A Stoichiometric Model of Early Plant Primary Succession

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abstract: The relative importance of plant facilitation and competition during primary succession depends on the development of ecosystem nutrient pools, yet the interaction of these processes remains poorly understood. To explore how these mechanisms interact to drive successional dynamics, we devised a stoichiometric ecosystem-level model that considers the role of nitrogen and phosphorus limitation in plant primary succession. We applied this model to the primary plant community on Mount St. Helens, Washington State, to check the validity of the proposed mechanisms. Our results show that the plant community is colimited by nitrogen and phosphorus, and they confirm previous suggestions that the presence of a nitrogen-fixing legume, *Lupinus lepidus*, can enhance community biomass. In addition, the observed nutrient supply rates may promote alternative successional trajectories that depend on the initial plant abundances, which may explain the observed heterogeneity in community development. The model further indicates the importance of mineralization rates and other ecosystem parameters to successional rates. We conclude that a model framework based on ecological stoichiometry allows integration of key biotic processes that interact nonlinearly with biogeochemical aspects of succession. Extension of this approach will improve the understanding of the process of primary succession and its application to ecosystem rehabilitation.

Keywords: primary succession, stoichiometry, nutrient limitation, resource competition, Mount St. Helens, facilitation.

Introduction

Primary succession—the development of an ecosystem from a substrate devoid of biological remnants—has been a subject of keen interest to ecologists for over a century (Clements 1916; Walker and del Moral 2003). Focusing mostly on plant communities and biogeochemical processes, ecologists have studied the development of ecosystems on glacial moraines (e.g., Matthews 1992; Chapin et al. 1994), volcanic substrates (e.g., del Moral and Bliss 1993; Tsuyuzaki and del Moral 1995; Vitousek 2004), sand dunes (e.g., Houle 1997), mine spoils (e.g., Smyth 1997), and other primary successional habitats (Walker and del Moral 2003). Since the rejection of the Clementsian theory of succession in the second half of the twentieth century, these studies have used empirical and statistical methods to discern relationships between populations and environments and tease out the mechanisms at work in a particular sere (e.g., Whittaker 1975). Conceptual models of succession are developed on the basis of the elucidated mechanisms in order to help understand and predict primary succession (Connell and Slatyer 1977; Pickett et al. 1987; Walker and Chapin 1987; Callaway and Walker 1997; del Moral et al. 2005).

This empirically driven approach to succession suffers several shortcomings. For example, due to the site-specific nature of empirical research, it is difficult to generalize about the presence and importance of mechanisms across seral communities, and only a few mechanisms (e.g., competition, facilitation, stochasticity) are explored (Walker and del Moral 2003). Furthermore, the complex interactions among successional mechanisms may not be amenable to experimental work, in part due to the temporal and spatial scales involved (Walker and del Moral 2003). The lack of generality, a limited understanding of interactions between mechanisms, and the intrinsic stochasticity of assembly processes combine to reduce ecologists' ability to predict community change (Walker and del Moral 2003).

To address these shortcomings, mechanistic mathematical models of succession have been developed (e.g., Pastor and Post 1986; Huston and Smith 1987). Their application to forest secondary succession has led to key insights concerning the importance of life-history traits and competition in succession (Huston and Smith 1987). However,

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this approach still does not necessarily lead to a general understanding of succession, as the models are tailored to specific seral communities such as forests (Walker and del Moral 2003). For greater generality, the models must be couched within a general theoretical framework that can be applied independently of the sere involved (Walker and del Moral 2003).

One such theoretical framework is ecological stoichiometry, which considers ecological interactions and processes at the chemical level (Sterner and Elser 2002). At the ecosystem level, many successional mechanisms, such as competition, facilitation, and resource availability, can be described in terms of exchanges of chemical compounds, which can allow for integration across levels of biological organization (Sterner and Elser 2002). At least one mechanistic stoichiometric model of marine succession has been developed and successfully applied, indicating the potential of the approach (Litchman et al. 2006).

Here we develop a mechanistic stoichiometric model of early plant primary succession based on early successional communities and biogeochemical processes at Mount St. Helens, a volcano in Washington State. We parameterized the model using data from field studies and the literature and compared the stoichiometric model's predictions with empirical results, finding qualitative agreement with both field observations and experimental manipulations. The model indicates that the plant community can enter different stable configurations on the basis of initial conditions, which has been hypothesized previously (del Moral et al. 2005). We conclude with a discussion on the impacts of the model for the study of primary succession.

Overview of Plant Primary Succession on Mount St. Helens

The eruption of Mount St. Helens in 1980 created a large area of primary successional habitat known as the Pumice Plain (Dale et al. 2005). The Pumice Plain lacked any biological remnants and contained no detectable nitrogen (del Moral and Clampitt 1985). The first plant to colonize the barren substrate was the prairie lupine (*Lupinus lepidus* var. *lobbii*), an herbaceous, short-lived, N-fixing legume (del Moral and Clampitt 1985; Bishop 2002). Because of its capacity to obtain N through its symbiotic association with *Bradyrhizobium* and its ability to tolerate stressful environmental conditions, *Lupinus* formed large monocultures across the Pumice Plain (Bishop et al. 2005).

In older colonies, *Lupinus* declined in dominance over time as the arrival of specialist herbivores and competing plant species reduced their numbers (Bishop 2002; del Moral and Rozzell 2005). Evidence suggests that *Lupinus* aided its own decline in dominance by facilitating the growth of competing plant species, presumably by im-

proving soil conditions and soil nutrient levels (Morris and Wood 1989; Halvorson et al. 1991*a*, 1991*b*, 1992; del Moral and Bliss 1993; Titus and del Moral 1998; Halvorson and Smith 2009). However, live *Lupinus* plants can actively inhibit the germination of competitors' seeds and sequester limiting resources such as N, P, and water (Morris and Wood 1989; Gill et al. 2006; Titus 2009). Furthermore, differences in community composition exist between areas with and without *Lupinus*, suggesting that certain plant species benefit most from associations with *Lupinus* (del Moral and Rozzell 2005; Titus 2009).

Recent experiments manipulating the levels of N and P available to the Pumice Plain plant community indicate that nutrient availability alters community composition and biomass (Gill et al. 2006; Bishop et al. 2010). With no nutrient additions, *Lupinus* dominated the experimental community, which also featured subdominant asters and grasses from the genus *Agrostis* (Gill et al. 2006). With additional N, the community became dominated by hairy cat's ear (*Hypochaeris radicata*; a weedy, nonnative composite), *Lupinus* decreased in biomass, and overall community biomass increased (Gill et al. 2006; Bishop et al. 2010). With additional P, *Lupinus* biomass increased over the short term, but other plant species experienced long-term benefit from N inputs by *Lupinus* (Gill et al. 2006; Bishop et al. 2010).

These results, combined with a lack of aboveground competition (Titus 2009), suggest that the change in community composition can be explained in terms of competition for nutrients and changes in nutrient availability, both of which are influenced by biotic and abiotic factors (Halvorson and Smith 2009). In addition, species differences in stoichiometries and the ability to fix N can alter both the competition for nutrients (Tyrrell 1999; Schade et al. 2005; Revilla and Weissing 2008) and nutrient availability through recycling (Daufresne and Hedin 2005; Ballantyne et al. 2008; Menge et al. 2009). Therefore, we develop a stoichiometrically explicit plant community model to explore how well ecological stoichiometry can explain the successional patterns seen at Mount St. Helens.

Modeling the Plant Community and Its Ecosystem

Because of the complex plant-soil-detritus interactions involved in primary succession, a good explanatory model for the community dynamics will need to keep track of nutrients in plant biomass, nutrients in the soil solution, and nutrients located within dead plant tissue (i.e., plant detritus). Each species j within our plant community will have a biomass B_j (mol C) and a certain amount of nutrient i per unit biomass, which is denoted by Q_{ij} (mol nutrient mol C^{-1}). Each plant will obtain nutrients from the soil solution depending on the concentration of each

nutrient i, denoted R_i (mol nutrient L^{-1}). When a plant dies, a portion of each nutrient i within it enters the plant detritus, denoted D_i (mol nutrient), and these nutrients can reenter the soil solution over time. The nutrient pathways between compartments are illustrated for the general case of n species with m nutrients (fig. 1).

Some simplifying assumptions are necessary to convert this conceptual framework into a mathematical model. For our model, we will assume a spatially homogeneous environment with temporally constant biotic and abiotic model parameters. We also assume that the plants considered here grow vegetatively (reproduction is ignored), have fixed amounts of C per unit biomass, have fixed allocation of biomass to roots and shoots, and compete solely through the reduction of belowground resources. We also assume that nutrients within the plant detritus are decomposed at the same rate, independent of the plant species from which they originated. The effects of violations of these assumptions will be addressed in "Discussion."

With these simplifying assumptions, we can describe the plant community, using a system of ordinary differential equations. The rate of change of nutrient i in the soil solution (left-hand term) is a function of the rate of nutrient supply (first two right-hand terms), the rate of uptake of nutrient i by the plant community (third term), and the rate of mineralization of nutrient i from the plant detritus (fourth term):

$$\frac{dR_i}{dt} = I_i - \phi_i R_i - \omega \sum_{j=1}^{n} f_{ij}(R_i, Q_{ij})B_j + \omega \delta_i D_i, \quad (1)$$

where I_i is the influx of nutrient i entering the soil solution, ϕ_i is the loss rate of nutrient i from the soil solution, ω is the reciprocal of the amount of water in the soil, f_{ij} is the uptake function of nutrient i for species j, and δ_i is the rate at which nutrient i is mineralized in the plant detritus. Note that the value of I_i depends on ω (see table 1) and that R_i is a concentration, and not a standing stock of nutrients as for plant biomass or plant detritus. Therefore changes in ω do not cause additional gains or losses in the total amount of nutrients present, but only in their concentrations in the soil solution.

The nutrient i taken up by species j enters into the plant's nutrient stores, whose dynamics (left-hand term) are governed by gains from uptake (first right-hand term) and dilution due to growth (second term):

$$\frac{dQ_{ij}}{dt} = f_{ij}(R_i, Q_{ij}) - \psi_j(Q_{1j}, \dots, Q_{ij}, \dots, Q_{nj})Q_{ij}, \quad (2)$$

where ψ_j is the growth function of species j, which depends solely on the amount of nutrients within its stores. Therefore, the dynamics of the biomass of species j (left-hand
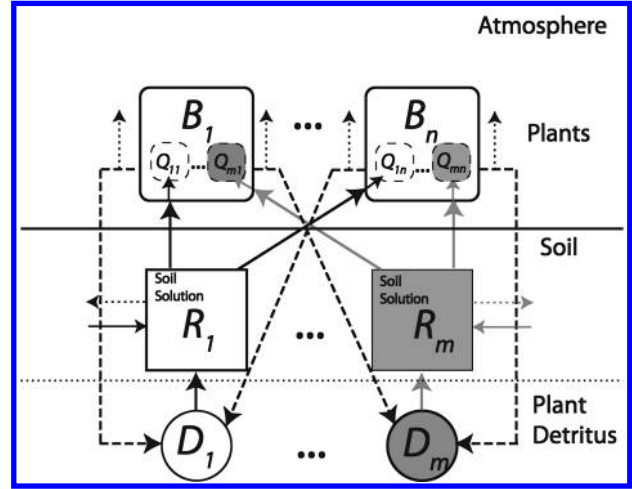

Figure 1: Conceptual diagram of the flows of m nutrients within an ecosystem with n plant species. Arrows with thin dotted lines indicate losses from the system, thick dashed arrows indicate the flow of nutrients from dead plants, and solid black and gray arrows indicate the flows of nutrients from plant detritus and the soil solution to plants and the flows of nutrients within the soil, respectively.

term) will be determined by the dynamics of the nutrient stores (first right-hand term), which control growth, and losses due to mortality (second term):

$$\frac{dB_j}{dt} = [\psi_j(Q_{1j}, \dots, Q_{ij}, \dots, Q_{nj}) - m_j]B_j, \quad (3)$$

where m_j is the mortality rate constant for species j. A portion of the nutrients lost to mortality ends up in the plant detritus compartment, whose dynamics (left-hand term) are governed by recycling (first right-hand term) and mineralization (second term):

$$\frac{dD_i}{dt} = \sum_{j=1}^{n} m_j B_j Q_{ij} \zeta_{ij} - \delta_i D_i, \quad (4)$$

where ζ_{ij} is the portion of nutrient i entering the plant detritus from species j. For the plant growth function, we assume that growth obeys Liebig's law of the minimum yielding a function that is identical to that used in most modeling studies with variable nutrient quotas (e.g., Klausmeier et al. 2004; Li and Smith 2007; Ballantyne et al. 2008; Revilla and Weissing 2008) known as the Droop function:

$$\psi_j(Q_{1j}, \dots, Q_{ij}, \dots, Q_{nj}) \quad (5)$$

$$= \mu_j \min\left(1 - \frac{Q_{\min, 1j}}{Q_{1j}}, \dots, 1 - \frac{Q_{\min, ij}}{Q_{ij}}, 1 - \frac{Q_{\min, nj}}{Q_{nj}}\right),$$

where μ_j is the maximum growth rate of plant species j at

Table 1: Definitions, dimensions, values, and sources for model parameters

Parameter (unit)	Definition	Value[a]	Data sources
I_i (μmol nutrient i day^{-1} L^{-1})	Influx of available nutrient i into ecosystem	(4.03 to 1,020) $\times$ ω for N, (100 to 867) $\times$ ω for P	Fagan et al. 2004; Gill et al. 2006; Halvorson and Smith 2009
ϕ_i (day^{-1})	Efflux of available nutrient i from ecosystem	1 (10^{-9} to 5) for N and P	Free parameter
ω (L^{-1})	Reciprocal of soil water content	.267 (.04 to .5)	Titus 2009
μ_j (day^{-1})	Maximum growth rate of species j at infinite Q	.218 for *Lupinus*, .352 (.252 to .352) for *Hypochaeris*, .140 (.120 to .140) for *Agrostis*	Fenner 1978; Van de Djik et al. 1982; Halvorson et al. 1991*a*; Rachmilevitch et al. 2006
m_j (day^{-1})	Mortality rate of species j	(.001 to .03) for all species	Tsuyuzaki et al. 1997; Braatne and Bliss 1999; Bishop 2002
$Q_{\max, Nj}$ (mol N mol C^{-1})	Maximum internal N concentration of species j	.0451 for *Lupinus*, .0509 for *Hypochaeris*, .0377 for *Agrostis*	Fagan et al. 2004; Bishop et al. 2010; Schoenfelder et al. 2010
$Q_{\min, Nj}$ (mol N mol C^{-1})	Minimum internal N concentration of species j	.0253 for *Lupinus*, .0115 for *Hypochaeris*, .0045 for *Agrostis*	Fagan et al. 2004; Bishop et al. 2010; Schoenfelder et al. 2010
$Q_{\max, Pj}$ (mol P mol C^{-1})	Maximum internal P concentration of species j	1.87×10^{-3} for *Lupinus*, 1.7×10^{-3} for *Hypochaeris*, 3.3×10^{-3} for *Agrostis*	Mamolos et al. 1995; Newberry et al. 1995; Fagan et al. 2004
$Q_{\min, Pj}$ (mol P mol C^{-1})	Minimum internal P concentration of species j	8.14×10^{-4} for *Lupinus*, 1.13×10^{-3} for *Hypochaeris*, 4.30×10^{-4} for *Agrostis*	Mamolos et al. 1995; Newberry et al. 1995; Fagan et al. 2004
ν_{Nj} (mol N day^{-1} mol C^{-1})	Maximum N uptake by species j	1.77×10^{-3} (1.49×10^{-3} to 1.77×10^{-3}) for *Lupinus*,[b] .127 (.0702 to .127) for *Hypochaeris*, .0183 (.0161 to .0183) for *Agrostis*	Van de Djik et al. 1982; Halvorson et al. 1992; Rachmilevitch et al. 2006
ν_{Pj} (mol P day^{-1} mol C^{-1})	Maximum P uptake by species j	2×10^{-3} (1.5×10^{-3} to 2×10^{-3}) for *Lupinus*,[c] 3.48×10^{-4} for *Hypochaeris*,[d] 1.87×10^{-3} (1.46×10^{-3} to 1.87×10^{-3}) for *Agrostis*,[e]	Loneragan and Asher 1967; Newberry et al. 1995; Esteban et al. 2003
K_{Nj} (μmol N L^{-1})	Half-saturation constant for N uptake by species j	115 (115 to 119) for *Lupinus*,[f] 7 (7 to 19) for *Hypochaeris*, 15 (15 to 30) for *Agrostis*[g]	Van de Djik et al. 1982; Barber 1995; Dunbabin et al. 2002
K_{Pj} (μmol P L^{-1})	Half-saturation constant for P uptake by species j	15.7 (15.7 to 16.7) for *Lupinus*,[c] .731 for *Hypochaeris*,[d] 3.7 (1.47 to 3.7) for *Agrostis*[h]	Loneragan and Asher 1967; Mouat 1983; Esteban et al. 2003
ζ_{ij}	Proportion of nutrient i recycled to detritus by species j	(0 to .99) for all species and all nutrients	Free parameter
δ_i (day^{-1})	Mineralization rate of nutrient i	.0015 (10^{-9} to 1) for N and P	Free parameter

[a] Where indicated, data in parentheses are ranges.

[b] Data based on season-end accumulation of N, with season equal to 100 growing days.

[c] Data from *Lupinus angustifolius* and *Lupinus pilosus*.

[d] Data from *Hypochaeris glabra*.

[e] Data from *Agrostis capillaris*.

[f] Data from *Lupinus albus*.

[g] Data from non-*Agrostis* grasses such as *Fescue*.

[h] Data from *Agrostis tenuis*.

infinite internal nutrients and $Q_{\min, ij}$ is the minimum amount of internal nutrient i for species j; the min function takes the smallest value found within the brackets of equation (5), which implements Liebig's law of the minimum. While the assumption of a theoretical maximum growth rate for all nutrient types is commonly used (e.g., Litchman et al. 2006; Ballantyne et al. 2008), its biological realism has been recently questioned (Cherif and Loreau 2010). Such concerns can be alleviated by having a theoretical maximum growth rate for each nutrient, that is, by using μ_{ij} instead of μ_j. We use the common theoretical maximum growth rate for analytical simplicity.

For the nutrient uptake function, we assume that increasing the soil solution nutrient concentration increases uptake but increasing the internal nutrient concentration decreases uptake. Such an uptake function has been argued for theoretically (Morel 1987; Grover 1997), has empirical support for both *Hypochaeris* and *Agrostis* (Van de Djik et al. 1982; Newberry et al. 1995), and likely captures the activation of high-affinity uptake systems of plants during periods of nutrient stress (Vance et al. 2003). To meet both assumptions, we use the following functional form:

$$f_{ij}(R_i, Q_{ij}) = \left(\frac{v_{ij}R_i}{K_{ij} + R_i}\right)\left(\frac{Q_{\max, ij} - Q_{ij}}{Q_{\max, ij} - Q_{\min, ij}}\right), \quad (6)$$

where v_{ij} is the maximum uptake rate of nutrient i by species j, K_{ij} is the half-saturation constant for nutrient i uptake by species j, and $Q_{\max, ij}$ is the maximum internal nutrient i concentration in species j. The units of the variables and the parameters involved in the model are listed in table 1.

To apply this general model to the Mount St. Helens plant community, we assume that N and P are the only limiting nutrients; this assumption is supported by previous studies (Wagner and Walker 1986; Gill et al. 2006). We also used net mineralization rates of N in areas with no plants as our estimate for I_N, and we calculated I_P by assuming that 0.5% of P that is potentially available for plants is in the soil solution, an assumption that is based on previous studies of P dynamics (Barber 1995; see app. A in the online edition of the *American Naturalist* for more details). Furthermore, we use *Lupinus lepidus*, *Hypochaeris radicata*, and *Agrostis scabra* (ticklegrass) as representative components of the plant community in our model to reduce model complexity. Each of these species represents a different plant functional group found on Mount St. Helens (legume, forb, and grass, respectively). As well, they are the dominant representatives of those functional groups in many locations, which further justifies the simplifying assumption (del Moral and Jones 2002; Gill et al. 2006; Schoenfelder et al. 2010).

We also modify equation (2) for the N stores of *Lupinus*,

as *Lupinus* is capable of fixing N and this will add N to the environment after *Lupinus* plants die. Because *Lupinus* species seem to maintain relatively constant uptake of N independent of soil solution N concentrations (Lee et al. 2003), we assume that *Lupinus* always achieves maximum N uptake:

$$\frac{dQ_{NL}}{dt} = v_{NL}\frac{Q_{\max, NL} - Q_{NL}}{Q_{\max, NL} - Q_{\min, NL}} - \mu_L \times$$

$$\min\left(1 - \frac{Q_{\min, NL}}{Q_{NL}}, 1 - \frac{Q_{\min, PL}}{Q_{PL}}\right)Q_{NL}. \quad (7)$$

This modification to equation (2) does not result in a change of $f_{NL}(R_N, Q_{NL})$ in equation (1). Even with these simplifications, the final three-species, two-nutrient model has 13 coupled ordinary differential equations and 43 model parameters (table 1). Many parameter values were obtained directly from the literature in the form of point estimates or ranges (table 1). However, some estimates were obtained by using statistical techniques on data series or by making simplifying assumptions about the biology of the plants. Other parameter estimates could be found only for species related to those studied here, which could impact the results of the model. Further details on model parameterization can be found in appendix A.

Model Analysis

Because the model defined by the above equations is high dimensional, many of our results were generated by numerical simulations. However, we did achieve some success in obtaining the local stability and existence conditions for many of the fixed points in the model, which were somewhat similar to those found by Li and Smith (2007; see app. B in the online edition of the *American Naturalist*). Conveniently, many of these conditions can be expressed graphically using previously developed techniques from resource-competition theory (e.g., Tilman 1980; Klausmeier et al. 2004; Daufresne and Hedin 2005).

Briefly, the graphical technique involves calculating the break-even resource levels for each plant j, known as R^* values, which are then combined to create the zero-net-growth isocline (ZNGI; Tilman 1980) for plant j (Z_j; fig. 2A). The species with the lowest R^* value for a particular resource is considered to be the best competitor for that resource. The ZNGIs help to establish the existence conditions for the possible steady states of our plant community. A coexistence steady state between species can occur only if the ZNGIs of the species intersect. Because N and P are essential resources, such isocline intersections occur only if different species are better competitors for different nutrients. Furthermore, there can be no three-
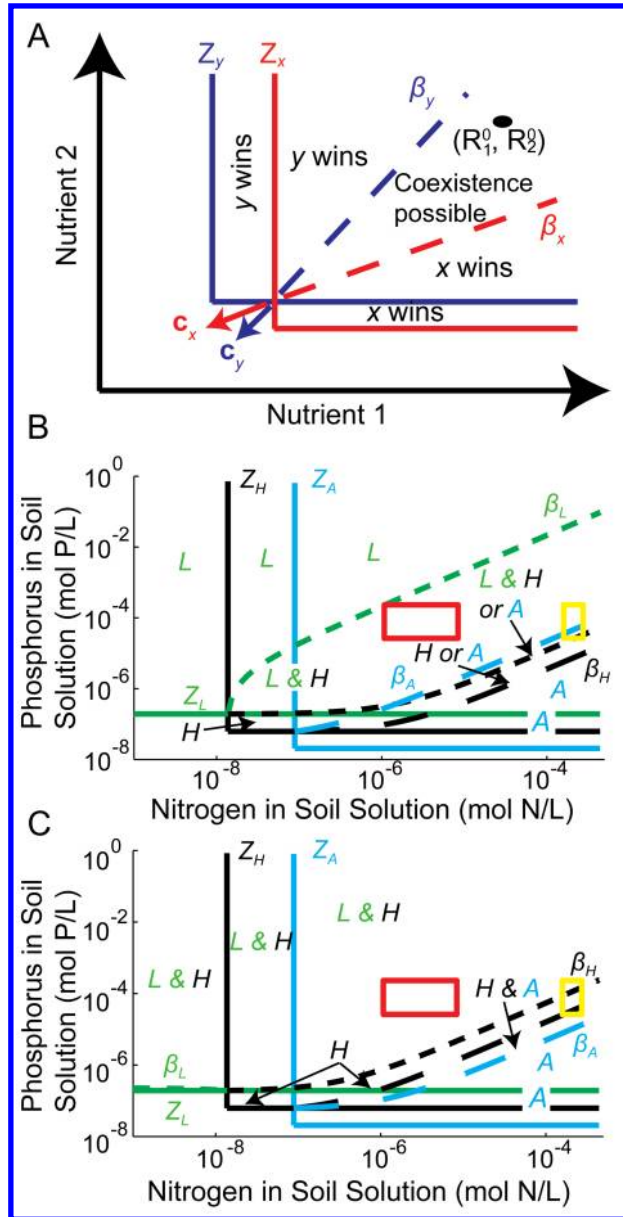
Figure 2: Outcomes of competition for nutrients between plants. Z_j is the zero-net-growth isocline (ZNGI) and β_j is the slope of net consumption vector (c_j) at equilibrium of species j. The regions delineated by the ZNGIs and the slopes of the net consumption vectors in the N-P plane determine what supply rates of N and P give rise to the existence and stability of the various steady states of the plant community. *A*, Theoretical example of competition between species *x* (*red lines*) and *y* (*blue lines*) for nutrients 1 and 2, where the coexistence steady state is stable. The location of the supply point (R_1^0, R_2^0) indicates that the ecosystem will go to the coexistence steady state. *B*, Outcomes of competition in the Mount St. Helens plant community with no recycling. *C*, Outcomes of competition in the Mount St. Helens plant community with recycling, $\zeta_{PL} = \zeta_{NL} = 0.01$, $\zeta_{PA} = \zeta_{NH} = 0.8$, $\zeta_{PH} = \zeta_{NA} = 0.1$. Outcomes of competition at steady state in each region of the N-P plane are denoted by

species coexistence steady states with only two essential nutrients, except in degenerate cases where species share the same R^* values, which does not occur here.

When there are coexistence steady states, the slopes of the net consumption vectors of each species j (β_j) found at each particular coexistence steady state, in conjunction with the ZNGIs, divide the nutrient plane into different areas, with each one having attracting steady states (fig. 2*A*). If the nutrient supply point is located in a certain area, then the system will go to specific steady states (fig. 2*A*). Hence, the β_j values determine the local stability of steady states in the ecosystem.

Whenever analytical techniques failed to yield stability conditions for certain fixed points, we performed extensive numerical simulations to obtain model results within the parameter regimes in question. The results of the simulations were nearly always in agreement with the qualitative results obtained by Daufresne and Hedin (2005), with possible dynamics including bistability and limit cycles. We obtained our numerical results by using one of Matlab's (Mathworks) stiff ordinary differential equation solvers (ode15s).

Results

Competitive Abilities and Possible Communities

The R^* values were calculated by setting equations (1)–(4) equal to 0 and solving for each variable while assuming that only one nutrient will be limiting plant growth at equilibrium. We obtained the following expression of R^* for plant species j being limited by nutrient i:

$$R_{ij}^* = \frac{\mu_j K_{ij}(Q_{ij}^* - Q_{\min, ij})(Q_{\max, ij} - Q_{\min, ij})}{\nu_{ij}(Q_{\max, ij} - Q_{ij}^*) - \mu_j(Q_{ij}^* - Q_{\min, ij})(Q_{\max, ij} - Q_{\min, ij})},$$ (8)

$$Q_{ij}^* = \frac{\mu_j Q_{\min, ij}}{\mu_j - m_j}.$$

Equations (8) indicate that R^* values are dependent on growth rate, mortality rate, nutrient uptake kinetics, and plant stoichiometry. Dependence on mortality rate poses some difficulties because the mortality rate is highly variable for all species found on Mount St. Helens (table 1). However, all three species considered here are small, short-lived perennials that should have similar average mortality rates, with the exception of *Lupinus*, as it suffers higher

L (*Lupinus*; *green lines*), H (*Hypochaeris*; *black lines*), and A (*Agrostis*; *cyan lines*). The ampersand indicates coexistence, while "*or*" indicates bistability. Boxes in *B* and *C* represent nutrient supply rates measured by Halvorson and Smith (2009; *red box*) and Gill et al. (2006; *yellow box*). Mortality rates are set at $m_L = 0.024$ day^{-1} and $m_A = m_H = 0.02$ day^{-1}.

morality due to herbivory (Bishop 2002). With such an assumption, we estimated the range of R^* values that were possible for each species for each nutrient at specific mortality rates (table 2).

Our investigation predicts a clear competitive hierarchy for N and P within the community (table 2). For N, *Lupinus* was the superior competitor, as it is not limited by N due to nitrogen fixation, followed by *Hypochaeris* and *Agrostis*. The order was reversed for P, with *Agrostis* dominating, followed by *Hypochaeris* and *Lupinus* (table 2). These results held for both low and high values of mortality (table 2).

Because of the ranking of competitive abilities, there are three possible two-species coexistence steady states; however, only the *Hypochaeris-Lupinus* and *Agrostis-Hypochaeris* steady states could be stable if all three species are initially present (fig. 2*B*). To determine graphically the regions of stability of each coexistence steady state, we calculated the slopes of the net consumption vectors of each species, which are given as

$$\beta_j = \frac{(1 - \zeta_{Nj})Q_{Nj}^{xy}}{(1 - \zeta_{Pj})Q_{Pj}^{xy}}, \tag{9}$$

where Q_{ij}^{xy} is the internal concentration of nutrient i of species j at the coexistence steady state of species x and y. Derivation of β_j can be found in appendix B.

If we ignore recycling, the *Hypochaeris-Lupinus* steady state is locally stable if it exists and the *Agrostis-Hypochaeris* steady state is unstable (fig. 2*B*). In addition, the empirically derived region of nutrient supply is located within both of these regions, indicating large potential shifts in community composition depending on the local environment (fig. 2*B*).

Nutrient recycling can affect competitive outcomes between the species on Mount St. Helens (fig. 2*C*). Nutrient recycling can allow for coexistence between *Agrostis* and

Hypochaeris as well as alter the region of coexistence between *Hypochaeris* and *Lupinus* (fig. 2*C*). However, this change from bistability to coexistence requires large differences in the amounts of N and P that are recycled for both species (about an eightfold difference in fig. 2*B*), which may not be biologically reasonable. Additionally, at the steady states observed here, *Lupinus* adds more N than it uptakes from the environment, which can allow other species to establish at lower nutrient supply levels than they could without *Lupinus* (note that *Hypochaeris* can establish in environments below its R^* value for N; fig. 2*C*).

Areas of bistability are of particular interest in successional studies because they support the possibility of multiple successional trajectories. Here, an area of parameter space exists where a stable *Hypochaeris-Lupinus* steady state overlaps with the unstable *Agrostis-Hypochaeris* steady state (fig. 2*B*). This area indicates that the eventual outcome is a community composed of either *Agrostis* alone or *Hypochaeris* and *Lupinus* together. Which outcome occurs depends on the initial conditions (e.g., plant densities, nutrient levels) and indicates that the region is bistable (fig. 2*B*).

Impacts of Lupinus *on Community Structure*

Lupinus can promote greater community biomass by supplying N to *Agrostis* and *Hypochaeris* (fig. 3). In low-N environments, *Hypochaeris* and *Agrostis* can establish, with *Hypochaeris* eventually excluding *Agrostis*, but total community biomass is low (fig. 3*A*). With the addition of *Lupinus*, community biomass increases drastically (fig. 3*B*). The beneficial effects of *Lupinus* on community biomass decline as the environment becomes richer in N and *Lupinus* experiences greater competition (fig. 3*C*).

Increasing *Lupinus* mortality does not increase the bio-

Table 2: Relative competitive abilities of *Lupinus*, *Hypochaeris*, and *Agrostis* for N and P

| Mortality rates (day^{-1}), species identity | R^* | |
	For N (mol N L^{-1})	For P (mol P L^{-1})
$m_L = .003$, $m_A = m_H = .00233$:		
Lupinus	...[a]	1.97×10^{-8}–2.8×10^{-8}
Hypochaeris	1.49×10^{-9}–7.32×10^{-9}	5.69×10^{-9}–5.73×10^{-9}
Agrostis	8.74×10^{-10}–20.0×10^{-10}	8.05×10^{-10}–26.0×10^{-10}
$m_L = .03$, $m_A = m_H = .029$:		
Lupinus	...[a]	2.58×10^{-7}–3.69×10^{-7}
Hypochaeris	2.07×10^{-8}–10.6×10^{-8}	1.04×10^{-7}–1.22×10^{-7}
Agrostis	1.41×10^{-7}–3.40×10^{-7}	1.30×10^{-8}–4.43×10^{-8}

[a] Because of its symbiotic relationship with N-fixing bacteria, *Lupinus* can maintain positive growth with no N in the environment and is not limited by N.
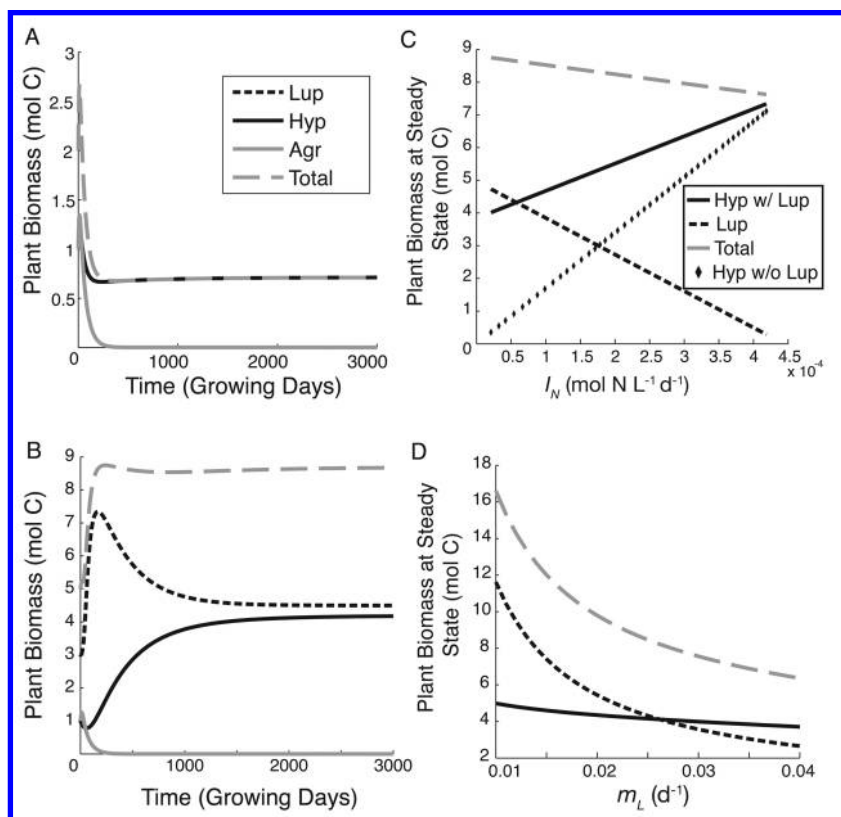
Figure 3: The effects of *Lupinus* (*dashed black line*) on *Agrostis* (*gray line*), *Hypochaeris* (*black line*), and total community biomass (*dashed gray line*) under different conditions. Recycling, mortality, and phosphorus influx rates, unless otherwise specified, are $\zeta_{NL} = 0.2$, $\zeta_{PA} = \zeta_{NH} = \zeta_{PH} = \zeta_{NA} = \zeta_{PL} = 0.1$, $m_L = 0.024$ day^{-1}, $m_A = m_H = 0.02$ day^{-1}, $I_P = 53.5$ μmol P L^{-1} day^{-1}, and $I_N = 41.85$ μmol N L^{-1} d^{-1}, respectively. *A*, *Lupinus* absent. *B*, *Lupinus* present. *C*, Community and *Hypochaeris* (*solid line* = with *Lupinus*; *diamonds* = without *Lupinus*) response to increasing nitrogen supply. *D*, Community response to increasing *Lupinus* mortality.

mass of other species (fig. 3*D*). Instead, it results in the exclusion of *Lupinus* and the elimination of any potential benefit from N fixation (fig. 3*D*). The community as a whole seems to benefit from decreased *Lupinus* mortality, with greater biomass for *Hypochaeris* (fig. 3*D*). The qualitative behavior of the simulation results in figure 3 generally holds for parameter values other than those used in the simulations.

Rates of Primary Succession

The time needed for the plant community to nearly reach a "steady state" for realistic parameter values and initial densities is between 5 and 20 years (500–2,000 growing days; fig. 3). The rates of succession match the timescales of vegetation development in patches seen at Mount St. Helens (del Moral and Bliss 1993), though they are dependent on mortality rates, initial community composition, and the rates at which nutrients within dead plant

material are recycled (particularly N; app. C in the online edition of the *American Naturalist*).

Effects of Enrichment on Community Structure

The model makes similar qualitative predictions to those found in field experiments at Mount St. Helens (e.g., Gill et al. 2006; Bishop et al. 2010; Schoenfelder et al. 2010), although the simulation results are sensitive to the parameter values because the model is attempting to capture transient behavior of the plant community. By simulating short-term additions of N, P, and both nutrients together, we found that *Hypochaeris* is most responsive to N additions, whereas P additions resulted in an increase in *Lupinus* biomass (fig. 4*A*–4*C*), in agreement with the experimental results (fig. C3). The model also predicts that when both nutrients are added, *Hypochaeris* dominates the community (fig. 4*D*), which is also seen in the experiment (fig. C3). However, *Lupinus* did not decline as observed in the experiments (fig. C3), which may indicate that an-
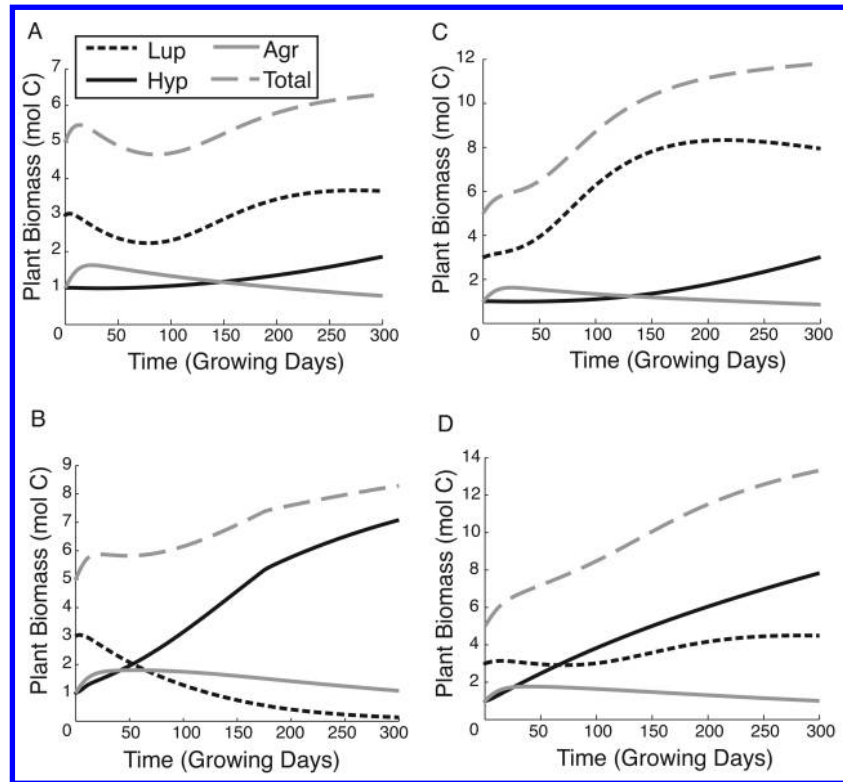
Figure 4: Simulation of the effects of short-term N and P additions on the dynamics of plant community (*dashed gray line*), *Lupinus* (*dashed black line*), *Hypochaeris* (*black line*), and *Agrostis* (*gray line*) biomasses. Recycling and mortality rates for all panels are $\zeta_{NL} = 0.2$, $\zeta_{PA} = \zeta_{NH} = \zeta_{PH} = \zeta_{NA} = \zeta_{PL} = 0.1$, $m_L = 0.018$ day^{-1}, $m_A = 0.004$ day^{-1}, and $m_H = 0.005$ day^{-1}, respectively. *A*, Control level of nutrients with influx $I_N = 12.93$ μmol N L^{-1} day^{-1} and $I_P = 20$ μmol P L^{-1} day^{-1}. *B*, N addition with $I_N = 129.3$ μmol N L^{-1} day^{-1} and I_P at control value. *C*, P addition with I_N at control value and $I_P = 40$ μmol P L^{-1} day^{-1}. *D*, N and P addition with I_N and I_P at addition values.

other process other than nutrient limitation is involved in *Lupinus* mortality (fig. 4*D*). Overall, the community is limited by both N and P, with P limiting *Lupinus* and N limiting the other species.

Discussion

We have developed a stoichiometrically explicit model of a plant community to explore plant community dynamics during primary succession. Our parameterized model matched many patterns observed at Mount St. Helens, such as the P limitation of *Lupinus* and the large biomass response of *Hypochaeris* to N additions (table 2; fig. 4). In addition, our model highlights the important facilitative role of *Lupinus* solely on the basis of N additions to the local ecosystem through mortality events. Furthermore, our model gives rise to more general results such as the important role of nutrient recycling in determining competitive outcomes (fig. 2). Overall, our results demonstrate the usefulness of ecological stoichiometry in explaining

and predicting plant community dynamics during primary succession.

Limitations to Approach

To make our model tractable and capable of elucidating the importance of ecological stoichiometry for plant community dynamics at Mount St. Helens, we made simplifying assumptions that reduced the realism of our model. Here, we highlight limitations to our approach due to assumptions about space, life-history traits, and interactions with nonplant organisms.

Our model assumes that the nutrients and organisms within the area considered are well mixed, a common assumption in resource-competition and stoichiometric models (e.g., Tilman 1980; Litchman et al. 2006). This assumption should hold only at small scales (<1 m²) because of patchy nutrient distribution, the limited zones of influence of plants on nutrient concentrations, and the effects of dispersal on plant distributions (Huston and DeAngelis 1994; Barber 1995; Nathan and Muller-Landau

2000). Therefore, our model should be applied only to local dynamics of the plant community, with appropriate modifications to address regional dynamics.

While many life-history traits are explicitly considered in the model (stoichiometry, uptake kinetics, growth and mortality rates), much has been simplified or ignored in the model. Differential allocation of resources to structures and reproduction, seed size, seed mortality, and size-dependent mortality are all traits that can influence the outcomes of plant competition, but they have been ignored here for simplicity (Huston and Smith 1987; Tilman 1988). These traits may explain why *Agrostis* can coexist with *Hypochaeris* and *Lupinus* at local scales in the field though our model predicts no coexistence (fig. 2; Gill et al. 2006). We also ignored the potential interactions between N and P acquisition, as N fixation can be affected by low soil P levels (Vitousek and Howarth 1991) and some N fixers, including *Lupinus* spp., can exude organic compounds that can increase P supply in the environment (e.g., Lambers et al. 2006).

Our model did not explicitly incorporate the population dynamics of herbivores and soil organisms or their effects on plant and nutrient dynamics. Herbivores contribute to the episodic mortality of *Lupinus*, which can accelerate the rate of succession by making the nutrients stored in *Lupinus* plants available for other plants and soil organisms (Bishop 2002; Fagan et al. 2004; Bishop et al. 2005). Herbivores can also promote the loss of nutrients from an ecosystem by converting them into volatile forms that can be lost through denitrification, volatilization, and leaching (de Mazancourt et al. 1999). Soil N losses at Mount St. Helens (Halvorson and Smith 2009) have coincided with herbivore-caused mortality and could explain the repeated reemergence of lupine dominance in the oldest colonization sites.

Soil organisms are reliant on carbon inputs provided by plants and herbivores and can control the growth of plants by immobilizing nutrients when carbon is lacking, leading to deceleration of succession (Halvorson and Smith 2009). These interactions cannot easily be incorporated into the current modeling framework, because of either spatial dependence (herbivores) or lack of knowledge concerning the interactions (soil organisms; Apple et al. 2009; Halvorson and Smith 2009). Therefore, we leave the incorporation of herbivores and soil organisms to future work.

Relevance to Mount St. Helens

Despite the limitations of our study, we believe that our work is relevant for Mount St. Helens in particular and primary succession in general. Our study is the first to develop a mathematical model of plant community dy-

namics for Mount St. Helens that is based on proposed mechanisms from earlier studies (del Moral and Bliss 1993; Dale et al. 2005). Other models for plant community dynamics were phenomenological, had mixed success at predicting the dynamics, and provided little explanation for the observed patterns (Childress et al. 1998; del Moral 2000; del Moral and Jones 2002). The lack of success of phenomenological models suggests that process-based (mechanistic) models incorporating abiotic and biotic processes are needed to predict primary succession (Childress et al. 1998). Our work with a stoichiometrically explicit model for primary succession suggests that developing such process-based models is feasible and could be applied to other successional systems.

In addition, we can compare our model results with previous hypotheses concerning the effects of *Lupinus* on the plant community (e.g., Morris and Wood 1989; Bishop 2002). Our model supports the hypothesis that *Lupinus* N inputs are large enough to have a net facilitative effect on other species growth, despite competition for other soil resources (fig. 3; Morris and Wood 1989). Our model did not support the hypothesis that higher mortality rates for *Lupinus* will accelerate succession at local scales because *Lupinus* populations became smaller, which resulted in less fixed nitrogen and poorer growth for other plant species (fig. 3; Bishop 2002). However, the differences between field observations and model results, in this instance, likely originate from the pulses of mortality observed in the field but not incorporated in the model (Braatne and Bliss 1999; Bishop et al. 2005). Further elaboration of our model with greater realism should allow us to investigate additional hypotheses concerning succession at Mount St. Helens.

Our study also helps to integrate results from several of the empirical studies on plant and herbivore stoichiometry previously conducted at Mount St. Helens (Fagan et al. 2004; Gill et al. 2006; Apple et al. 2009; Schoenfelder et al. 2010). Some studies highlight how mismatches between plant and herbivore stoichiometry combined with spatial variation in plant stoichiometry, which can be explained by succession, result in unexpected herbivory patterns that can halt the spread of plant species (Fagan et al. 2004, 2005; Apple et al. 2009). Other studies have focused on how nutrient limitation and competition for nutrients interact with plant stoichiometry to structure the plant community (Gill et al. 2006; Bishop et al. 2010; Schoenfelder et al. 2010). While our current model addresses the second set of studies, we can extend our approach to include herbivores and their impacts on the plant community. This natural extension of our model should provide insights into how herbivory, competition, and nutrient limitation jointly control succession at Mount St. Helens.

Ecological Stoichiometry and Primary Succession

Most successional theories and models have been developed for secondary succession, with the focus mostly being on life-history traits and biotic interactions (Connell and Slatyer 1977; Pastor and Post 1986; Huston and Smith 1987; Pickett et al. 1987; Walker and Chapin 1987; Callaway and Walker 1997). Although these factors are important, abiotic factors can be just as or more influential during primary succession (Walker and Chapin 1987; Matthews 1992; Walker and del Moral 2003; del Moral et al. 2005). This fact limits the applicability of current models of succession to primary succession (Pickett et al. 1987; Walker and Chapin 1987; Walker and del Moral 2003). Only frameworks that can incorporate and investigate the interactions between abiotic and biotic factors will provide ecologists with the tools needed to understand and predict primary succession. Furthermore, the frameworks must allow for the development of models that can explain the mutual feedbacks between ecosystem development and biotic interactions.

Our study suggests that ecological stoichiometry provides such a framework. It allowed us to integrate ecosystem processes such as nutrient cycling with community processes like competition. Using information only on soil nutrients, plant stoichiometry, and plant physiology, we were able to predict qualitatively the competitive hierarchies observed at Mount St. Helens, the facilitative effects of *Lupinus* on other species, and the responses of each species to nutrient enrichment (figs. 2–4). Such results, combined with those from Gill et al. (2006) and Apple et al. (2009), indicate the powerful explanatory and synthetic potential of a stoichiometric framework for primary succession.

This potential extends beyond primary succession, as several of our results demonstrate. First, our model demonstrates that the recycling of nutrients by plants can lead to starkly different competitive outcomes by shifting the effective rate of resource supply (fig. 2). The shift is caused by differences in stoichiometry and nutrient retention between competing species, which can be seen only when nutrient recycling and nutrient dynamics are explicitly considered (Daufresne and Hedin 2005). This result, combined with the influence of other trophic levels on nutrient limitation (Daufresne and Loreau 2001; Cherif and Loreau 2009), suggests that the differences in stoichiometry and nutrient retention across species should be explicitly considered in ecological communities.

Second, we demonstrate that alternative successional trajectories may be created and maintained through the deterministic competitive and facilitative interactions, which promote destabilizing nutrient consumption at the coexistence steady state, combined with variation in initial floristic composition (fig. 2). This supports the view that stochastic assembly plays a key role in succession (del Moral et al. 2005). Third, our model shows the important role of P in determining the availability of N in an ecosystem by controlling the biomass of *Lupinus* (fig. 4). Our result lends support to the idea that N limitation in many ecosystems is caused by the P limitation of N fixers (Vitousek and Howarth 1991; Vitousek 2004). Overall, these results demonstrate how the explicit incorporation of abiotic and biotic mechanisms into a common framework can lead to important, general insights for ecological problems.

Conclusions

Our model demonstrates that some of the vegetation patterns found on Mount St. Helens during primary succession can be explained and predicted through ecological stoichiometry. This suggests that our model may be useful for predicting patterns of successional dynamics more broadly, which is needed for applications to ecosystem restoration and the potential invasibility of local communities.

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