Rastetter E, R Barnes R, Buma B, Gavin D, Gerhart L, Gillson L, Hietz P, Mack M, McNeil B, Perakis S. 2016. A framework to assess biogeochemical response to ecosystem disturbance using nutrient partitioning ratios. Ecosystems 19:387-395.

Kroeger, KD. 2003. Controls on magnitude and species composition of groundwater-transported nitrogen exports from glacial outwash plain watersheds. Dissertation. Boston University, Boston, Massachusetts, USA.

Lambers, H, Raven, JA, Shaver, G, Smith, SE. 2008. Specialized nutrient-acquisition strategies reflect plant adaptations to changing N and P status as soils change over geological time scales. Trends in Ecology and Evolution 23: 95-103

Lazarus 2.0.4 on http://www.lazarus-ide.org. 2019.

Lovett, GM, Goodale, CL, Ollinger, SV, Fuss, CB, Ouimette, AP, Likens, GE. 2018. Nutrient retention during ecosystem succession: A revised conceptual model. Front. Ecol. Environ. 16:532-538.

Matson, PA, Naylor R, Ortiz-Monasterio I. 1998. Integration of environmental, agronomic, and economic aspect of fertilizer management. Science 280:112-115.

Mayes, M, Melillo, J, Neill, C, Palm, C, Nyadzi, G. 2019. Nitrogen cycle patterns during forest regrowth in an African miombo woodland landscape. J Geophysical Res BiogeoSci 124:1591-1603.

McHale, MR, Mitchell MJ, McDonnell JJ, Cirmo CP. 2000. Nitrogen solutes in an Adirondack forested watershed: importance of dissolved organic nitrogen. Biogeochemistry **48**:165–184.

Nagy, RC, Rastetter, EB, Neill, C, Porder, S. 2017. Nutrient limitation in tropical secondary forests following different management practices. Ecol. Appl. 27:734-755.

Newbold, JD, O'Neill RV, Elwood JW, Van Winkle W. 1982. Nutrient spiraling in streams: implications for nutrient limitation and invertebrate activity. American Naturalist **120**:628–652.

Odum, EP. 1969. The strategy of ecosystem development. Science 164: 262-270.

Odum, WE, Odum EP, Odum HT. 1995. Nature's pulsing paradigm. Estuaries 18: 547–555.

Pearce, AR, Rastetter EB, Bowden WB, Mack MC, Jiang Y, Kwiatkowski BL. 2015. Recovery of arctic tundra from thermal erosion disturbance is constrained by nutrient accumulation: a modeling analysis. Ecological Applications 25:1271-1289

Perakis, SS, Hedin LO. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. Nature **415**:416–419.

Perakis, SS, Matkins JJ, Hibbs DE. 2012. N_2-fixing red alder indirectly accelerates ecosystem nitrogen cycling. Ecosystems 15: 1182-1193.

Post, WM, Pastor J, Zinke PJ, Stangenberger AG. 1985. Global patterns of soil nitrogen storage. Nature 317:613-616.

Press, WH, Flannery, BP, Teukolsky, SA, Vetterling, WT, 1986. Numerical Recipes: The Art of Scientific Computing. Cambridge University Press, Cambridge, UK.

Qualls, RG, Haines BL, Swank WT, Tyler SW. 2002. Retention of soluble organic nutrients by a forested ecosystem. Biogeochemistry **61**:135–171.

Rastetter, EB. 2011. Modeling coupled biogeochemical cycles. Frontiers in Ecology and the Environment 9:68-73.

Rastetter, EB. 2017. Modeling for understanding v. modeling for numbers. Ecosystems 20:215-221

Rastetter, EB, Ågren GI. 2002. Changes in Individual Allometry Can Lead to Species Coexistence without Niche Separation. Ecosystems 5: 789-801.

Rastetter EB, Shaver GR. 1992. A model of multiple element limitation for acclimating vegetation. Ecology 73:1157–74.

Rastetter, EB, Vitousek PM, Field C, Shaver GR, Herbert D, Ågren GI. 2001. Resource Optimization and Symbiotic N Fixation. Ecosystems 4:369-388

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. Ecological Applications 23:621-642.

Rastetter, EB, Perakis SS, Shaver GR, Ågren GI. 2005. Carbon Sequestration in Terrestrial Ecosystems Under Elevated CO_2 and Temperature: Role of Dissolved Organic N Loss. Ecological Applications 15:71-86.

Risser, PG, Parton WJ. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342-1351.

Roskoski, J. P. 1980. Nitrogen fixation in hardwood forests of the northeastern United States. Plant Soil (54) 33− 44.

Running, S. 2008. Ecosystem disturbance, carbon, and climate. Science 321:652-653.

Schimel, DS, Braswell, BH, McKeown, R, Ojima, DS, Parton, WJ, Pulliam, W. 1996. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochemical Cycles 10:677-692.

Segel LA, Slemrod M. 1989. The quasi-steady-state assumption: a case study in perturbation. SIAM Review 31: 446-477.

Shaver, GR, W. Billings WD, Chapin FS, III, Giblin AE, Nadelhoffer KJ, Oechel WC, Rastetter EB. 1992. Global change and the carbon balance of arctic ecosystems. BioScience 42(6):433-441.

Sollins, P, Grier CC, McCorison FM, Cromack K, Jr, Fogel R, Fredricksen RL. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in Western Oregon. Ecol. Monogr. 50:261-285.

Thornton, PE, Doney, SC, Lindsay, K, Moore, JK, Mahowald, N, Randerson, JT, Fung, I, Lamarque, J-F, Feddema, JJ, Lee, Y-H. 2009. Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: Results from an atmosphere-ocean general circulation model. Biogeosciences 6:2099-2120.

Thornton, PE, Lamarque, J-F, Rosenbloom, NA, Mahowald, NM. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. Global Biogeochemical Cycles 21: GB4018.

Thornton, PE, Law, BE, Gholz, HL, Clark, KL, Falge, E, Ellsworth, DS, Goldstein, AH, Monson, RK, Hollinger, D, Falk, N, Chen, J, Sparks, JP. 2002, Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, Agric. For. Meteorol., 113: 185– 222.

van Cleve, K, Dyrness CT, Viereck LA. Fox J, Chapin FS, III, Oechel W. 1983. Taiga ecosystems in interior Alaska. BioScience 33:39-44.

Vitousek, P. 2004. Nutrient Cycling and Limitation; Hawai'i as a Model System. Princeton University Press, Princeton NJ USA.

Vitousek, P, Matson, P. 1984. Mechanisms of nitrogen retention in forest ecosystems: A field experiment. Science 225: 51-52.

Vitousek, PM, Reiners WA. 1975. Ecosystem succession and nutrient retention: A hypothesis. BioScience 25: 376-381.

Vitousek, PM, Cassman, Cleveland C, Crews T, Field CB, Grimm N, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent J. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57/58:1-45.

Vitousek, PM, Porder S, Houlton BZ, Chadwick OA. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecological Applications 20:5-15.

Walker, TW, Syers JK. 1976. The fate of phosphorus during pedogenesis. Geoderma 15:1-19.

Whittaker, RH, Likens GE, Bormann FH, Eaton JS, Siccama TG. 1979. The Hubbard Brook ecosystem study: forest nutrient cycling and element behavior. Ecology 60:203–20.

Woodmansee RG, Duncan DA. 1980. Nitrogen and phosphorus dynamics and budgets in annual grasslands. Ecology 61:893-904. Knapp, AK, Briggs JM, Hartnettz DC, Collins SL. 1998. Grassland Dynamics. Oxford University Press, New York, New York, USA.

Yanai, RD. 1992. Phosphorus Budget of a 70-Year-Old Northern Hardwood Forest. Biogeochemistry 17:1-22.

Yanai, RD, Vadeboncoeur, MA, Hamburg, SP, Arthur, MA, Fuss, CB, Groffman, PM, Siccama, TG, Driscoll, CT. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a Northern Hardwood Forest. Environ. Sci. Technol (47) 11440-11448.

Tables:

Table 1: Model Equations. Variables and parameters defined in Table 2.

	CARBON		**NITROGEN**		**ALLOMETRY & STOICHIOMETRY CONSTRAINTS**
1	$\frac{dB_C}{dt} = P_s - L_{itC} - R_a$	2	$\frac{dB_N}{dt} = U_N - L_{itN}$		
3	$\frac{dD_C}{dt} = L_{itC} - R_h - Q_{CR}$	4	$\frac{dD_N}{dt} = L_{itN} + U_{Nm} - N_{min} - Q_{NR}$		
		5	$\frac{dN}{dt} = N_{in} + N_{min} - U_N - U_{Nm} - Q_{DIN}$		
6	$P_s = \frac{g_C}{\boldsymbol{\Psi}} S \frac{C_a}{k_C + C_a}$	7	$U_N = g_N \, \boldsymbol{\Psi} \, S \frac{N}{k_N + N}$	8	$S = B_C \frac{(\propto B_C + 1)}{(\gamma \, B_C + 1)}$
9	$L_{itC} = m_{CB} \, B_C$	10	$L_{itN} = \frac{m_{NB}}{\boldsymbol{\Psi}} B_N$	11	$\boldsymbol{\Psi} = \frac{B_C}{B_N \, q_B}$
12	$R_a = r_B \, B_C \, \boldsymbol{\Psi}$	13	$U_{Nm} = g_{Nm} \, \boldsymbol{\Phi} \, D_C \frac{N}{k_{Nm} + N}$	14	$\boldsymbol{\Phi} = \frac{D_C}{D_N \, q_D}$
15	$R_h = r_D \, D_C \, \boldsymbol{\Phi}$	16	$N_{min} = \frac{m_{Nm}}{\boldsymbol{\Phi}} \, D_N$		
17	$Q_{CR} = q_{DOM} \, Q_{NR}$	18	$Q_{NR} = \beta_{NR} D_N$		
		19	$Q_{DIN} = \beta_N \, N$		

Table 2: Variable and parameter definitions, symbols, and units

Variable or parameter	Symbol	Units
Vegetation C	B_C	g C m^{-2}
Detrital C	D_C	g C m^{-2}
Vegetation N	B_N	g N m^{-2}
Detrital N	D_N	g N m^{-2}
Inorganic N	N	g N m^{-2}
Photosynthesis	P_s	g C m^{-2} yr^{-1}
Autotrophic respiration	R_a	g C m^{-2} yr^{-1}
Litter-fall C	L_{itC}	g C m^{-2} yr^{-1}
Heterotrophic respiration	R_h	g C m^{-2} yr^{-1}
Vegetation N uptake	U_N	g N m^{-2} yr^{-1}
Litter-fall N	L_{itN}	g N m^{-2} yr^{-1}
Gross N mineralization	N_{min}	g N m^{-2} yr^{-1}
N immobilization	U_{Nm}	g N m^{-2} yr^{-1}
Inorganic N losses	Q_{DIN}	g N m^{-2} yr^{-1}
Refractory N losses	Q_{NR}	g N m^{-2} yr^{-1}
Refractory C losses	Q_{CR}	g C m^{-2} yr^{-1}
Allometric constraint	S	g C m^{-2}
Vegetation stoichiometric constraint	Ψ	none
Soil stoichiometric constraint	Φ	none
Atmospheric CO2	C_a	μmol mol^{-1}
N inputs	N_{in}	g N m^{-2} yr^{-1}
Allometric parameter 1	α	m^{2} g^{-1} C
Allometric parameter 2	γ	m^{2} g^{-1} C
Optimum vegetation C:N	q_B	g C g^{-1} N
Optimum soil C:N	q_D	g C g^{-1} N
Photosynthesis rate parameter	g_C	yr^{-1}
CO$_2$ half-saturation constant	k_C	μmol mol^{-1}
Autotrophic respiration constant	r_B	yr^{-1}
Vegetation C turnover rate constant	m_{CB}	yr^{-1}
Vegetation N-uptake rate parameter	g_N	g N g^{-1} C yr^{-1}
Vegetation N half-saturation constant	k_N	g N m^{-2}
Vegetation N turnover rate constant	m_{NB}	yr^{-1}
Heterotrophic respiration constant	r_D	yr^{-1}
Microbial N-uptake rate parameter	g_{Nm}	g N g^{-1} C yr^{-1}
Microbial N half-saturation constant	k_{Nm}	g N m^{-2}
Soil organic N turnover constant	m_{Nm}	yr^{-1}
C:N of DOM loss	q_{DOM}	g C g^{-1}N
N loss-rate parameter	β_N	yr^{-1}
Refractory N loss parameter	β_{NR}	yr^{-1}

Table 3: Vegetation, soil, and total N accumulation rates during the first forty years of the simulations. BG - simulations of ecosystem development from bare ground. BD – "blowdown" simulation transferring vegetation biomass to soils. 0% - removal of vegetation but leaving soil intact. 30% - removal of vegetation and 30% of soil organic matter. BG 400 - for comparison, N accumulation rates in the simulations of development from bare ground once 400 g N m^{-2} has accumulated in the ecosystem as an indicator of Phase 3 N accumulation rates.

g N m^{-2} yr^{-1}		**Ecosystem**							
		1	2	3	4	5	6	7	8
		Without refractory N losses				**With refractory N losses**			
		10% N in vegetation		**5% N in vegetation**		**10% N in vegetation**		**5% N in vegetation**	
		N_{in}= 3% U_N	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**
BG	Vegetation	0.08	0.27	0.04	0.14	0.08	0.32	0.04	0.14
	Soil	0.15	0.89	0.09	0.62	0.16	1.19	0.09	0.73
	Total	0.22	1.16	0.13	0.76	0.24	1.51	0.13	0.87
BD	Vegetation	1.41	1.19	0.85	0.80	1.52	1.49	0.87	0.87
	Soil	-3.46	-4.75	-1.01	-1.56	-1.86	-2.99	-0.88	-0.95
	Total	-2.05	-3.56	-0.16	-0.76	-0.34	-1.50	-0.01	-0.08
0%	Vegetation	1.41	1.17	0.93	0.83	1.71	1.58	0.97	0.98
	Soil	-4.01	-5.34	-1.29	-2.20	-2.24	-3.51	-0.99	-1.10
	Total	-2.60	-4.18	-0.36	-1.36	-0.53	-1.93	-0.02	-0.12
30%	Vegetation	1.16	0.98	0.73	0.69	1.35	1.33	0.75	0.78
	Soil	-2.30	-3.27	-0.88	-1.32	-1.44	-1.71	-0.72	-0.57
	Total	-1.14	-2.29	-0.14	-0.63	-0.09	-0.38	0.03	0.21
BG 400	Vegetation	0.007	0.038	0.002	0.014	0.009	0.057	0.003	0.017
	Soil	0.067	0.392	0.053	0.323	0.092	0.595	0.055	0.397
	Total	0.073	0.430	0.055	0.337	0.102	0.652	0.058	0.414

Figure captions:

Figure 1: A simple model of coupled carbon (C) and nitrogen (N) interactions in an ecosystem. **Stocks** - B_C autotrophic C, D_C detrital & heterotrophic C, B_N autotrophic N, D_N detrital & heterotrophic N, N available N. **Processes** - P_s photosynthesis, R_a autotrophic respiration, L_{itC} C in litterfall, R_h heterotrophic respiration, U_N autotrophic N uptake, L_{itN} N in litterfall, N_{min} gross N mineralization, U_{Nm} N uptake by heterotrophs, N_{in} inorganic N inputs, Q_{DIN} inorganic N losses, Q_{NR} refractory N loss, Q_{CR} refractory C loss.

Figure 2: Balanced-accumulation, ecosystem-development, and recovery trajectories on vegetation N versus soil N phase-plane plots for the four ecosystems with no refractory N losses. Thick, long-dashed line - balanced-accumulation trajectory. Solid gray lines - isopleths of total ecosystem N (vegetation plus soil N). Solid black line – ecosystem development from bare ground. Dotted line – blowdown simulations in which steady-state vegetation biomass is transferred to the soil. Dashed line – 0% soil removal simulation in which vegetation biomass is removed, but no soil is removed. Dash-dot line – 30% soil removal in which vegetation biomass is removed, and 30% of the steady-state soil is removed.

Figure 3: Balanced-accumulation, ecosystem-development, and recovery trajectories on vegetation N versus soil N phase-plane plots for the four ecosystems with refractory N losses. Lines and symbols as in Fig. 2.

Figure 4: Recovery of total, vegetation, and soil C and N for Ecosystem 6 following removal of vegetation but soil left untouched. This simulation was selected because it lost the most N and therefore illustrates the 3 phases most clearly. Time is presented on a log scale to make dynamics early in recovery more visible. Letters at the top of the figure delineate the four phases of recovery identified by Bormann and Likens (1994): R - *Reorganization*, A - *Aggradation*, T - *Transition*, and S - *Steady State*. Dash-dot lines in upper two panels represent the total C and N levels if N accumulation stopped and the ecosystem reached a steady state at the end of the Transition Phase in the Bormann and Likens conceptual model. Vertical black lines and numbers at the top separate the three recovery phases in our conceptual model. In Phase 1,

vegetation accumulates N but not as fast as N is lost from soil. Total N therefore continues to decline. Initially, total C is also lost during Phase 1. However, because the C:N ratio of vegetation is so much larger than that of soil, total C increases substantially later in Phase 1. In Phase 2, total N begins to accumulate and vegetation and soil-microbial processes come into balance. Most of the N is re-accumulated in Phase 3. In the lower two panels, increments on left and right are the same so slopes can be compared between vegetation and soil.

Figure 5: Gains and losses of N by the ecosystems during phases 1, 2, and 3 of recovery for the blowdown disturbance (BD: steady-state biomass transferred to soil), removal of vegetation but soil left undisturbed (0%), and removal of vegetation and 30% of the soil organic matter (30%). Each bar is an average for the four ecosystems with the specified characteristic listed at the bottom. Data for individual ecosystems are listed in appendix Table A2.

Figures:

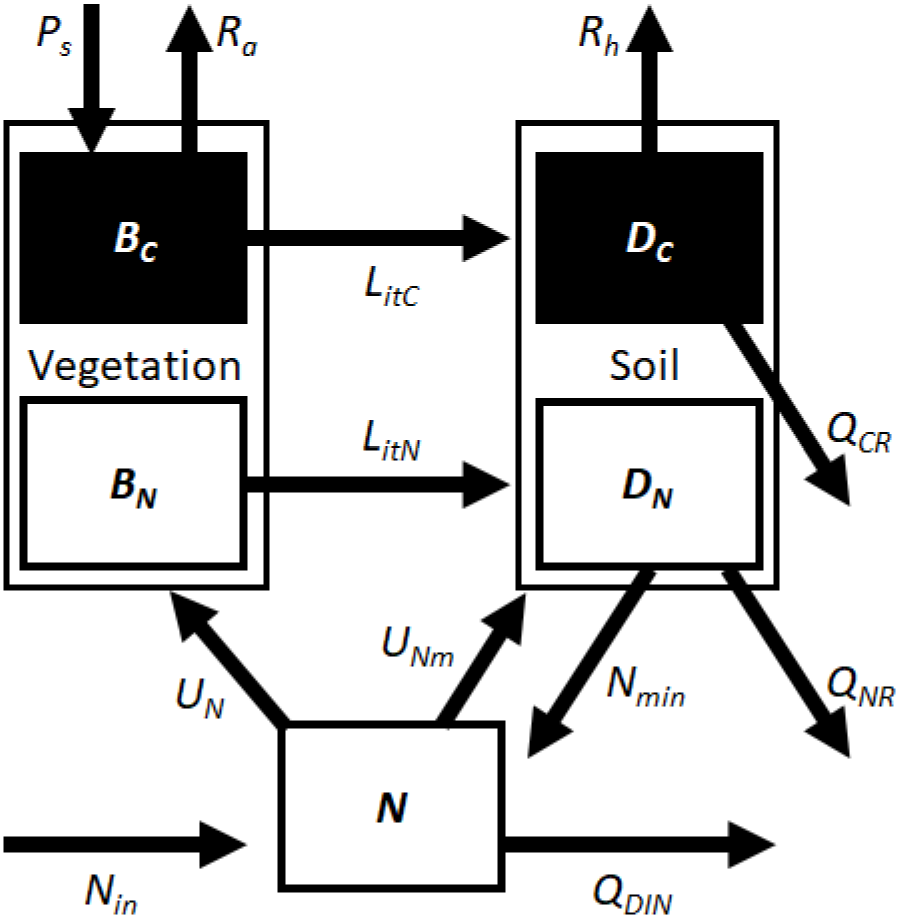

Figure 1

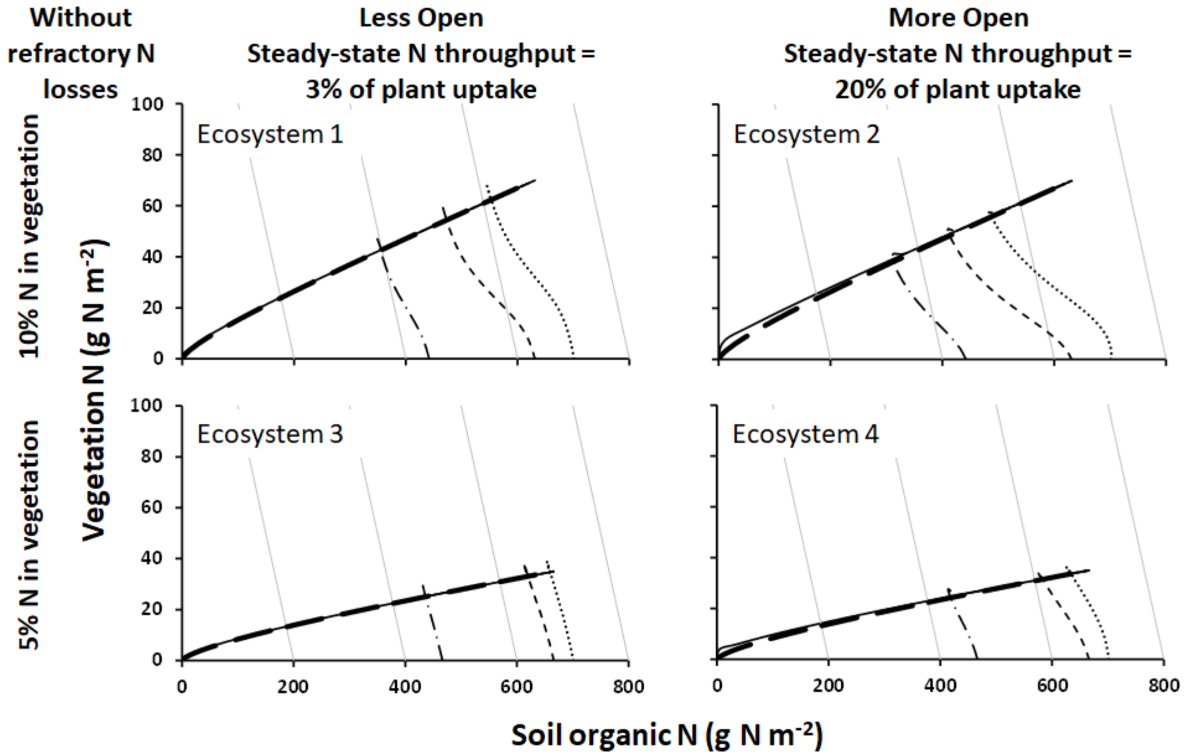
Without refractory N losses
Less Open
Steady-state N throughput = 3% of plant uptake
More Open
Steady-state N throughput = 20% of plant uptake
10% N in vegetation
5% N in vegetation
Vegetation N (g N m^{-2})
Soil organic N (g N m^{-2})
Ecosystem 1
Ecosystem 2
Ecosystem 3
Ecosystem 4
0
20
40
60
80
100
0
200
400
600
800

Figure 2

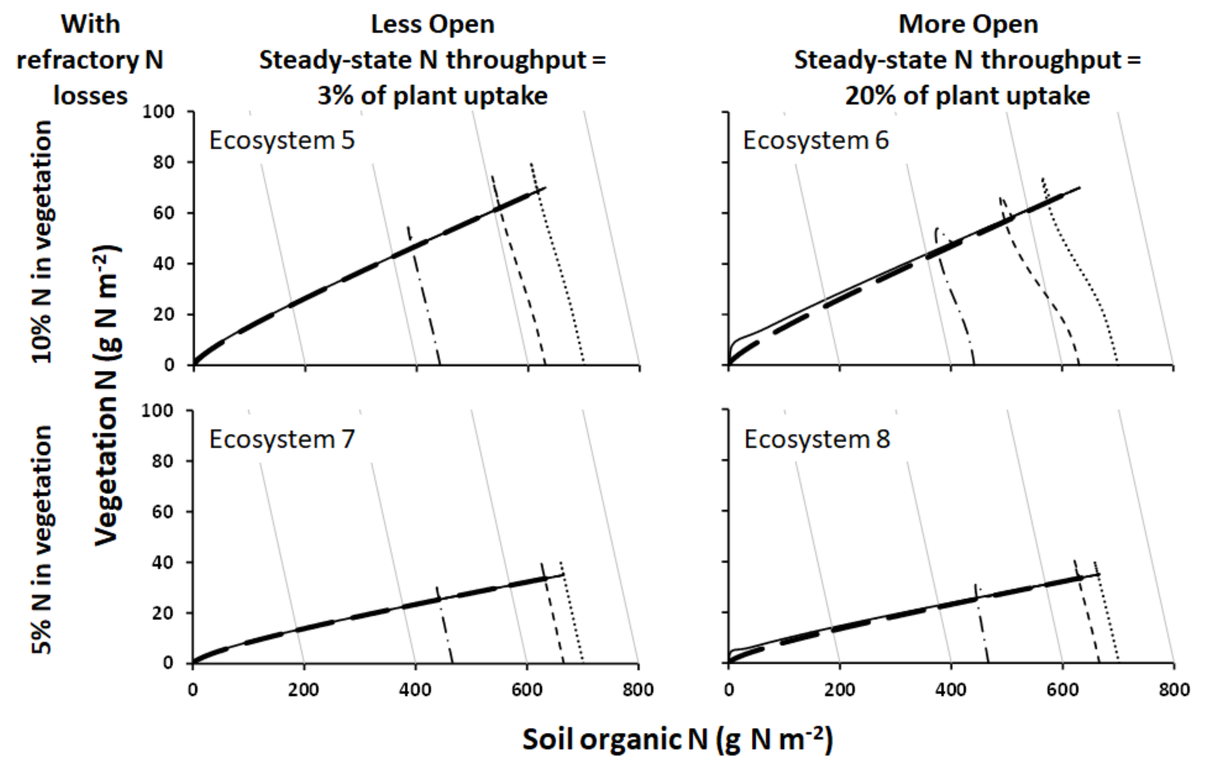
With refractory N losses
Less Open
Steady-state N throughput = 3% of plant uptake
More Open
Steady-state N throughput = 20% of plant uptake
10% N in vegetation
5% N in vegetation
Vegetation N (g N m-2)
Ecosystem 5
Ecosystem 6
Ecosystem 7
Ecosystem 8
0
20
40
60
80
100
0
200
400
600
800
Soil organic N (g N m-2)

Figure 3

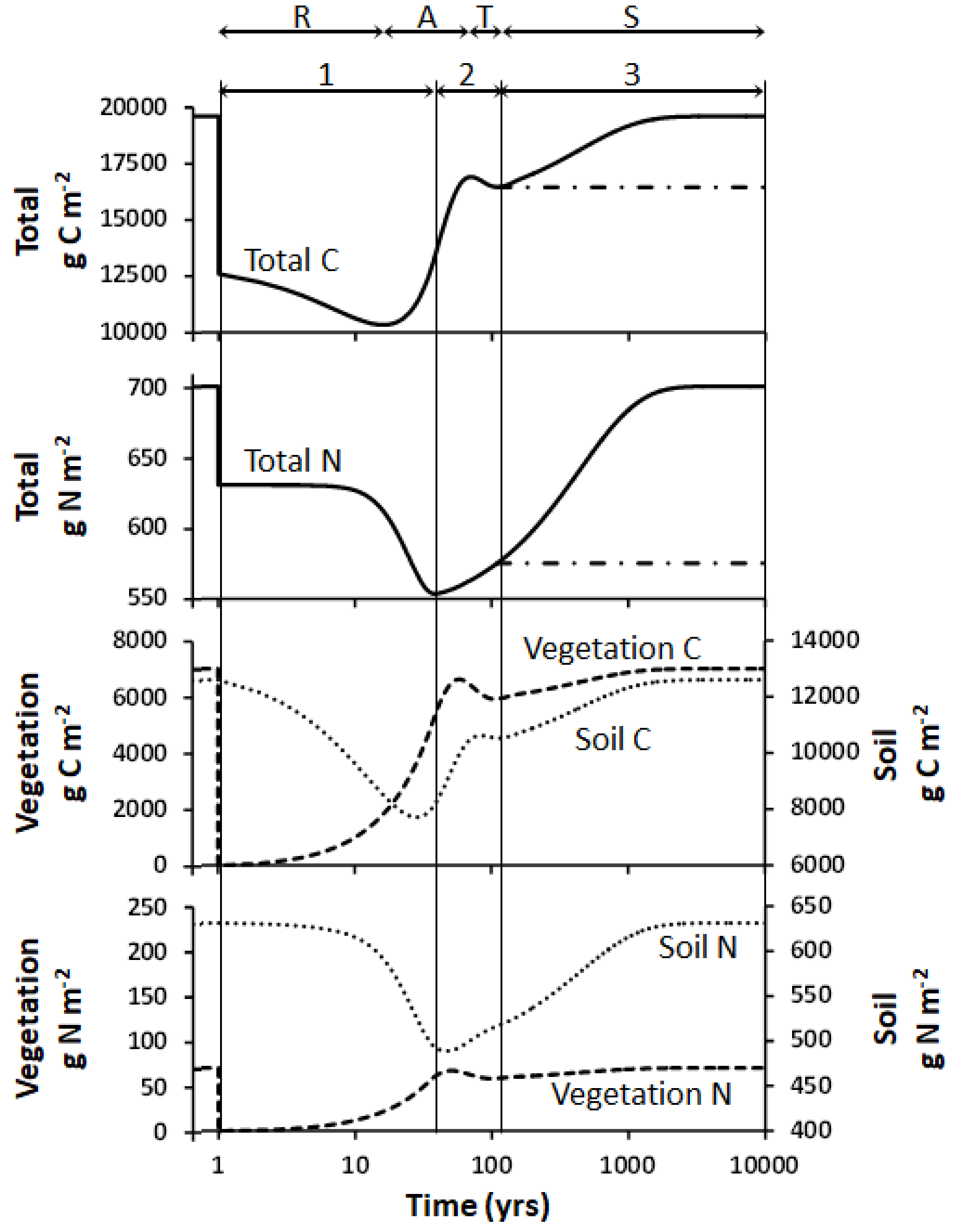

Figure 4

931

932

933

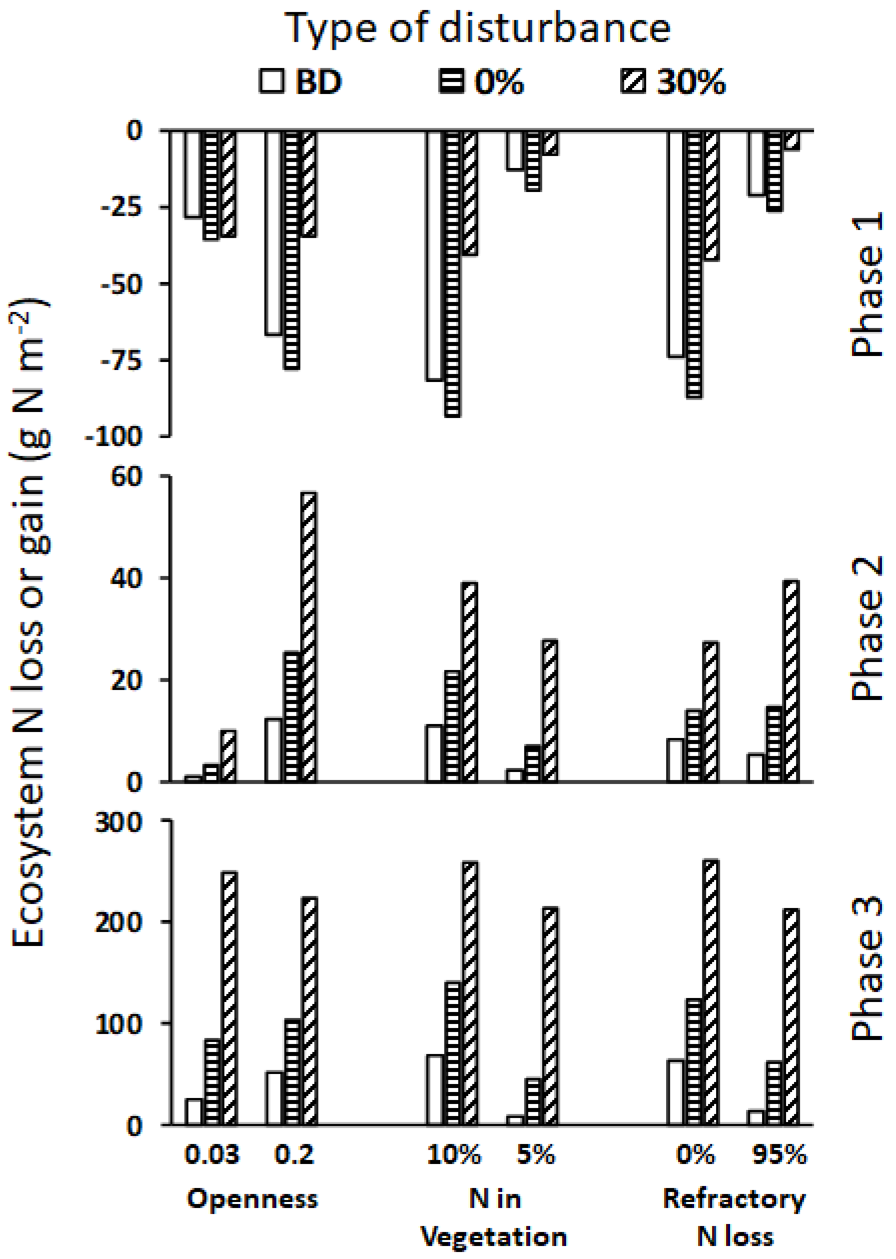
Type of disturbance
☐ BD
⊟ 0%
▨ 30%
Ecosystem N loss or gain (g N m^{-2})
0
-25
-50
-75
-100
Phase 1
60
40
20
0
Phase 2
300
200
100
0
Phase 3
0.03
0.2
Openness
10%
5%
N in Vegetation
0%
95%
Refractory N loss

Figure 5

Appendix: Biogeochemical Recovery from Disturbance: Model Parameterization, Recovery Statistics, and Ancillary Results.

In this appendix we present details on the parameterization of the model for the eight ecosystems (Table A1) and the properties of these ecosystems in relation to the properties of some ecosystems reported in the literature (Fig. A1).

We also present statistics on the timing and gains and losses of N by the eight ecosystems during the three-phase recovery in relation to the ecosystem properties and the severity of disturbance (Table A2).

Finally, we present results for several simulations. We again present the simulated recovery of Ecosystems 7 and 8 from a removal of vegetation and 30% of the soil organic matter. These simulations are presented as a phase plane plot in the main text (Fig. 3). Here we plot C and N stocks against time (Figs. A2 & A3). We also present the results of repeated vegetation removal on a 300-year cycle (Fig. A4) and of symbiotic N fixation on ecosystem development from bare ground and on recovery from disturbance (Fig. A5).

Tables:

Table A1: Steady-state variables and parameters (4 significant digits). State variables are listed first, followed by processes, drivers, and parameters. Bold type - constant across all eight ecosystems.

	Ecosystem							
	1	2	3	**4**	**5**	**6**	**7**	**8**
	Without refractory N losses				**With refractory N losses**			
	10% N in		**5% N in**		**10% N in**		**5% N in**	
	N_{in}= 3% U_N	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**
B_C	7000	7000	3500	3500	7000	7000	3500	3500
D_C	12600	12600	13300	13300	12600	12600	13300	13300
B_N	70	70	35	35	70	70	35	35
D_N	630	630	665	665	630	630	665	665
N	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
P_s	798.9	798.9	448.7	448.7	798.9	798.9	448.7	448.7
R_a	350	350	175	175	350	350	175	175
L_{itC}	448.9	448.9	273.7	273.7	448.9	448.9	273.7	273.7
R_h	448.9	448.9	273.7	273.7	440.9	395.7	269.2	243.9
U_N	7.989	7.989	4.487	4.487	7.989	7.989	4.487	4.487
L_{itN}	7.989	7.989	4.487	4.487	7.989	7.989	4.487	4.487
N_{min}	42.64	42.64	41.06	41.06	42.41	41.12	40.93	40.21
U_{Nm}	34.65	34.65	36.58	36.58	34.65	34.65	36.58	36.58
Q_{DIN}	0.2397	1.598	0.1346	0.8974	0.01198	0.07989	0.006731	0.04487
Q_{NR}	0	0	0	0	0.228	1.518	0.128	0.853
Q_{CR}	0	0	0	0	7.969	53.124	4.476	29.840
S	79.89	79.89	44.87	44.87	79.89	79.89	44.87	44.87
Ψ	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Φ	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
C_a	**400**	**400**	**400**	**400**	**400**	**400**	**400**	**400**
N_{in}	0.2397	1.598	0.1346	0.8974	0.2397	1.598	0.1346	0.8974
α	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
γ	**0.100**	**0.100**	**0.100**	**0.100**	**0.100**	**0.100**	**0.100**	**0.100**
q_B	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**
q_D	**20**	**20**	**20**	**20**	**20**	**20**	**20**	**20**
g_C	**20**	**20**	**20**	**20**	**20**	**20**	**20**	**20**
k_C	**400**	**400**	**400**	**400**	**400**	**400**	**400**	**400**
r_B	**0.05**	**0.05**	**0.05**	**0.05**	**0.05**	**0.05**	**0.05**	**0.05**
m_{CB}	0.06412	0.06412	0.07821	0.07821	0.06412	0.06412	0.07821	0.07821
g_N	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**
k_N	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
m_{NB}	0.1141	0.1141	0.1282	0.1282	0.1141	0.1141	0.1282	0.1282
r_D	0.03562	0.03562	0.02058	0.02058	0.03499	0.03141	0.02024	0.01834
g_{Nm}	**0.0055**	**0.0055**	**0.0055**	**0.0055**	**0.0055**	**0.0055**	**0.0055**	**0.0055**
k_{Nm}	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
m_{Nm}	0.06768	0.06768	0.06175	0.06175	0.06732	0.06527	0.06156	0.06047
q_{DOM}	**35**	**35**	**35**	**35**	**35**	**35**	**35**	**35**
β_N	0.2397	1.598	0.1346	0.8974	0.01198	0.07989	0.006731	0.04487
β_{NR}	0	0	0	0	3.614 x10^{-04}	2.409 x10^{-03}	1.923 x10^{-04}	1.282 x10^{-03}

Table A2: Recovery statistics. BD – “blowdown” simulation transferring vegetation biomass to soils. 0% - removal of vegetation but leaving soil intact. 30% - removal of vegetation and 30% of soil organic matter.

	Ecosystem							
	1	2	3	**4**	**5**	**6**	**7**	**8**
	Without refractory N losses				**With refractory N losses**			
	10% N in vegetation		**5% N in vegetation**		**10% N in vegetation**		**5% N in vegetation**	
	N_{in}= 3% U_N	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**	**N_{in} = 3% U_N**	**N_{in} = 20% U_N**
Phase 1 duration (years)								
BD	64	63	71	69	55	48	63	60
0%	52	51	58	55	43	37	39	39
30%	42	40	40	38	31	29	0	0
Phase 2 duration (years)								
BD	141	105	174	162	163	159	264	191
0%	142	104	180	160	161	160	206	202
30%	145	104	165	162	161	158	209	209
Initial loss (g N m^{-2})								
BD	0	0	0	0	0	0	0	0
0%	-69.99	-69.99	-34.99	-34.99	-69.99	-69.99	-34.99	-34.99
30%	-258.99	-258.99	-234.49	-234.49	-258.99	-258.99	-234.49	-234.49
Phase 1 N loss (g N m^{-2})								
BD	-87.78	-159.93	-8.44	-38.96	-16.17	-63.35	-0.57	-3.70
0%	-105.18	-170.61	-15.33	-57.33	-21.33	-77.45	-0.73	-4.99
30%	-45.74	-91.50	-5.76	-25.27	-4.14	-20.17	0.00	0.00
Phase 2 N gain (g N m^{-2})								
BD	3.20	21.68	0.60	7.74	0.97	19.22	0.06	0.97
0%	5.98	32.38	2.02	16.39	4.91	44.33	1.40	9.17
30%	10.73	48.30	7.13	43.05	13.92	82.97	8.86	52.77
Phase 3 N gain (g N m^{-2})								
BD	84.58	138.26	7.84	31.22	15.20	44.13	0.51	2.73
0%	169.20	208.22	48.30	75.93	86.41	103.11	34.32	30.81
30%	294.00	302.19	233.12	216.71	249.21	196.19	225.63	181.72

Appendix Figure Captions:

Figure A1: Model experimental setup relative to some terrestrial ecosystems. Open circles show the characteristics of the ecosystems simulated in this study. Data were compiled for tropical rain forest by Nagy and others (2017), for temperate evergreen forest by Rastetter (2011), for northern hardwood by Rastetter et al. (2013), for arctic tundra by Pearce and others (2015), for annual grassland by Woodmansee and Dugan (1980), and for two prairies (1) by Blair and others (1998; soil to 25 cm) and (2) by Risser and Parton (1982; soil to 1 m). Openness of the annual grassland is high because of the high reported rates of symbiotic N fixation – over 70% of the total N inputs. Only four open circles in left panel because refractory losses are not illustrated in this figure, only two open circles in right panel because total ecosystem N is the same in all simulations.

Figure A2: Recovery of total, vegetation, and soil C and N for Ecosystem 7 following removal of vegetation and 30% of the soil. Time is presented on a log scale to make dynamics early in recovery more visible. Letters at the top of the figure delineate the four phases of recovery identified by Bormann and Likens (1994): R - *Reorganization*, A - *Aggradation*, T - *Transition*, and S - *Steady State*. Dash-dot lines in upper two panels represent the total C and N levels if N accumulation stopped and the ecosystem reached a steady state at the end of the Transition Phase in the Bormann and Likens conceptual model. Vertical black lines and numbers at the top separate the recovery phases in our conceptual model. Phase 1 is missing because the ecosystem begins to accumulate N immediately after the disturbance. In Phase 2, total N accumulates and vegetation and soil-microbial processes come into balance. Almost all the N is re-accumulated in Phase 3. In the lower two panels, increments on left and right are the same so slopes can be compared between vegetation and soil.

Figure A3: **R**ecovery of total, vegetation, and soil C and N for Ecosystem 8 following removal of vegetation and 30% of the soil. Lines and notations are as in Fig. A2.

Figure A4: Recovery trajectories on vegetation N versus soil N phase-plane plots for Ecosystem 8 on a 300-year harvest cycle. Solid black line –accumulation trajectory from bare ground; black dot – steady state distribution of N between vegetation and soil; dashed lines – recovery trajectories for ten sequential harvests, on a 300-year harvest cycle, with 99% of vegetation removed and soil left untouched. The recovery trajectories approach a stable limit cycle as the amount of N lost in subsequent harvests decreases to the amount the ecosystem can sequester in the 300-year recovery period. The first harvest is to the right and each subsequent harvest is displaced to the left as more and more N is lost from the ecosystem.

Figure A5: Accumulation from bare ground and recovery trajectories on vegetation N versus soil N phase-plane plots for Ecosystem 7 with and without N fixation. To constrain N fixation to early succession, N fixation is simulated as $F = F_0(1 - (S/S_{max})^2)$ if $S < S_{max}$, $F = 0$ otherwise; with $F_0 = 3$ and $S_{max} = 30$. The thick solid line in the upper panel is the accumulation trajectory from bare ground with N fixation held constant at 3 g N m^{-2} yr^{-1}. The dashed gray line in the upper panel is the accumulation trajectory from bare ground without N fixation (same trajectory as in the lower panel). The lower panel shows the same simulations as those in the panel for Ecosystem 7 in Fig. 3. All other lines and symbols are as in Fig. 2. Nitrogen-fixing species generally turn over N more rapidly (Vitousek and others 2002), which shifts the distribution of N from vegetation to soil (recovery trajectories tilt more to the right in the upper panel than the lower panel). Once the N-fixing species is excluded during succession, the recovery trajectories shift back toward the balanced-accumulation trajectory for an ecosystem with lower total N at steady state (tilt back to the left). Thus, the recovery trajectory with early-succession N fixation rapidly accumulates N and accelerates the N cycle under the influence of the symbiotic N fixer (Perakis and others 2012). Then, with the loss of the N fixer, the ecosystem transitions back toward a more-closed, less rapid N cycle and potentially loses some of the accumulated N; overall resulting in a recovery that arches out to the right then back to the left.

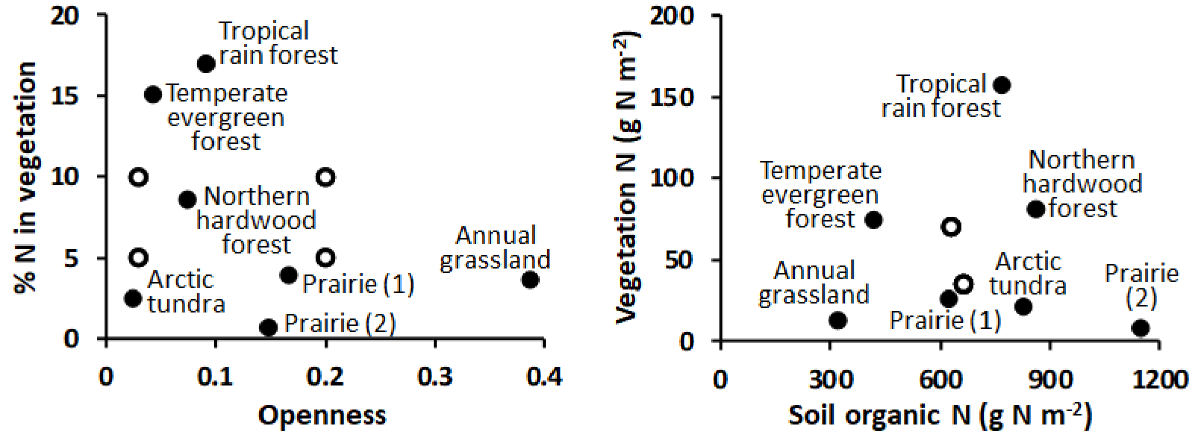
% N in vegetation
20
15
10
5
0
0
0.1
0.2
0.3
0.4
Openness
Tropical rain forest
Temperate evergreen forest
Northern hardwood forest
Arctic tundra
Prairie (1)
Prairie (2)
Annual grassland
Vegetation N (g N m-2)
200
150
100
50
0
0
300
600
900
1200
Soil organic N (g N m-2)
Tropical rain forest
Temperate evergreen forest
Northern hardwood forest
Annual grassland
Prairie (1)
Arctic tundra
Prairie (2)

Figure A1

1031

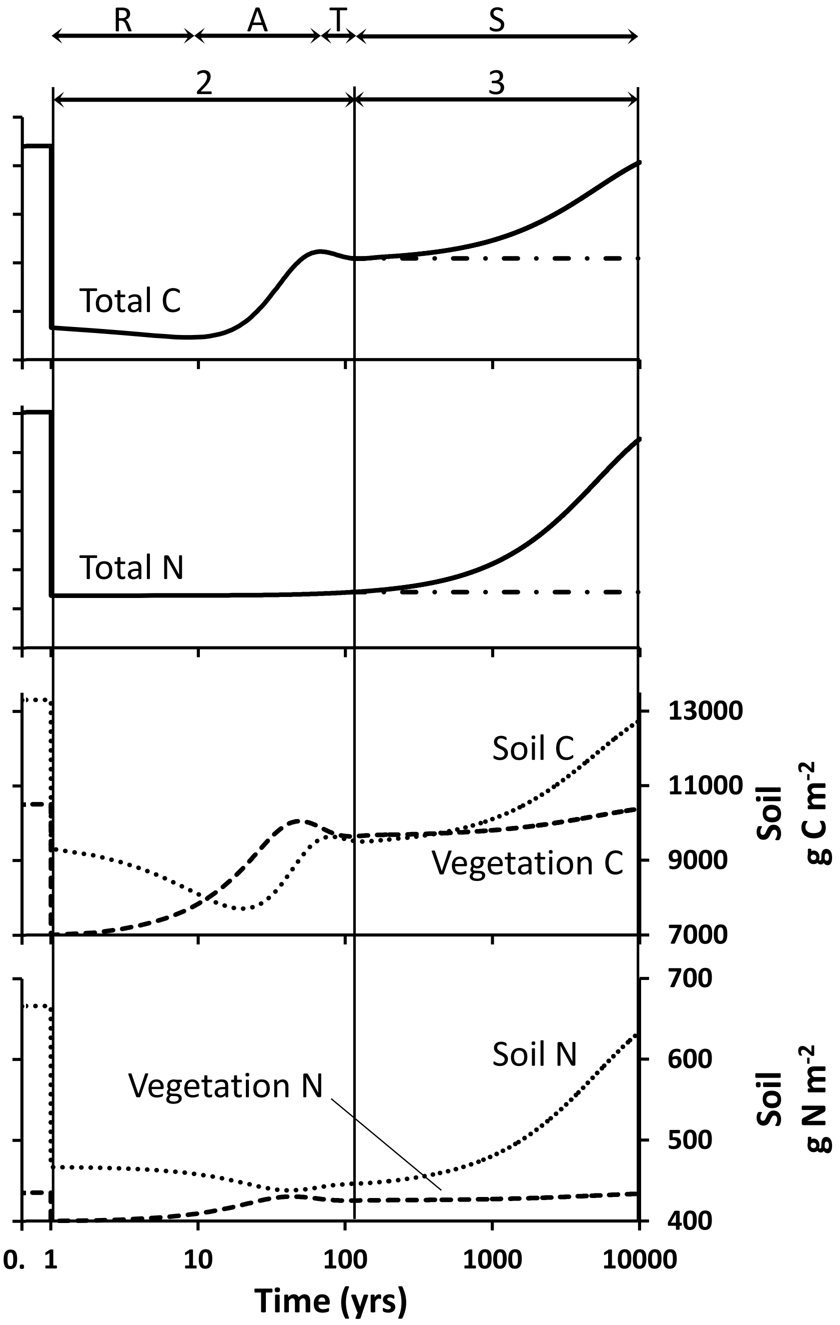

Figure A2

1032
1033

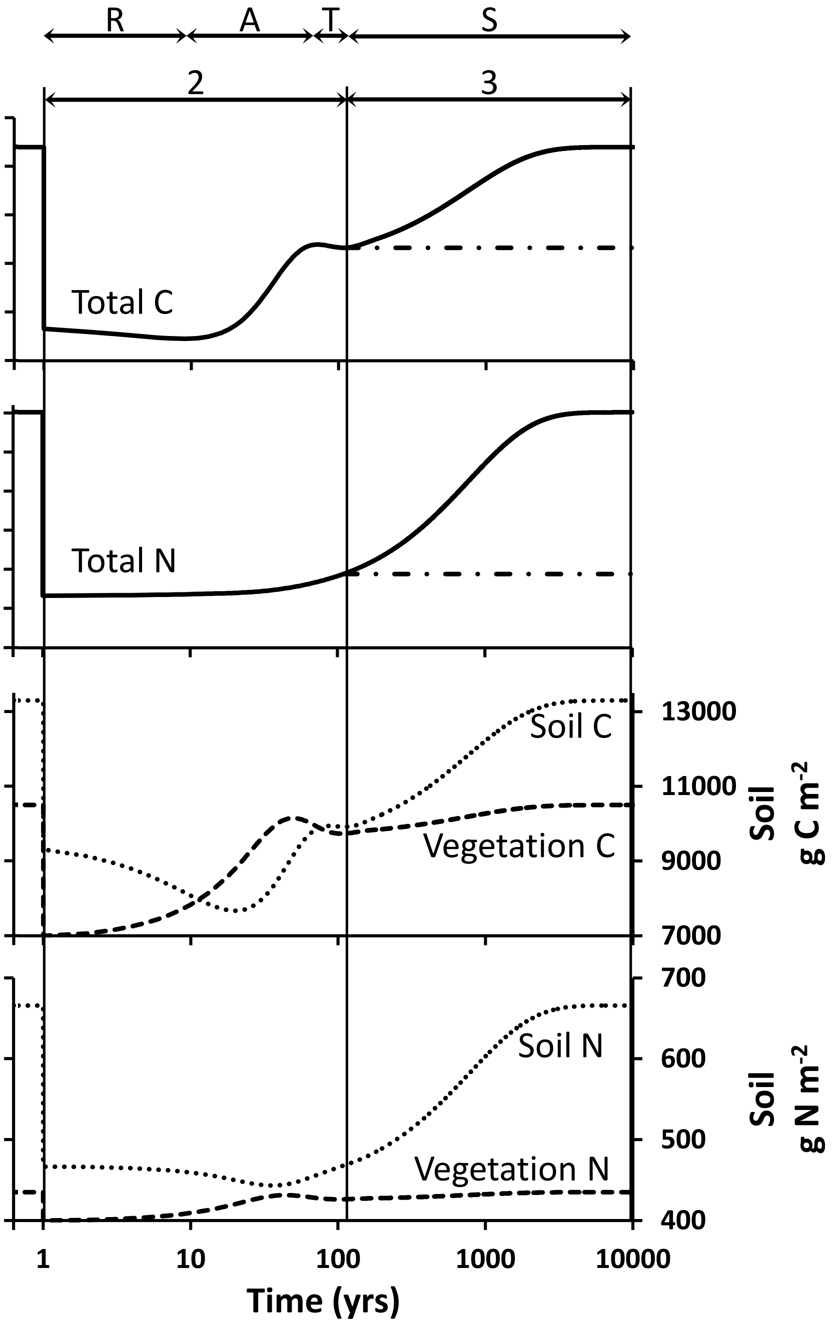

Figure A3

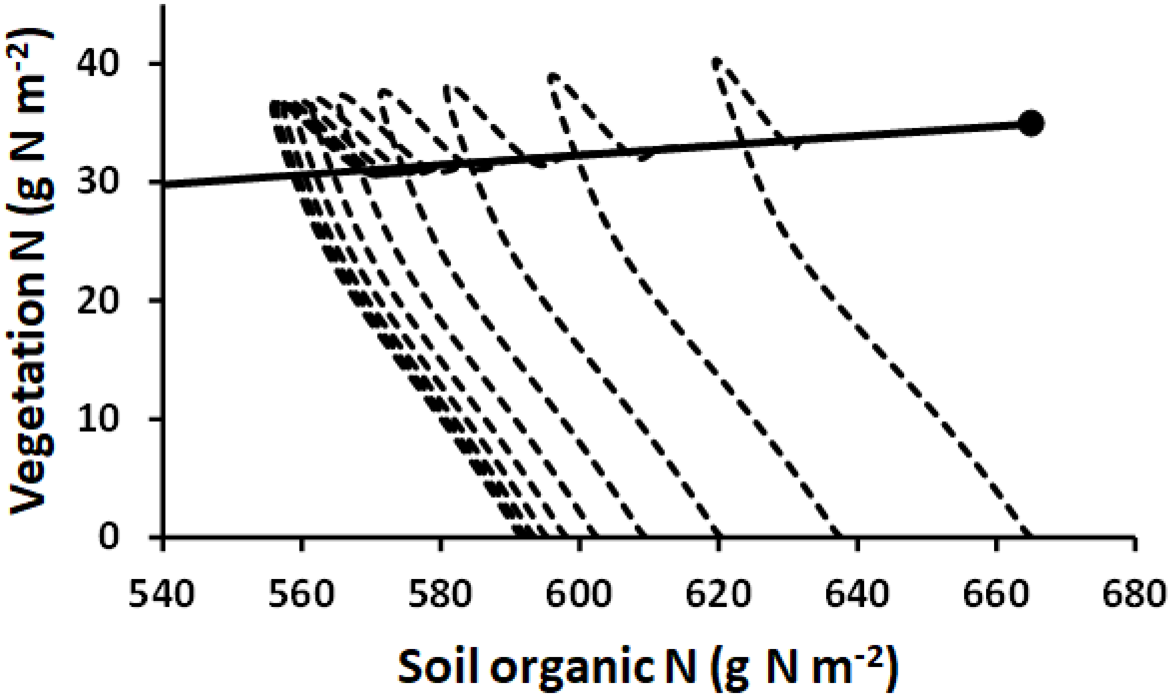
Vegetation N (g N m^{-2})
40
30
20
10
0
540
560
580
600
620
640
660
680
Soil organic N (g N m^{-2})

Figure A4

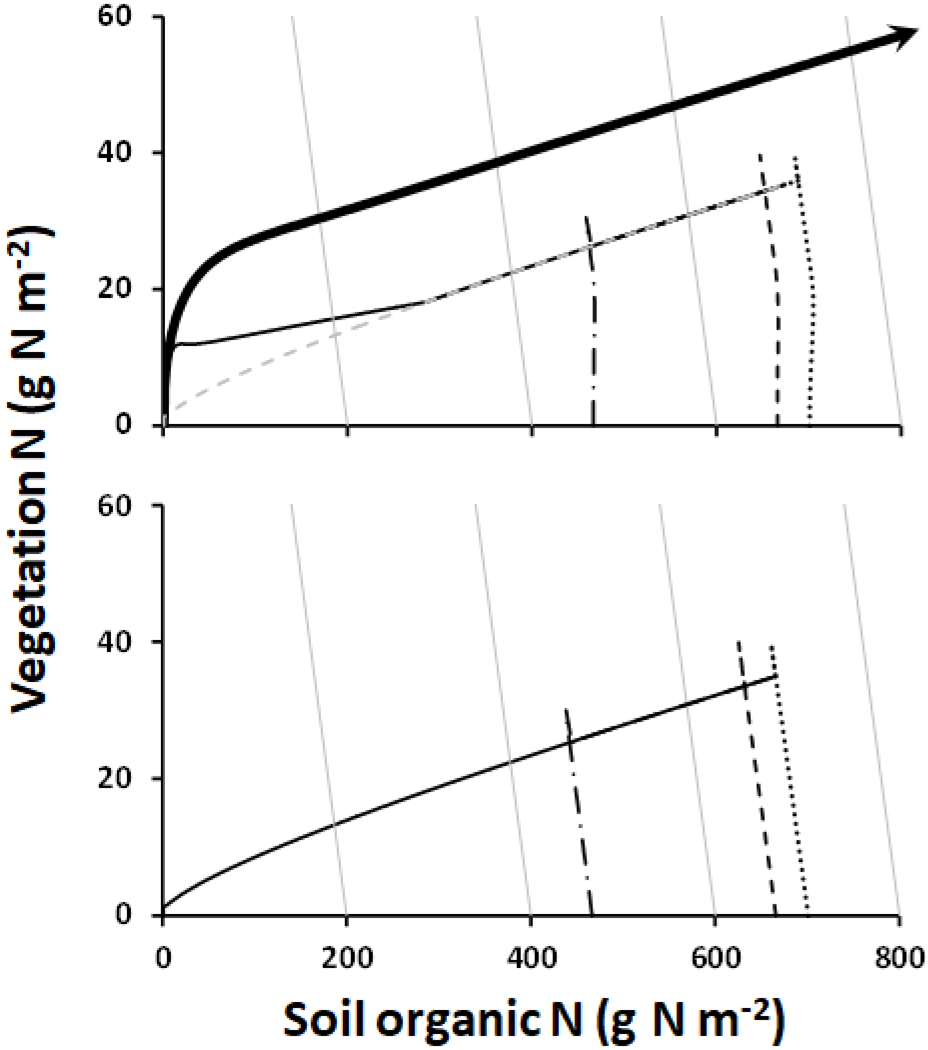
Vegetation N (g N m^{-2})
Soil organic N (g N m^{-2})
0
20
40
60
0
20
40
60
0
200
400
600
800

Figure A5