

**A framework to assess biogeochemical response to ecosystem  
disturbance using nutrient partitioning ratios**

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1 **Abstract**

2           Disturbances affect almost all terrestrial ecosystems, but it has been difficult to  
3 identify general principles regarding these influences. To improve our understanding of  
4 the long-term consequences of disturbance on terrestrial ecosystems, we present a  
5 conceptual framework that analyzes disturbances by their biogeochemical impacts. We  
6 posit that the ratio of soil and plant nutrient stocks in mature ecosystems represents a  
7 characteristic site property. Focusing on nitrogen (N), we hypothesize that this  
8 partitioning ratio (soil N: plant N) will undergo a predictable trajectory after disturbance.  
9 We investigate the nature of this partitioning ratio with three approaches: (1) nutrient  
10 stock data from forested ecosystems in North America, (2) a process-based ecosystem  
11 model, and (3) conceptual shifts in site nutrient availability with altered disturbance  
12 frequency. Partitioning ratios could be applied to a variety of ecosystems and  
13 successional states, allowing for improved temporal scaling of disturbance events. The  
14 generally short-term empirical evidence for recovery trajectories of nutrient stocks and  
15 partitioning ratios suggests two areas for future research. First, we need to recognize and  
16 quantify how disturbance effects can be accreting or depleting, depending on whether  
17 their net effect is to increase or decrease ecosystem nutrient stocks. Second, we need to  
18 test how altered disturbance frequencies from the present state may be constructive or  
19 destructive in their effects on biogeochemical cycling and nutrient availability. Long-  
20 term studies, with repeated sampling of soils and vegetation, will be essential in further  
21 developing this framework of biogeochemical response to disturbance.

22

- 23 **Keywords:** Disturbance, fire regime, succession, Multiple Element Limitation (MEL)
- 24 model, nitrogen stocks, nutrient ratio

25 **1. Introduction**

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

41 Biogeochemical cycles of carbon (C) and nutrients exhibit a range of responses to  
42 disturbance over ecologically meaningful time scales (Running 2008). In turn,  
43 biogeochemical cycles and their interactions can influence the pattern and pace of  
44 ecosystem recovery from disturbance; both disturbance legacies and feedbacks between  
45 plant regrowth and soil element stores are particularly influential in shaping recovery  
46 (Gough et al. 2007, Pearce et al. 2015). Feedbacks among C accumulation, nutrient  
47 recycling, and other ecosystem processes may interact with whole-ecosystem constraints

48 on element supply and loss (Belyea and Baird 2006). These constraints on the various  
49 individual and feedback processes can result in surprisingly consistent patterns in  
50 biogeochemical cycling after disturbance across a wide range of ecosystem types  
51 (Davidson et al. 2007, Rastetter et al. 2013). Yet, key uncertainties remain in both the  
52 consequences of disturbance events and their impacts at landscape scales. Thus it has  
53 been difficult, for example, to quantify the direction and magnitude of biotic disturbances  
54 on forest C cycling in the United States and Canada (i.e., Hicke et al. 2012). Nonetheless,  
55 generalization of disturbance ecology would benefit from a theoretical biogeochemical  
56 framework which would apply across single and multiple events, in multiple biomes.

57 For many terrestrial ecosystems, both the infrequent nature of disturbance events  
58 and slow post-disturbance processes complicate efforts to empirically study  
59 biogeochemical responses on long timescales. While a single disturbance event has the  
60 potential to create a significant biogeochemical impact (Paré et al. 2002, Foster et al.  
61 2003, Romme et al. 2011), over the long term a shift in the disturbance regime itself and  
62 its associated successional pathways may combine to affect ecosystems more profoundly  
63 (e.g., directional change, Reiners 1983). Detecting shifts in disturbance regimes  
64 necessitates extending the temporal scale of disturbance history beyond the time period of  
65 direct or historical observations (Marlon et al. 2012). Recent studies have provided  
66 increasingly clear characterizations of disturbance regimes (at least for fire and storm  
67 regimes) on millennial timescales (Donnelly and Woodruff 2007, Higuera et al. 2014),  
68 including return intervals, spatial extent and intensity (Baker 2009). Several lines of  
69 evidence indicate incipient or ongoing shifts in disturbance regimes during the past few  
70 decades, with larger and more frequent fire events (Dennison et al. 2014) and seemingly

71 unprecedented bark beetle outbreaks (Raffa et al. 2008). Projecting the future  
72 biogeochemical trajectory of disturbed systems requires the ability to identify how  
73 profoundly a disturbance regime has departed from the present state (Walker and Wardle  
74 2014).

75         Here, we introduce a conceptual framework using the ratio of plant and soil  
76 nutrient stocks to characterize the relative stasis of mature ecosystems and to hypothesize  
77 the consequences of a single disturbance event on nutrient loss and recovery. We suggest  
78 this framework will improve ecosystem comparisons of biogeochemical response to  
79 multiple disturbances over time. This framework is designed for temporal scaling and it is  
80 flexible with regard to disturbance mechanism, ecosystem type, and spatial extent. We  
81 develop this framework with three different approaches: (1) nutrient stock data from  
82 forested ecosystems in North America, (2) a process-based ecosystem model, and (3)  
83 conceptual shifts in site nutrient availability with altered disturbance frequency. We  
84 expect that this framework will be sufficiently robust to improve our understanding of  
85 biogeochemical outcomes across new disturbance types, regimes, and interactions.

## 86 **2. Characterizing terrestrial ecosystems by partitioning ratios**

87         In a mature terrestrial ecosystem (i.e., when aboveground biomass accumulation  
88 has plateaued), nutrients are entrained into ecosystem cycles and accumulate  
89 predominantly in soils and vegetation. For this accumulation to occur, a balance has to be  
90 maintained between soil and plant processes; soil organic matter (SOM) cannot  
91 accumulate without the litter produced by vegetation and the vegetation cannot grow and  
92 continue to produce organic matter without the nutrients mineralized from the SOM. In  
93 addition, the accumulation of nutrients has to be synchronized; N cannot accumulate in

94 the ecosystem unless P and other vital nutrients also accumulate and *vice versa*. We posit  
95 that the ratio between soil and plant nutrient stocks represents a characteristic property of  
96 an ecosystem that can be quantified empirically, both to better allow cross-system  
97 comparisons and to provide insight into the fluxes between pools (given that internal  
98 cycling fluxes are often much larger than input and output fluxes) (Rastetter et al. 2013).  
99 We call this value the **partitioning ratio**.

100         There is empirical support for characteristic differences in the partitioning ratio  
101 among ecosystems at the biome scale. For illustrative purposes we focus our discussion  
102 on nitrogen (N), the most commonly limiting nutrient in terrestrial ecosystems, although  
103 it should be recognized this element has unique characteristics such as significant organic  
104 forms, multiple loss pathways, and multiple biotically-mediated transformations . As an  
105 example, six types of North American forests ranging from boreal moist in British  
106 Columbia to subtropical dry in Texas exhibit wide variability in soil N: vegetation N,  
107 spanning 1.3 to 40.9 across total soil N pools ranging from 724 to 6929 kg ha<sup>-1</sup> (Figure  
108 1a) (Ponder et al. 2012). However, for the four forest types with sufficient sample size,  
109 there are separate, unique values of soil N: vegetation N (Figure 1b). These results  
110 suggest that boreal and temperate forested biomes as a whole may demonstrate consistent  
111 and predictable partitioning ratios, at least in late successional stages.

112         This partitioning ratio concept may extend to other biomes beyond temperate  
113 forests. For example, grasslands contain large belowground N stocks in the soil pool  
114 relative to aboveground biomass. A prairie in Oklahoma (U.S.A.) had a partitioning ratio  
115 of 232 over a three-year period in the 1970s (Risser et al. 1981). Deserts of the  
116 southwestern U.S. generally have both low aboveground biomass and low soil organic



117 matter stocks. Their N partitioning ratios range from 4 to 203 depending on the dominant  
118 vegetation type [e.g. mesquite, sagebrush, creosote, and paloverde (West and Skujins  
119 1978)]. Tropical forests with relatively organic-poor soils have low soil nutrient stocks  
120 relative to vegetation nutrient stocks and exhibit partitioning ratios of 1.6 to 4.8 (Jordan  
121 1985). Thus, the quantification of soil and plant nutrient stocks *via* a partitioning ratio  
122 appears to be a useful characteristic descriptor of biomes.

### 123 **3. Single disturbance events and recovery of nutrient stocks**

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

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

140 limiting during recovery, there will tend to be a net loss from the ecosystem and the  
141 recovery trajectory will be below and to the left of the isopleths of total ecosystem  
142 nutrient. This redistribution trajectory should approach the predisturbance baseline as  
143 plant and soil processes come back into balance. Once the balance is reestablished, the  
144 ecosystem will be more effective at entraining and retaining nutrients in the ecosystem  
145 cycle and from that point on, the recovery trajectory should coincide with characteristic  
146 partitioning ratio of the ecosystem. DeAngelis (1980) hypothesized that this recovery  
147 time reflected system energetics, in particular the mean transit time of essential and  
148 nonessential nutrients recycled between soils and vegetation during succession.

149         Several post-disturbance sampling sequences indicate some degree of predictable  
150 temporal change in soil N: vegetation N over time (Johnson and Turner 2014). In  
151 lodgepole pine forests of the Greater Yellowstone ecosystem, soil N and vegetation N  
152 stocks recovered at different rates during 331 years after stand-replacing fires, converging  
153 on a characteristic partitioning ratio over time (Smithwick et al. 2009). In tropical  
154 rainforests of the Andean foothills in western Amazonia, the partitioning ratio changed  
155 from 39 at three years post-disturbance, to 7.25 at 25-30 years post-disturbance, relative  
156 to a ratio of 2.2 in primary forest (Scott 1978). While we emphasize ratios because of the  
157 balance struck between plant:soil nutrient cycles in the conceptual model, the absolute  
158 amounts of ecosystem nutrient capital (isopleths in Figure 2) could also be a vital  
159 measure of biogeochemical recovery under many applications.

160         The initial effect of a disturbance on the partitioning ratio and nutrient stocks  
161 depends on the specific mechanism because the biogeochemical consequences of  
162 disturbance events are not simply loss of nutrients. Disturbances can also increase

163 ecosystem nutrient stocks or change their distributions among pools. This argues for the  
164 need to expand current definitions of disturbance. Examples of disturbance increasing  
165 nutrient stocks (either concurrent with the disturbance event or displaced over time)  
166 include deposition of calcium-rich volcanic ash (Ayriss and Delmelle 2012), post-fire N  
167 fixation by early successional plants such as alder (Perakis et al. 2011), sediment  
168 deposition during floodplain disturbances (Appling 2012), thermokarst delivery of  
169 phosphorus (P) to tundra, or anthropogenic N additions (Block et al. 2012). These types  
170 of **accreting disturbance** events are an important counterexample to the traditional view  
171 of disturbance as reducing terrestrial ecosystem nutrient stocks.

172

#### 173 **4. Modeling nutrient stock recovery to a disturbance event across contrasting** 174 **ecosystems**

175 To illustrate how ecosystems with differing partitioning ratios may recover N  
176 stocks following a disturbance event, we used the Multiple Element Limitation (MEL)  
177 model with parameters as described by Rastetter et al. (2013) (Figure 3). The MEL model  
178 was used to simulate three broadly contrasting ecosystems in the U.S.A.: (1) the mixed  
179 deciduous and coniferous forest of Hubbard Brook Experimental Forest, located in New  
180 Hampshire (Bormann and Likens 1979), (2) temperate wet coniferous forest of the H. J.  
181 Andrews Experimental Forest in Oregon (Harmon 1992), and (3) Arctic tundra at the  
182 Toolik Lake Long Term Ecological Research site in Alaska (Hobbie and Kling 2014).  
183 We calculated the partitioning ratio for N (soil N: vegetation N) at steady state for each  
184 ecosystem. The partitioning ratios at Hubbard Brook, H. J. Andrews, and Toolik Lake  
185 were 10.1, 5.5, and 52.7, respectively. A disturbance was simulated in the model by

186 removing 90% of the aboveground biomass. To simulate a range of successional  
187 pathways, 80% or 100% of the pre-disturbance biomass was added to the soil and coarse  
188 woody debris pools following the disturbance event.

189 In all three modeled ecosystems there was a temporal trajectory of return to the  
190 original partitioning ratio after the disturbance event but at greatly different rates because  
191 the mechanisms of recovery differed among the three ecosystems (Figure 3). The  
192 quantity of biomass returned to the system has a slight effect on the rate of recovery, but  
193 recovery pathways are quite similar. Symbiotic N fixation is not thought to be a major  
194 component of the recovery at Hubbard Brook or Toolik Lake, but it is a major contributor  
195 to the N budget during the recovery at H.J. Andrews. Hence the N trajectory for H.J.  
196 Andrews indicates a net gain of N by the ecosystem soon after the disturbance, which is  
197 then lost during later stages of succession. Note that the recovery trajectories following  
198 disturbance converge at a lower point in succession rather than returning directly to  
199 predisturbance levels. This convergence results from the loss of nutrients in the  
200 disturbance and in the early recovery phase. These nutrients need to be recovered before  
201 the relative stasis of a mature ecosystem can be reached. There is potentially a high  
202 capacity for predicting post-disturbance trajectories with this framework. In addition to  
203 measuring the immediate effects of a disturbance (accreting or depleting in terms of any  
204 given soil nutrient stock, such as a reduction in soil N), the relative ratio change through  
205 time could be predicted based on known successional ratio development.

206

207 **5. Assessing biogeochemical vulnerability to disturbances**

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

218           Stability ratios have in many cases not been empirically confirmed, but this is an  
219 area of active research through programs such as the Long-term Soil Productivity Study  
220 (LTSP) (Powers 2006) and the Centre for International Forestry Research (Saint-André et  
221 al. 2008). Over the first ten years of the LTSP study the complete site-level organic  
222 matter removal treatment has not yet resulted in significant, overall declines in  
223 regenerating stand productivity (Ponder et al. 2012), but early trends indicate some  
224 differing sensitivities to nutrient loss by forest soil type (e.g., deeply weathered  
225 subtropical soils vs. less developed glacial soils) that may corroborate the partitioning  
226 ratio concept. More significant effects of nutrient capital removal may appear after  
227 canopy closure, when regenerating forests place greater demands on soil nutrients  
228 (Thiffault et al. 2011), but it is also possible that losses in nutrient stocks will result in  
229 only temporary, rather than permanent, reductions in growth capacity as soil processes  
230 recover (Egnell 2011). For example, recent studies in the Brazilian Cerrado

231 forest/savanna ecotone suggest that less fertile sites are more sensitive to changes in fire  
232 frequency, likely because fire-induced losses of nutrients greatly exceed the supply of  
233 nutrients (de Dantas et al. 2013, Pellegrini et al. 2014). Alternatively, there is evidence  
234 that tropical savannas are well adapted to fire (Bond 2008, Staver et al. 2011), and the  
235 long-term nutrient balance of these biomes seems to not be altered, as N supply can keep  
236 pace with losses from periodic, low intensity disturbance.

237

## 238 **6. Stability of nutrient stocks under shifting disturbance frequencies**

239 It might be argued that, as illustrated by the modeling exercise, a single  
240 disturbance event may be less a question of ‘if’ nutrient stocks recover but rather a  
241 question of ‘when’. We suggest more fundamental alterations in nutrient stocks and  
242 partitioning ratios may require changes in disturbance frequency or intensity over  
243 multiple generations of a plant community (e.g., many decades for grasslands, many  
244 centuries for forests). A number of mechanisms have been identified or hypothesized as  
245 drivers in the biogeochemical response of ecosystems to disturbance frequency and  
246 intensity (Gorham et al. 1979), such as bryophyte- and lichen-associated N-fixation,  
247 water table fluctuations, mineral weathering rates, forest floor accumulations, and inputs  
248 of ericaceous plant roots (Antoine 2004, Zackrisson et al. 2004, Simard et al. 2007,  
249 Hazlett et al. 2011, Clemmensen et al. 2013). Quantification of these processes further  
250 develops the concept of accreting or depleting disturbances by identifying mechanisms of  
251 biogeochemical change. Both processes might even occur simultaneously, as in the  
252 positive and negative aspects of forest floor accumulation and loss (Prescott et al. 2000).  
253 The strength of these constructive and destructive processes may mean that shifts in

254 disturbance frequency could push biogeochemical cycles to support either an altered  
255 productive capacity of the ecosystem, or perhaps an entirely new, alternative stable state  
256 (Reiners 1983).

257         We have conceptually portrayed these possible interactions of site properties with  
258 disturbance frequency to illustrate how ecosystems may respond with increased,  
259 decreased, or no change in long-term nutrient supply rates (Figure 4). Ecosystems  
260 exhibiting low sensitivity to excessive disturbance (*i.e.* showing small changes in total  
261 nutrient capital, point A in Figure 4) would theoretically have rapid vegetation recovery  
262 with a significant component of N-fixing plants, soils with high buffering capacity,  
263 weatherable minerals for P and base cation replenishment, and a high allocation of site  
264 nutrients in belowground pools. Ecosystems exhibiting high sensitivity to excessive  
265 disturbance (point B) would be relatively slow to revegetate, highly prone to nutrient  
266 leaching (high precipitation regime, low retention capacity of the soil) and nutrient  
267 volatilization (deep, dry surface organic accumulations), low rates of symbiotic and  
268 asymbiotic N-fixation, highly weathered soils, and a high allocation of site nutrients in  
269 aboveground pools. Ecosystems with low sensitivity to reduced disturbance frequency  
270 (point C) would have efficient and sustainable nutrient cycling between soils and  
271 vegetation (low loss rates), adequate on-going replenishment of sequestered nutrients (via  
272 mineral weathering and N-fixation), and balanced organic matter inputs (e.g., wood, litter,  
273 roots, bryophytes) and outputs (decomposition). Mechanisms leading to a high sensitivity  
274 to infrequent disturbances (point D) would be excessive nutrient immobilization through  
275 biomass sequestration, detrimental changes over time in soil thermal properties or  
276 drainage (cooling via forest floor accumulations, paludification), reduced rhizodeposition,

277 and high inputs of low-quality litter such as peat or ericaceous plants. These  
278 characterizations of ecosystem properties and responses to multiple disturbances should  
279 generate several testable hypotheses suitable for cross-biome synthesis.

## 280 **7. Conclusions**

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



299 • Further development of this framework could focus on multiple elements in state  
300 space. Our modeling results indicate that the post-disturbance ecosystem  
301 trajectories reflect cycling rates and stoichiometry in plant and soil pools.  
302 Stoichiometry is also likely to be important in post-disturbance trajectories of the  
303 empirical partitioning ratio.  
304

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315

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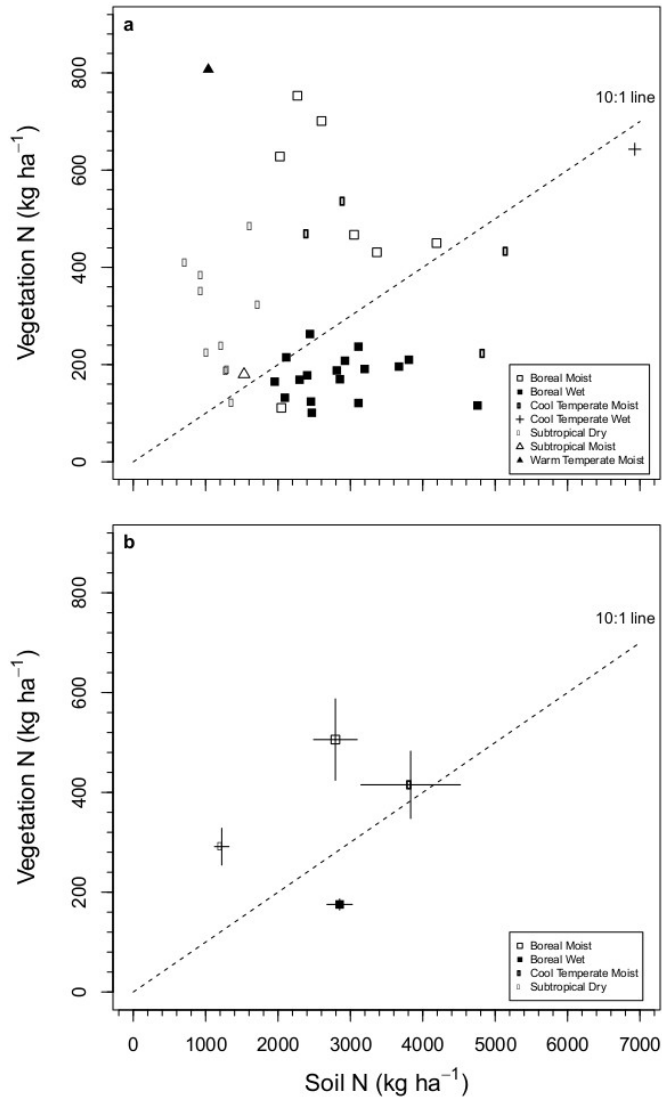
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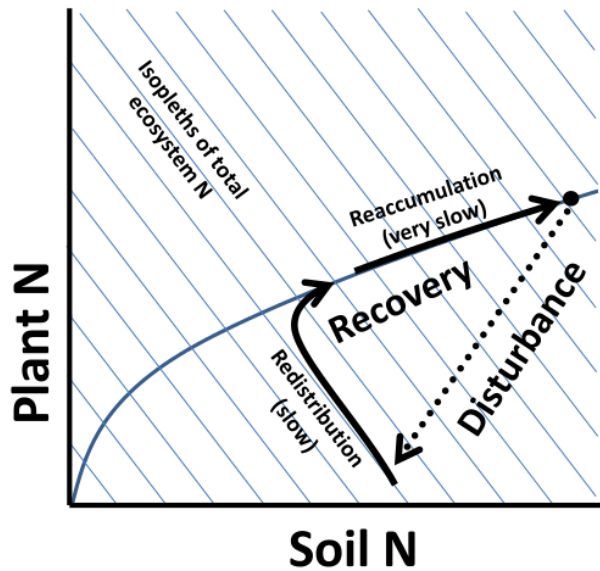
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469 **Figure 1.** a) Ratios of soil N and vegetation N pools in 41 forests in North America that  
 470 are part of the Long-Term Soil Productivity network (Ponder et al. 2012). b) Mean values  
 471 for four Holdridge life zones with one standard error for both soil and vegetation N.

472 Vegetation N includes both tree bole and tree crown N, while soil N includes both O  
 473 horizon and mineral soil N measured to 20 cm depth. Sites represent a variety of

474 successional stages, climate types, and dominant species. Locations: British Columbia,

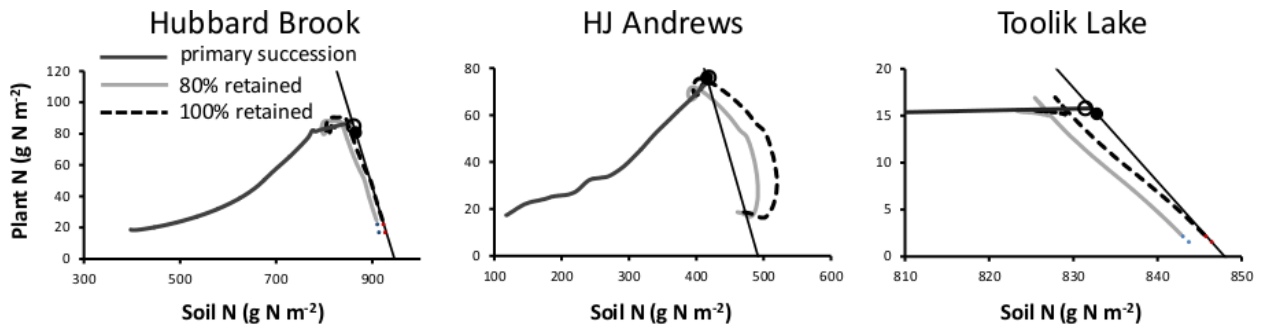
475 Ontario, Louisiana, Mississippi, Texas, Washington, Missouri, North Carolina, and Idaho.



476

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

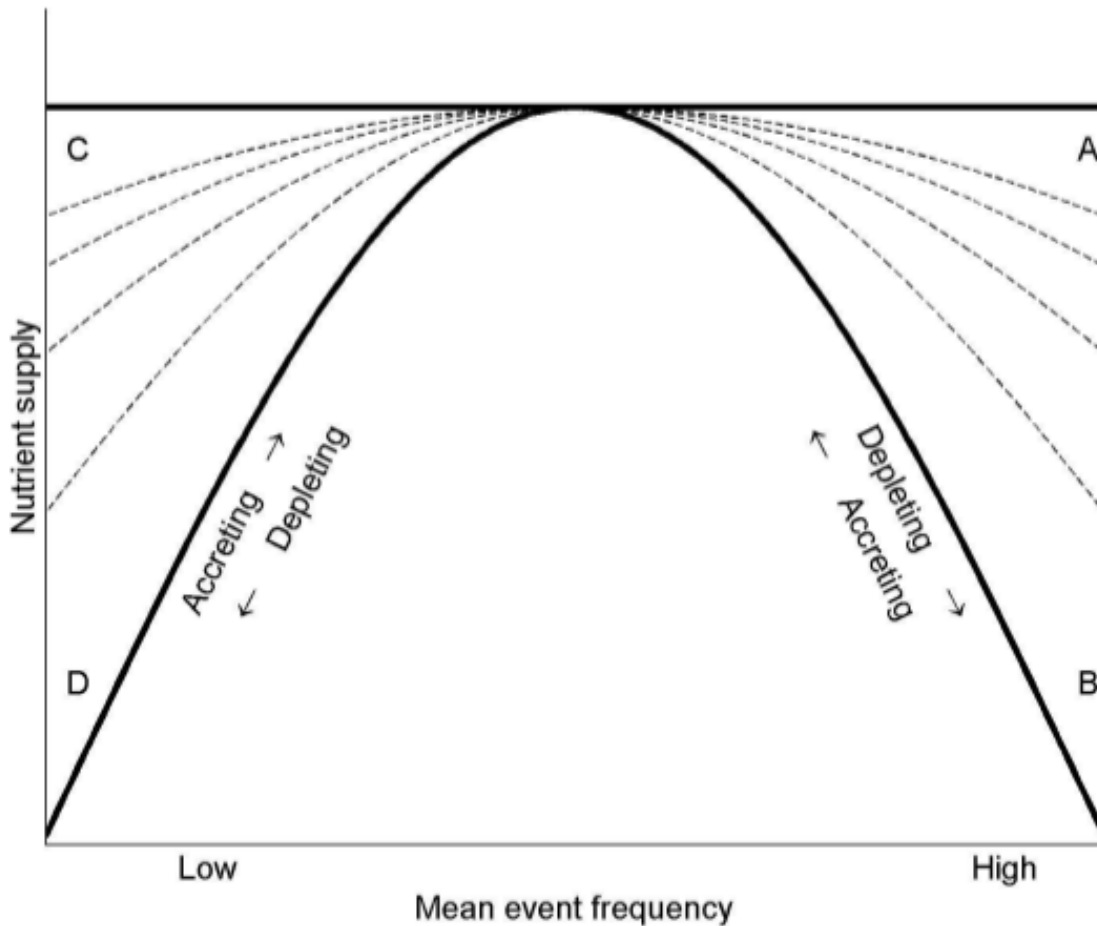
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486

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

496



497

498 **Figure 4.** Conceptual figure of how disturbance frequency can balance the potentially  
 499 accreting and depleting processes affecting ecosystem nutrient capital. Projected response  
 500 ranges from complete loss (lower portion of the converse black curve) to no effect (top,  
 501 flat black line) of disturbance frequency on nutrient supply. Points A through D represent  
 502 four contrasting ecosystem responses as described in the text; for example, a coniferous  
 503 forest that requires a sufficient return interval of fire to sustain productivity because  
 504 nutrients immobilized in stand biomass and forest floors of old-growth are released for a  
 505 new cycle of growth (left side of the black curve moving towards the center, marked D).  
 506 Higher fire frequency, however, could be destructive (moving from center to the right  
 507 side of the black curve, marked B) because nutrients are depleted faster than they can be

508 replaced, thereby lowering ecosystem productivity. Every ecosystem and site type could  
509 occupy a unique spot in the conceptual figure, helping researchers formulate specific  
510 hypotheses on how disturbance frequency may be constructive, destructive or of no  
511 consequence to nutrient supply and ecosystem productivity.