

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

J. Marty Kranabetter, Ministry of Forests, Lands, and Natural Resource Operations, PO

Box 9536 Stn Prov Govt, Victoria BC V8W 9C4, Canada

Marty.Kranabetter@gov.bc.ca

Kendra K. McLauchlan, Department of Geography, Kansas State University, 118 Seaton

Hall, Manhattan KS 66506, USA

Sara K. Enders, Department of Land, Air, & Water Resources, University of California,

One Shields Avenue, Davis CA 95616-8627, USA

Jennifer M. Fraterrigo, Department of Natural Resources and Environmental Sciences,

University of Illinois, 1102 South Goodwin Ave, Urbana IL 61810, USA

Philip E. Higuera, Department of Forest Rangeland and Fire Sciences, University of

Idaho, 875 Perimeter Drive, Moscow ID 83844, USA

Jesse L. Morris, Department of Forest, Rangeland, and Fire Sciences, University of Idaho,

875 Perimeter Drive, Moscow ID 83844, USA

Edward B. Rastetter, The Ecosystem Center, The Marine Biological Laboratory, 7 MBL

Street, Woods Hole MA 02543, USA

Rebecca Barnes, Environmental Program, Colorado College, 14 E Cache La Poudre,

Colorado Springs CO 80903, USA

Brian Buma, University of Alaska Southeast, 11120 Glacier Hwy, Juneau AK 99801,

USA

Daniel G. Gavin, Department of Geography, 1251 University of Oregon, Eugene OR
97403-1251, USA

Laci M. Gerhart, Department of Geography, Kansas State University, 118 Seaton
Hall, Manhattan KS 66506, USA

Lindsey Gillson, Plant Conservation Unit, Department of Biological Sciences University
of Cape Town, Private Bag X3 7701, South Africa

Peter Hietz, Institute of Botany, University of Natural Resources and Life Sciences,
Gregor Mendel-Str.33, 1180 Vienna, Austria

Michelle C. Mack, Center for Ecosystem Science and Society, Northern Arizona
University, PO Box 5620, Flagstaff AZ 86011, USA

Brenden McNeil, West Virginia University, Department of Geology and Geography, P.O.
Box 6300, Morgantown WV 26506, USA

Steven Perakis, US Geological Survey, Forest and Rangeland Ecosystem Science Center,
3200 SW Jefferson Way, Corvallis OR 97331, USA

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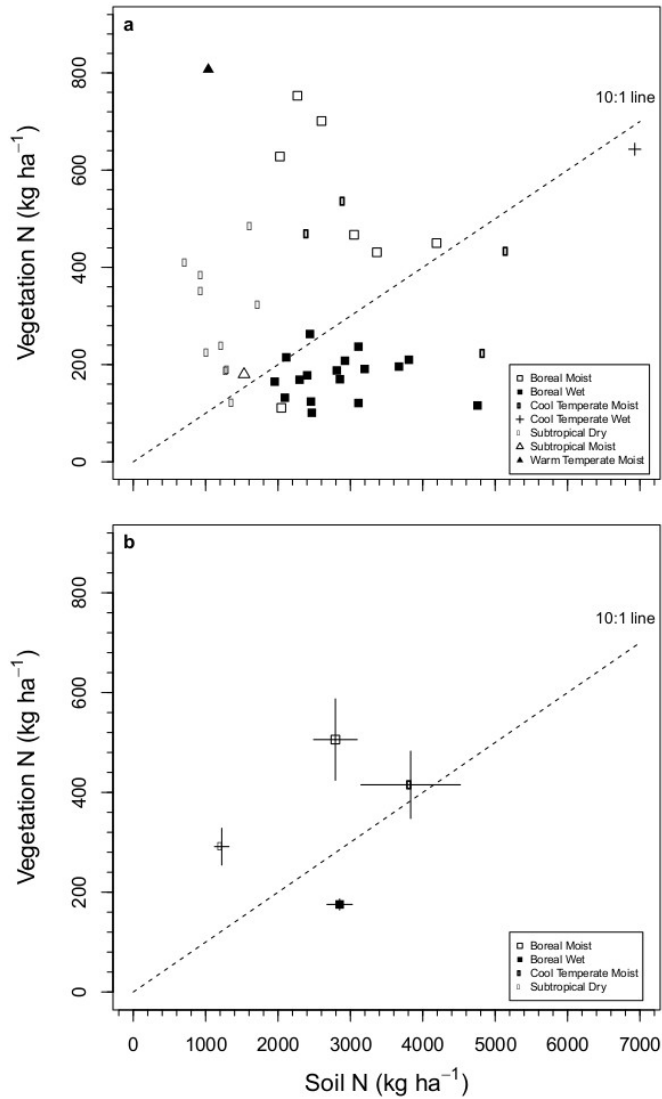
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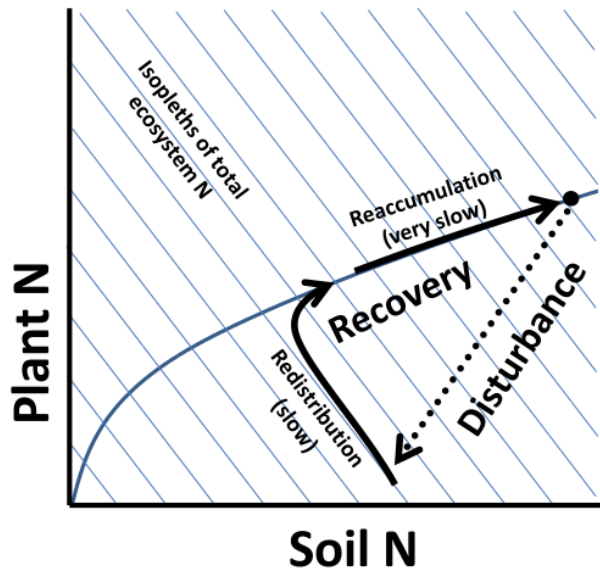
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469 **Figure 1.** a) Ratios of soil N and vegetation N pools in 41 forests in North America that
 470 are part of the Long-Term Soil Productivity network (Ponder et al. 2012). b) Mean values
 471 for four Holdridge life zones with one standard error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

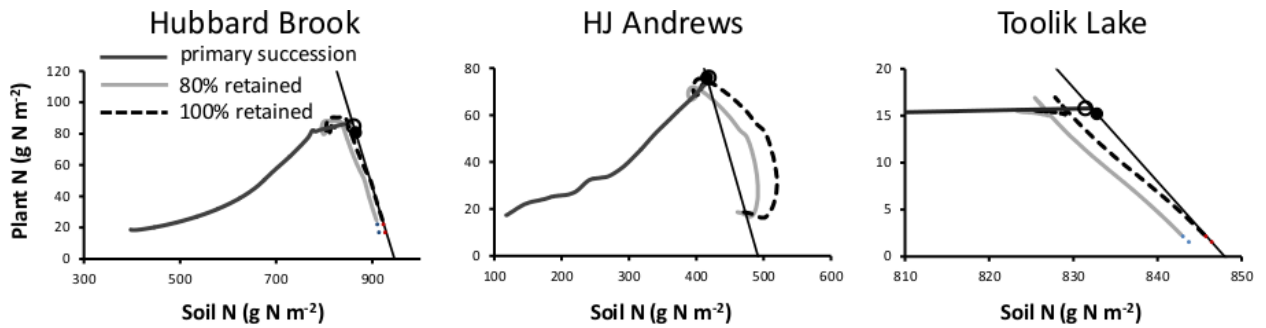
475 Ontario, Louisiana, Mississippi, Texas, Washington, Missouri, North Carolina, and Idaho.



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.

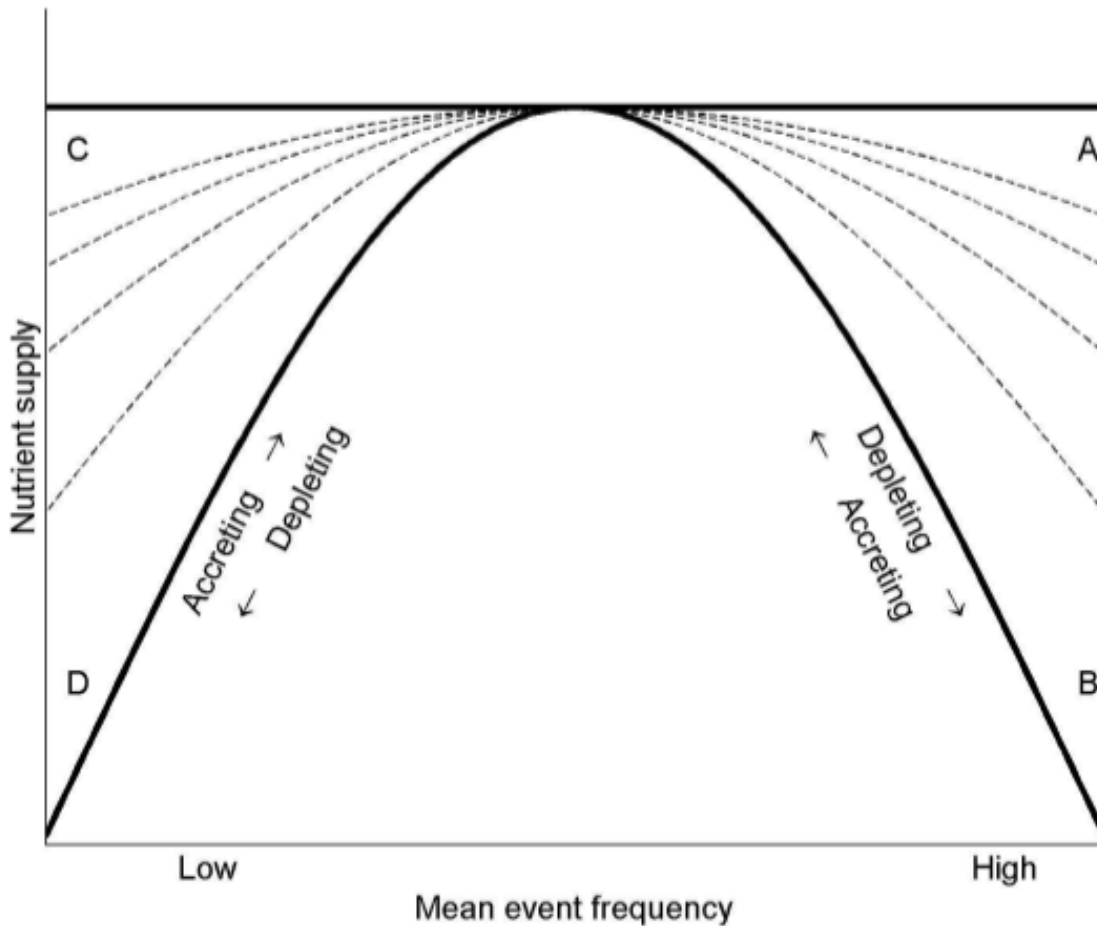
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487 **Figure 3.** Trajectory of N recovery in vegetation versus soil following disturbance at the
 488 Hubbard Brook, H.J. Andrews, and Toolik Lake LTER sites as predicted by the Multiple
 489 Element Limitation (MEL) model. The filled circles are 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.