

Boom and bust carbon–nitrogen dynamics during reforestation



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ABSTRACT

Legacies of historical land use strongly shape contemporary ecosystem dynamics. In old-field secondary forests, tree growth embodies a legacy of soil changes affected by previous cultivation. Three patterns of biomass accumulation during reforestation have been hypothesized previously, including monotonic to steady state, non-monotonic with a single peak then decay to steady state, and multiple oscillations around the steady state. In this paper, the conditions leading to the emergence of these patterns is analyzed. Using observations and models, we demonstrate that divergent reforestation patterns can be explained by contrasting time-scales in ecosystem carbon–nitrogen cycles that are influenced by land use legacies. Model analyses characterize non-monotonic plant–soil trajectories as either single peaks or multiple oscillations during an initial transient phase controlled by soil carbon–nitrogen conditions at the time of planting. Oscillations in plant and soil pools appear in modeled systems with rapid tree growth and low initial soil nitrogen, which stimulate nitrogen competition between trees and decomposers and lead the forest into a state of acute nitrogen deficiency. High initial soil nitrogen dampens oscillations, but enhances the magnitude of the tree biomass peak. These model results are supported by data derived from the long-running Calhoun Long-Term Soil–Ecosystem Experiment from 1957 to 2007. Observed carbon and nitrogen pools reveal distinct tree growth and decay phases, coincident with soil nitrogen depletion and partial re-accumulation. Further, contemporary tree biomass loss decreases with the legacy soil C:N ratio. These results support the idea that non-monotonic reforestation trajectories may result from initial transients in the plant–soil system affected by initial conditions derived from soil changes associated with land-use history.

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1. Introduction

Ecosystem transitions between agricultural and forest land uses occur across the globe and are associated with transient changes in biogeochemical cycling. It is estimated that 64% of the world's forests are regenerating from disturbance caused by human activities (FAO, 2010). Land use legacy effects originating from such transitions include altered species composition, water fluxes, soil chemistry, soil carbon and nitrogen storage, and ecosystem nitrogen cycling (Richter et al., 1994, 2000; Guo and Gifford, 2002; Farley

et al., 2005; Berthrong et al., 2009; Bain et al., 2012; Bernal et al., 2012; Vadeboncoeur et al., 2012).

Several modes of transient forest recovery after disturbance have been recognized. Peet (1981) summarized biomass recovery trajectories across a gradient of increasing time lag between recruitment and mortality: saturating growth to steady state (no lag), overshoot of and subsequent decay to steady state (moderate lag), and multiple oscillations around the steady state (long lag) (Fig. 1a). Consistent with Peet's (1981) "asymptotic yield" curve with no lag, reforestation trajectories are commonly characterized by a monotonic, saturating approach to a relatively stable live tree biomass (Fig. 1b) (e.g., Odum 1969; Dewar 1991; Dewar and Cannell, 1992; Ryan et al., 1997; Amiro et al., 2000; Williams et al., 2012; Wang et al., 2014). In contrast, many stands exhibited non-monotonic reforestation trajectories with overshoot or oscillations (Fig. 1c) (e.g., Peet and Christensen, 1987; Aakala and Keto-Tokoi,

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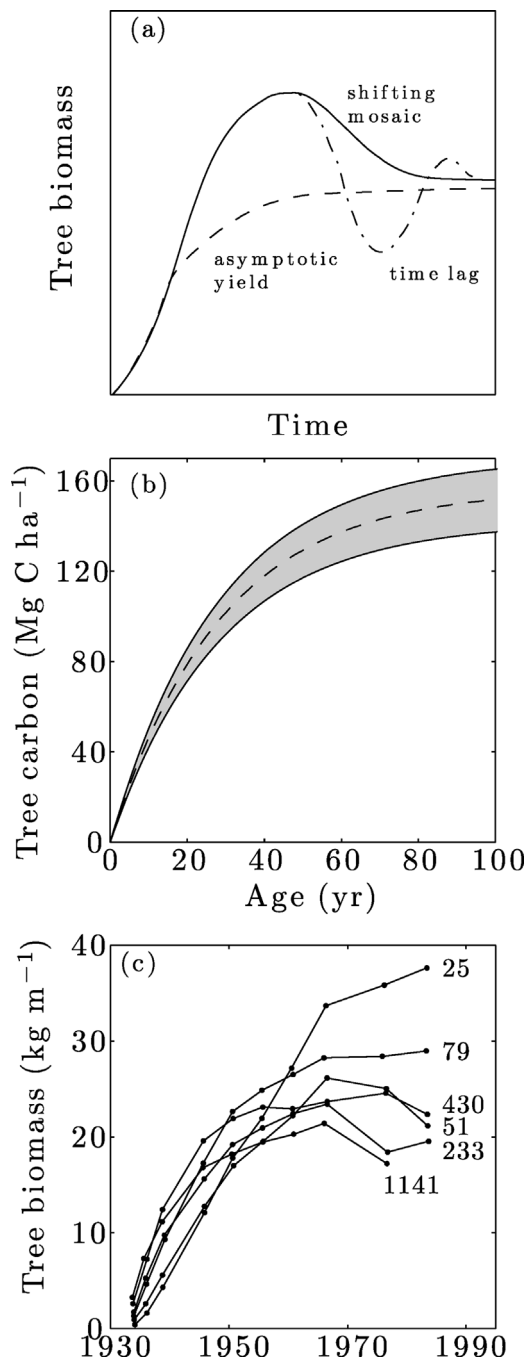


Fig. 1. Alternative perspectives on reforestation dynamics: (a) three hypothesized reforestation trajectories, including asymptotic yield, shifting mosaic, and time lag (redrawn from Peet, 1981); (b) monotonic, saturating reforestation trajectory fit to the USFS Forest Inventory and Analysis dataset for Slash Pine in the Southeast US (Williams et al., 2012); and (c) observed biomass change over 60 years at Duke Forest exhibiting both saturation and overshoot (redrawn from Peet and Christensen, 1987). In (c), the numbers correspond to initial planting density (stems per 0.1 acres).

2011; Mobley 2011), often termed “boom-and-bust cycles” in other complex systems (Brander and Taylor, 1998; Rodrigues et al., 2009).

Proposed mechanisms that underlie non-monotonic, boom-and-bust reforestation trajectories include temporal changes in age-structure and soil resource availability. The “shifting mosaic” hypothesis contends that planted even-aged stands grow to a peak biomass that is greater than that of the steady-state mixed-aged stand (Bormann and Likens, 1979; Peet and Christensen, 1987). The transition from peak even-aged biomass to the lower all-aged

steady state biomass occurs as age-related mortality in the original cohort is offset by heterogeneous gap recruitment and regeneration. Secondly, changes in soil nutrient availability over time (e.g., Richter et al., 2000) imply that the strength of nutrient limitation of productivity may also change with forest age (Peet 1981). In the Duke Forest, volume of 44-year old loblolly pine was strongly positively correlated with site index, determined by A horizon depth and B horizon plasticity (Peet 1981). Stands with high site index exhibited monotonic increases in tree volume, whereas stands with low site index exhibited a peak and subsequent losses of tree volume (Peet 1981).

The flow of carbon and nitrogen in ecosystems may capture how soil resource availability affects reforestation trajectories. Forest biogeochemical cycles are complex, multi-dimensional systems composed of abiotic-biotic interactions tightly coupled through the stoichiometric requirements of autotrophic and heterotrophic metabolism. In particular, the carbon-nitrogen ratio (C:N), an index of soil organic matter (SOM) quality, is a soil property that integrates the cycling of these essential elements between plants and soil (Manzoni et al., 2010). Plant-soil trajectories during reforestation arise from internal feedbacks regulated by SOM quality, which include plant nutrient uptake, canopy re-translocation, litterfall, mortality and other biomass turnover, and nitrogen mineralization through decomposition of plant residue and SOM. As in any system with a large number of interacting states, such feedback interactions between plants and soil may produce complex, non-monotonic dynamics, even in the absence of external oscillatory forcing or excitation (Murray, 2002; Bechhoefer, 2005) (e.g., disturbance or climate extremes). Indeed, consumer-resource oscillations have been noted in bacteria- or decomposer-substrate systems (Zelenev et al., 2000; Manzoni and Porporato, 2007; Raupach, 2007; Sanchez-Vila et al., 2013), but have not been extended to coupled plant-soil systems.

Models can be used to distill the complexities of reforestation mechanisms and outcomes (Neubert and Caswell, 1997; Baisden and Amundson, 2003; Wang et al., 2014). From a systems perspective, biomass overshoot and oscillations indicate an interaction exists between at least two ecosystem components. As noted above, either forest age structure or soil resource availability provides the additional degree of freedom that allows biomass to vary in a non-monotonic way. Therefore, at a minimum, a quantitative description of the three hypothesized reforestation trajectories depicted in Fig. 1 must couple the dynamics of tree biomass to forest age structure or a soil resource.

A logical starting point for a quantitative analysis of reforestation dynamics is an aggregated, stand-level forest model that does not explicitly represent age structure. While age-structured models are useful in many situations, they are represented as systems of coupled partial differential equations that are not easily analyzed (Friend et al., 1997; Moorcroft et al., 2001; Strigul et al., 2008). Stand-level models, on the other hand, can be represented as systems of ordinary differential equations (e.g., Parton et al., 1988; Thornton et al., 2002) with opportunity for detailed mathematical analysis. Stand-level models are commonly used in the study of harvest impacts on reforestation and some are known to produce non-monotonic reforestation trajectories (Neubert and Caswell, 1997; Baisden and Amundson, 2003; Wang et al., 2014), which is why they are selected for the starting point of the analysis. Finally, ecosystem processes aggregated at the population level, such as productivity, are related to age structure (van Straalen, 1985; Moorcroft et al., 2001), providing a link between the results of stand-level and age-structured models.

In this paper, models of coupled plant-soil carbon and nitrogen cycles are developed and used to identify mechanisms intrinsic to forest carbon-nitrogen cycles that may lead to alternative asymptotic, overshoot, and oscillation reforestation trajectories. In a case

study, the models are applied to the Calhoun Long-Term Soil-Ecosystem Experiment (LTSE) in South Carolina (now the Calhoun Critical Zone Observatory), where oscillations between tree and soil nitrogen pools were observed during reforestation of loblolly pine (*Pinus taeda* L.) from bare, abandoned cotton fields. At the Calhoun LTSE, tree and soil carbon and nitrogen pools were previously sampled multiple times over 50 years of reforestation, providing a unique dataset to explore mechanisms of non-monotonic reforestation dynamics following land use change. This synthesis of model and case study results provides a basis for generating insight and hypotheses designed to unfold the relative roles of internal, biogeochemical and external, disturbance drivers of biomass accumulation and loss during reforestation and succession.

2. Methods

A dynamical systems modeling approach (e.g., Strogatz, 1994; Murray, 2002) with two models of contrasting complexity is employed to evaluate the internal ecosystem drivers of reforestation dynamics. First, a simple two-pool model with linear, donor-controlled plant-soil nitrogen (N) flows is introduced. Although this model is oversimplified, it represents the minimum level of complexity (i.e., second order) needed to produce the hypothesized reforestation trajectories (Peet 1981) and permits an analytical solution that explicitly relates tree biomass dynamics to the model parameters and initial conditions. Second, a more complex model with five ecosystem carbon (C) and N pools is developed. This model incorporates the plant, SOM, and decomposer C:N and was found to represent the minimum level of complexity needed to reproduce the plant and soil C and N trajectories observed in the Calhoun LTSE case study.

2.1. Calhoun long-term soil-ecosystem experiment, South Carolina: pine reforestation following cotton field abandonment

The Southern Piedmont is an important agricultural region in North America with a history of intensive use and recovery (Richter et al., 2000). Prior to European settlement, the Southern Piedmont uplands were mixed deciduous forest, composed primarily of oak and hickory stands, and periodically burned by indigenous people. By the early 1800s, extensive tracts of this forest had been cut, burned, and converted to agriculture. Between 1800 and 1920, fields were managed for cotton, tobacco, and wheat production, with increased fertilizer use during the latter part of this time period. Soils were severely eroded and degraded under cultivation and, consequently, agriculture was abandoned throughout the early and mid-20th century. Widespread regrowth of pine and mixed pine-hardwood forest ensued and much of the area is now actively managed timberland.

Reforestation on abandoned agricultural fields at the Calhoun LTSE, in Sumter National Forest near Union, South Carolina, has been monitored over several decades and is used here as prototypical of such ecosystem dynamics (Richter et al., 1994, 1999, 2000; Mobley, 2011; Mobley et al., 2013, 2015). Mean annual precipitation is 1272 mm and mean annual temperature is 15.7 °C. The soils are classified as fine, kaolinitic, thermic oxaquic Kanhapludults of the Cataula series with gentle slopes (<3%). Abandoned fields were planted with loblolly pine in 1956 and 1957 and have not been fertilized, thinned, or burned since planting. Although some late successional hardwood species are found in the forest, a 2005 inventory established that the hardwood understory comprised less than 5% of aboveground biomass. Further details about the site and measurements can be found in the references noted above.

Previously collected data used in this paper include C and N in trees, coarse woody debris (CWD), soil O horizon, and mineral

soil horizons at four depths (0–7.5 cm, 7.5–15 cm, 15–35 cm, and 35–60 cm). For tree biomass C and N, data were collected in eight permanent 0.1 ha plots, with four plots planted at each of two tree spacings, 2.4 m and 3.0 m (Mobley, 2011). Tree biomass was measured in 1972, 1982, 1987, 1991, 1997, 2003, and 2007. Mineral soil was sampled on the same eight plots up to 60 cm depth in 1962, 1968, 1977, 1982, 1990, 1997, and 2005. CWD was sampled in 2007 on 12 plots and the temporal trajectory of CWD was constructed by combining estimates of CWD age and a linear decay model (Mobley et al., 2013). Lastly, the O horizon was sampled in 1956, 1992, 1997, and 2005 on the eight permanent plots (Mobley 2011; Mobley et al., 2015). For comparison to the model results, CWD, O horizon, and mineral soil were summed into total soil C and total soil N pools. Because separate pools were sampled in different years, data were interpolated linearly from the two nearest measurements to estimate values in missing years. Further, error estimates for total soil pools were based on mineral soil samples, which were most frequent over time and were found to contribute most of the variability in the total soil pool sums.

2.2. Reduced two-pool model

A reduced order two-pool model is developed as a minimalist description of plant N trajectories (henceforth referred to as the reduced model, illustrated in Fig. 2a). The reduced model includes the effects of both internal plant-soil interactions (i.e., uptake and litterfall) and external factors (i.e., aerial deposition and leaching) on transient reforestation dynamics.

The reduced model describes the dynamics of plant and total soil N, N_p and N_t (g N m^{-2}), with the two state equations,

$$\frac{dN_p}{dt} = UP - LF_N \quad (1a)$$

$$\frac{dN_t}{dt} = DEP + LF_N - UP - L_N \quad (1b)$$

where uptake ($UP = k_{up}N_t$), litterfall ($LF_N = m_N N_p$), and leaching ($L_N = k_s N_t$) are assumed to be linear, donor-controlled processes with rates k_{up} , m_N , and k_s (yr^{-1}), respectively. N input (DEP , $\text{g N m}^{-2} \text{ yr}^{-1}$) is assumed constant and may include inputs via aerial deposition and biological nitrogen fixation (Cleveland et al., 1999; Reed et al., 2011). While the assumption of linear, donor-controlled nutrient cycling processes neglects other environmental or biological controls on their rates (DeAngelis 1992; Agren and Bosatta, 1996; Baisden and Amundson, 2003), Eq. (1) is exponentially stable under physically realistic conditions and, as will be shown in the results, unequivocally links the modeled trajectories to model structure, parameters, and initial conditions.

Eq. (1) is solved analytically given initial conditions for N_p and N_t . For a transition from abandoned agricultural field to secondary forest, the system initially contains zero plant N (i.e., $N_p(0) = 0$) and a given mass of legacy soil N (i.e., $N_t(0)$). For these initial conditions,

$$N_p(t) = (\alpha - N_p^*) \exp(\lambda_1 t) - \alpha \exp(\lambda_2 t) + N_p^* \quad (2)$$

where $N_p^* = \frac{k_{up} DEP}{m_N k_s}$ is the reduced model steady state,

$$\lambda_{1,2} = -\frac{m_N + k_{up} + k_s}{2} \left[1 \mp \left(1 - \frac{2m_N k_s}{(m_N + k_{up} + k_s)^2} \right)^{1/2} \right] \quad (3)$$

are the system eigenvalues, and

$$\alpha = \frac{k_{up}}{\lambda_1 - \lambda_2} \left[N_t(0) + \frac{\lambda_1 DEP}{m_N k_s} \right] \quad (4)$$

accounts for the initial condition through $N_t(0)$ and external forcing through DEP . Here, $\lambda_1 - \lambda_2 \neq 0$.

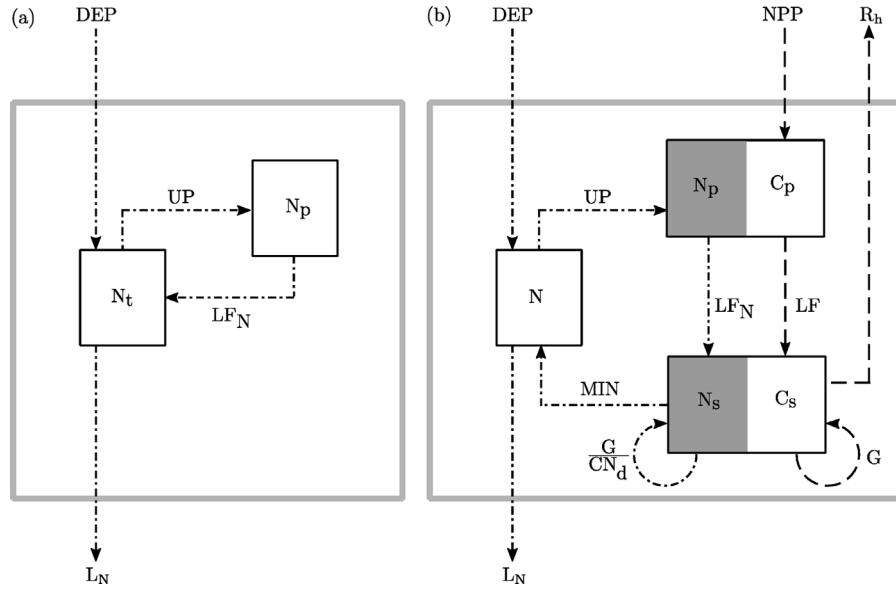


Fig. 2. Schematics for the (a) reduced and (b) extended models of ecosystem plant-soil carbon-nitrogen dynamics. The dashed lines represent carbon fluxes and the dot-dashed lines represent nitrogen fluxes. The model states are: C_p , plant carbon; N_p , plant nitrogen; C_s , soil organic matter carbon; N_s , soil organic matter nitrogen; and N , soil inorganic nitrogen. In the reduced model, N_s and N are combined into a total soil nitrogen pool, N_t . The model fluxes are: DEP , deposition; NPP , net primary productivity; R , decomposer respiration; LF_C , litterfall carbon flux; LF_N , litterfall nitrogen flux; MIN , mineralization; UP , plant uptake; G , decomposer growth (with C:N ratio CN_d); and L_N , inorganic nitrogen losses.

2.3. Extended five-pool ecosystem carbon-nitrogen model

To develop a more appropriate representation of the coupled plant-soil system that includes both carbon and nitrogen pools (e.g., Manzoni et al., 2007; Parolari and Porporato, 2016), a five-pool ecosystem C-N model is now proposed (henceforth referred to as the extended model, illustrated in Fig. 2b). The extended model consists of two C pools, plant (C_p) and SOM (C_s), and three N pools, plant (N_p), SOM (N_s), and inorganic (N). The extended model is described by a system of five coupled ordinary differential equations,

$$\frac{dC_p}{dt} = NPP - LF_C \quad (5a)$$

$$\frac{dN_p}{dt} = UP - LF_N \quad (5b)$$

$$\frac{dC_s}{dt} = LF_C - R \quad (5c)$$

$$\frac{dN_s}{dt} = LF_N - MIN \quad (5d)$$

$$\frac{dN}{dt} = DEP + MIN - UP - L_N \quad (5e)$$

where the fluxes not previously defined are: net primary productivity (NPP), litterfall C (LF_C), decomposer respiration (R), and N mineralization (MIN).

Similar to the reduced model, litterfall, uptake, and leaching are modeled as linear, donor-controlled processes. Because plant C and N are now modeled as two separate pools, LF_C is modeled separate from LF_N as

$$LF_C = m_C C_p, \quad (6)$$

where m_C is the plant C turnover rate. The relative values of m_C and m_N can be adjusted to represent faster turnover of high N leaves compared to low N stem and wood tissue.

In the plant carbon pool, NPP is modeled as a logistic growth function with the growth rate dependent on plant N given by

$$NPP = gN_p \left(1 - \frac{C_p}{K}\right) \quad (7)$$

where g is a density-independent, N-specific growth rate ($g C g N^{-1} yr^{-1}$) and K ($g C m^{-2}$) is the ecosystem carrying capacity, taken in terms of plant C (Agren and Bosatta, 1996). Eq. (7) captures the saturating recovery of forest NPP after disturbance (Amiro et al., 2000; Williams et al., 2012) and increased productivity with canopy N (Birk and Vitousek, 1986). Other representations of NPP can be accommodated.

SOM decomposition and N mineralization-immobilization are linked by the size and N requirements of the heterotrophic decomposer population (Manzoni and Porporato, 2007). In the extended model, decomposer biomass is not modeled explicitly but the N requirements of decomposition relative to the N availability in SOM substrate is accounted for as follows. Decomposer growth, G ($g C m^{-2} yr^{-1}$), and respiration, R ($g C m^{-2} yr^{-1}$), are assumed to be controlled by a decomposition rate, k_d (yr^{-1}), the SOM C pool size, and the dimensionless decomposer C use efficiency, e (Manzoni et al., 2010),

$$G = ek_d C_s \quad (8)$$

and

$$R = (1 - e)k_d C_s. \quad (9)$$

Decomposer respiration (Eq. (9)) represents a flux of C lost from the system to the atmosphere as CO_2 , whereas decomposer growth (Eq. (8)) is recycled within the SOM C pool (i.e., decomposer biomass is considered as part of the SOM C pool). Mineralization-immobilization, the net N flux between the SOM and the inorganic N pools, is assumed to be the difference between N released from SOM N during the decomposition process and the N demand for decomposer growth,

$$MIN = k_d N_s - \frac{ek_d C_s}{CN_d} \quad (10)$$

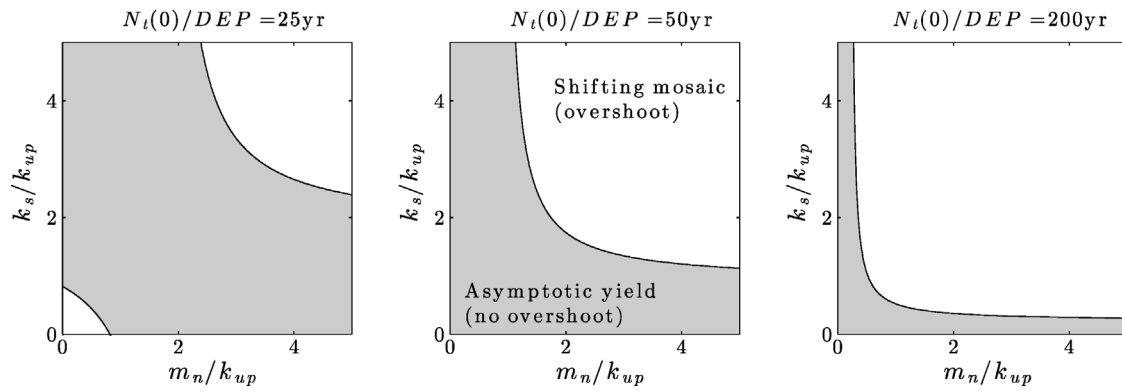


Fig. 3. Reforestation dynamics delineated in the reduced two-pool model parameter space. Using dimensional analysis, the two-pool model parameter space is defined by two dimensionless parameters: the ratio of the turnover and uptake rates (horizontal axis) and the ratio of the leaching and uptake rates (vertical axis). The white regions correspond to asymptotic reforestation trajectories with no peak and the gray regions correspond to overshooting reforestation trajectories with a peak in plant N. The panels from left to right correspond to increasing values of the soil N depletion time-scale imposed by the initial soil N (Eq. (14)) and $k_{up} = 0.02 \text{ yr}^{-1}$.

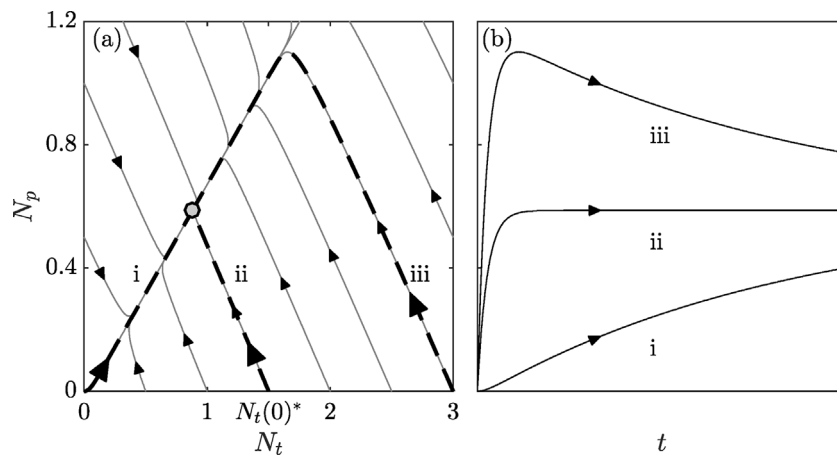


Fig. 4. Reduced model phase portrait (a) and time trajectories (b) demonstrating tree nitrogen overshoot. Panel (a) illustrates how both N_t (horizontal axis) and N_p (vertical axis) change over time. Each line in (a) corresponds to a model trajectory with different initial conditions and the gray circle marks the model steady state. The bold dashed lines in (a) correspond to different values of initial soil N: (i) zero; (ii) the critical value for tree N overshoot, $N_t(0)^*$ (Eq. (14)); and (iii) twice $N_t(0)^*$. The corresponding time trajectories of N_p are plotted in panel (b). Parameters are $k_{up} = 0.05 \text{ yr}^{-1}$, $k_s = 0.0067 \text{ yr}^{-1}$, $m_n = 0.075 \text{ yr}^{-1}$, and $DEP = 5.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The arrows indicate the direction of time.

where CN_d is the decomposer C:N ratio. Eq. (10) is a minimal description of soil N mineralization-immobilization processes, representing direct assimilation of organic N by decomposers (Manzoni and Porporato, 2007). This scheme prioritizes organic N retention in the SOM pool over release to the inorganic N pool, which reduces the amount of inorganic N available for plant uptake and leaching losses. When the SOM quality is sufficient to meet the decomposer demand (i.e., $eCN_s < CN_d$), net mineralization proceeds and $MIN > 0$. Alternatively, when decomposer N demand exceeds that available in the SOM pool (i.e., $eCN_s > CN_d$), decomposers supplement organic N with inorganic N, net immobilization proceeds, and $MIN < 0$.

To assess whether the extended model is adequate to investigate hypothesized mechanistic explanations for reforestation trajectories, extended model simulation results were compared to the Calhoun LTSE data. Extended model parameters were estimated from other published studies and from previous empirical studies at the Calhoun LTSE. Estimated parameters and sources are summarized in Table 1. Simulations are initialized in the year 1962, which is the earliest date with reliable estimates for all plant and soil pools. The total soil pools are compared, such that modeled C_s (or $N+N_s$) corresponds to the sum of measured O horizon, mineral horizon, and coarse woody debris C (or N). The code for both the

reduced and extended models is included in the supplementary material.

3. Results and discussion

The results and discussion are organized as follows. In Section 3.1, the reduced two-pool model analytical solutions and phase space are presented to demonstrate the roles of plant-soil feedbacks and initial conditions in reforestation trajectories. In Section 3.2, numerical solutions to the extended model are presented to expand the theoretical analysis to systems with plant-soil feedbacks dependent on both C and N fluxes. Then, in Section 3.3, the Calhoun LTSE observations are used as empirical support for the hypotheses generated by the model analyses. Finally, the internal C-N drivers of reforestation trajectories identified in the first three sections are discussed in comparison to other drivers of forest biomass loss, including age-related mortality and external disturbances such as ice/wind storms, drought, and pests.

3.1. Reduced two-pool model

In the context of regenerating forests, overshoot refers to a reforestation trajectory in which the tree biomass initially exceeds and then decreases to the stable, or steady state, biomass for the for-

Table 1
Extended model parameters.

Parameter		Units	Value	Source
Carrying capacity	K	Mg C ha ⁻¹	250	Estimated from model steady-state ^a
Growth rate	g	kg C kg N ⁻¹ yr ⁻¹	49	Mobley (2011)
Plant turnover	m _c	yr ⁻¹	0.066	White et al. (2000), Tatarinov and Cienciala (2006), Mobley (2011), Mobley et al. (2013)
N deposition	m _N	yr ⁻¹	0.14	Jorgensen et al. (1980), Richter et al. (2000)
N leakage coefficient	DEP	kg N ha ⁻¹ yr ⁻¹	5.9	Richter et al. (2000)
N uptake coefficient	k _s	yr ⁻¹	0.006	Richter et al. (2000)
Microbial C efficiency	k _{up}	yr ⁻¹	0.052	Jorgensen et al. (1980); Richter et al. (2000)
Microbe C:N	e	–	0.30	Sinsabaugh et al. (2013)
Decomposition rate	CN _d	kg C kg N ⁻¹	12.5	Manzoni et al. (2010)
	k _d	yr ⁻¹	0.15	Jorgensen et al. (1980), Gonzalez-Benecke et al. (2016)

^a The carrying capacity, K , was estimated from the steady-state solution for C_p , using the other estimated parameters and assuming $C_p^* = 120 \text{ Mg C ha}^{-1}$ (Williams et al., 2012).

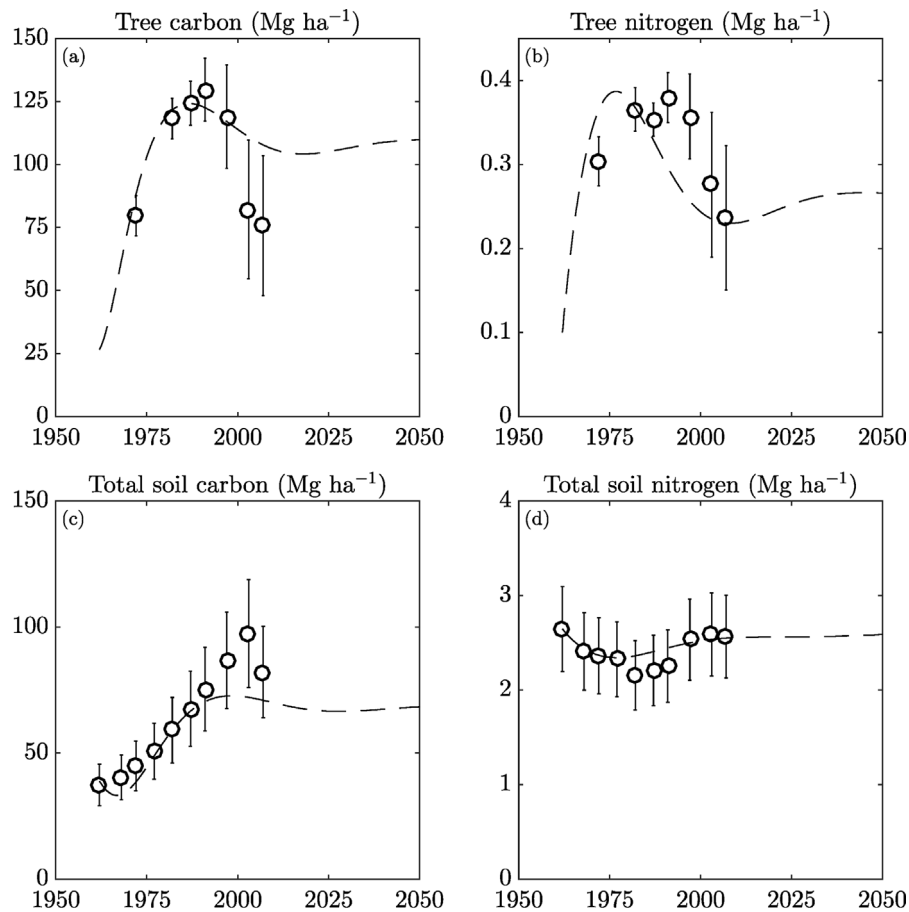


Fig. 5. Comparison of the extended model output (dashed lines) with observed plant and soil carbon and nitrogen pools (open circles): (a) tree carbon; (b) tree nitrogen; (c) total soil carbon; and (d) total soil nitrogen. Observed total soil carbon and nitrogen pools include O horizon, mineral horizons, and coarse woody debris. For the tree pools, error bars indicate the standard deviation estimated from 8 replicates. For the soil pools, error bars indicate a standard deviation estimated from the mineral soil samples only ($n=8$) (see text). Parameters are listed in Table 1. All oscillations in modeled variables are the outcome of endogenous boom-bust dynamics and exclude any time-dependent forcing or parameters.

est. The forest exhibits oscillations when multiple peaks occur as the forest approaches a stable state. Single overshoot and multiple oscillations correspond to the shifting mosaic and time lag regimes introduced by Peet (1981) (Fig. 1a), respectively. The reduced model provides a simple method to discriminate the conditions that lead to either reforestation regime.

Overshoot occurs in second-order systems under two conditions defined by the eigenvalues, $\lambda_{1,2}$ (Eq. (3)) (e.g., see Strogatz, 1994). When the eigenvalues are complex, the system is under-

damped and exhibits multiple oscillations characteristic of the long lag hypothesis (Fig. 1a). In critically- and over-damped systems with real eigenvalues, a single overshoot characteristic of the shifting mosaic hypothesis (Fig. 1a) may occur as an initial transient with a magnitude that depends on the initial conditions. For the reduced model, the eigenvalues are real for all positive parameter combinations, indicating multiple oscillations are not possible and overshoot occurs only as a single peak above the steady state.

Overshoot requires N_p to reach a maximum during the reforestation trajectory. The occurrence of a maximum N_p is evaluated by setting the time-derivative of Eq. (2) equal to 0 to obtain,

$$\frac{dN_p(t)}{dt} = \lambda_1 (\alpha - N_p^*) \exp(\lambda_1 t) - \lambda_2 \alpha \exp(\lambda_2 t) = 0. \quad (11)$$

Eq. (11) is satisfied at the steady state (i.e., for $t \rightarrow \infty$) and for a finite value of t given by,

$$t_p = (\lambda_2 - \lambda_1)^{-1} \ln \left[\frac{\lambda_1 (\alpha - N_p^*)}{\lambda_2 \alpha} \right]. \quad (12)$$

A maximum N_p occurs when $t_p > 0$, which for $\lambda_1 > \lambda_2$ occurs when,

$$\frac{\lambda_1 (\alpha - N_p^*)}{\lambda_2 \alpha} > 0. \quad (13)$$

Note that for asymptotically stable systems with $\lambda_1 < \lambda_2 < 0$, the left-hand side of Eq. (13) is strictly less than or equal to 1, such that $t_p \geq 0$. Therefore, N_p overshoots its steady-state when,

$$N_t(0) > -DEP \frac{\lambda_2}{\omega_n^2}. \quad (14)$$

where $\omega_n = \sqrt{m_N k_s}$ is the undamped natural frequency of the system. Eq. (14) states there is a critical initial soil N that increases the initial plant growth rate sufficiently for plant N to overshoot its steady state. This critical initial soil N is the product of the external system forcing (DEP) and a time-scale defined as the ratio of the faster (i.e., more negative) eigenvalue to the square of the undamped natural frequency ($-\lambda_2/\omega_n^2$). Similar to ω_n , recall from Eq. (3) that λ_2 is a combination of the N flow rate parameters for uptake, litterfall, and leaching; or the N flows controlled by internal N cycling processes.

The two reforestation trajectories possible in the reduced model, asymptotic yield or single overshoot, are delineated in the reduced model parameter space in Fig. 3. The reduced model parameter space can be delineated by two dimensionless parameters identified by dimensional analysis. These are the ratio of turnover to uptake rates, m_N/k_{up} , and the ratio of leaching to uptake rates, k_s/k_{up} . When the time-scale imposed by the initial condition (i.e., $N_t(0)/DEP$) is large, overshoot occurs for nearly all parameter combinations. For intermediate time-scales, systems with high plant turnover and leaching losses relative to uptake exhibit overshoot. However, as the time-scale decreases further, systems with high uptake relative to plant turnover and leaching losses also exhibit overshoot. This result demonstrates the complex dependence of reforestation response on plant-soil feedback and the soil nutrient status at the time of planting.

The magnitude of tree N overshoot above the model steady state increases with the initial soil N. That is, the more soil N at the time of planting, the more tree biomass N accumulation during the boom phase, and the more tree biomass N loss during the bust phase (Fig. 4). The reduced model has a single steady state, $N_p^* = \frac{k_{up} DEP}{m_N k_s}$ and $N_t^* = \frac{DEP}{k_s}$ that is independent of the initial condition and only depends on the system parameters. Therefore, the reduced model predicts that the plant-soil system will return to this steady state following any perturbation to either state variable.

3.2. Extended five-pool model

While the reduced model only considers plant and soil N pools, biogeochemical cycling in real forests is controlled by the relative availability of C and N to decomposers. By simulating interactions between plant and soil C and N pools, results from the extended model allow for exploration of a more detailed mechanistic link between reforestation trajectories and soil C-N conditions. The

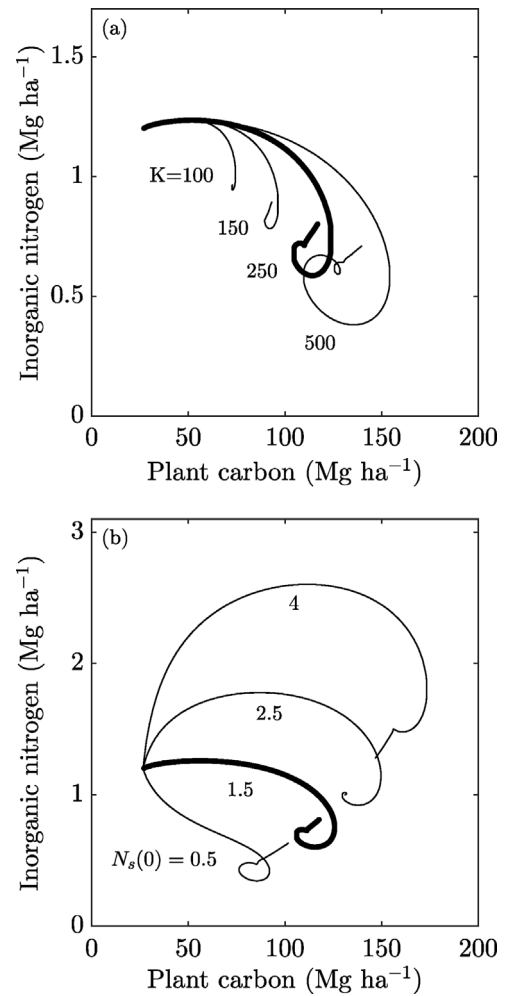


Fig. 6. Extended model plant carbon and soil inorganic nitrogen phase portrait for several values of (a) tree carrying capacity, K (Mg C ha^{-1}); and (b) initial SOM nitrogen pool, $N_s(0)$ (Mg N ha^{-1}). The bold lines correspond to the parameters in Table 1 and the thin lines correspond to a range of parameter values, as labeled.

extended model with the estimated parameters in Table 1 compares favorably with the reforestation dynamics observed at the Calhoun LTSE (Fig. 5). The modeled trajectory is an initial transient away from the system steady state that exhibits under-damped oscillations between tree and soil pools. That is, the eigenvalues are complex. Under-damped plant-soil dynamics are common in the extended model parameter space, discussed further below.

In the extended model, boom and bust reforestation dynamics are associated with feedback between plant biomass accumulation and SOM mineralization. Weak damping of the initial conditions and the appearance of plant-soil oscillations result from intense competition between trees and decomposers for soil inorganic N. From the plant perspective, this is associated with efficient N users (i.e., large g or K) that initially grow rapidly and return low quality litter to the SOM pool (Figs. 6a and 7a). At the same time, the initial SOM pool must be sufficiently low in N to stimulate low mineralization rates and possibly net N immobilization (Figs. 6b and 7b). Initially, the system simultaneously accumulates plant biomass and mineralizes SOM N. As SOM N is mineralized and replaced with low quality plant litter, mineralization decreases while plant biomass accumulation continues. Eventually, competition for soil inorganic N becomes so intense that plant biomass turnover exceeds NPP and trees enter the bust phase. Tree biomass loss subsequently reduces plant uptake, which increases soil N availability and allows miner-

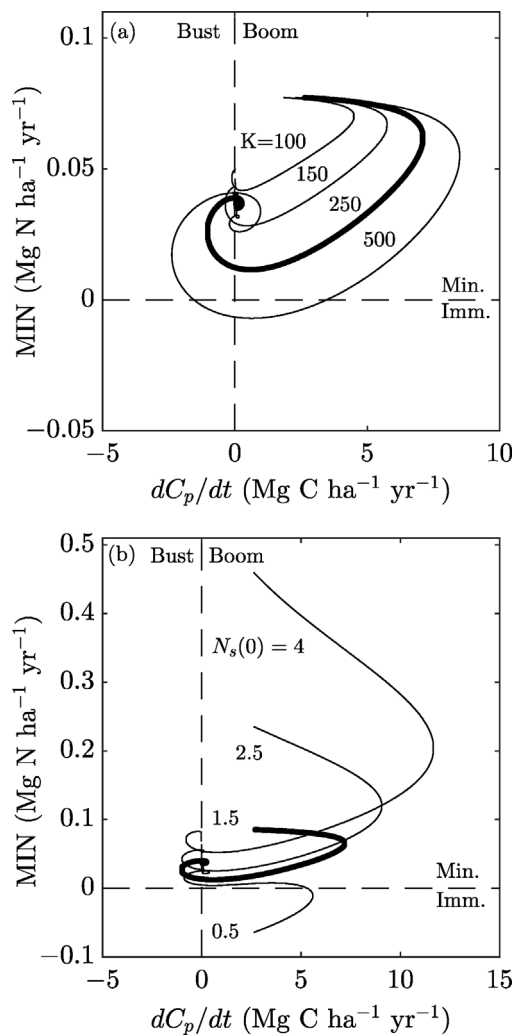


Fig. 7. Relation between the plant carbon accumulation rate and soil nitrogen mineralization rate in the extended model for several values of (a) tree carrying capacity, K (Mg C ha^{-1}); and (b) initial SOM nitrogen pool, $N_s(0)$ (Mg N ha^{-1}). The bold lines correspond to the parameters in Table 1 and the thin lines correspond to a range of parameter values, as labeled.

alization to increase. In weakly damped systems, trees may enter another boom phase as soil N availability rises again.

Elevated initial SOM N both strengthens damping (i.e., smooths oscillations) and increases the magnitude of tree biomass overshoot in the modeled trajectories (Fig. 6b). This results from the simultaneous effects of SOM N on mineralization and NPP. High initial N availability ensures continued net mineralization, which minimizes oscillations. On the other hand, it also increases initial NPP beyond that which can be sustained at steady state. Therefore, it is anticipated that plant-soil systems with high initial soil N availability (i.e., low soil C:N ratio) will exhibit the largest biomass loss after the peak, a model prediction that is tested with experimental data in Section 3.3 below. The extended model results are consistent with the reduced model and specifically illustrate the role of plant, soil, and decomposer C:N ratios in reforestation dynamics. Similar to the reduced model, the extended model has a single steady state (omitted for brevity) to which the perturbed system always returns. Hence, the extended system can be viewed as a generalization of the reduced system, which only considers N dynamics.

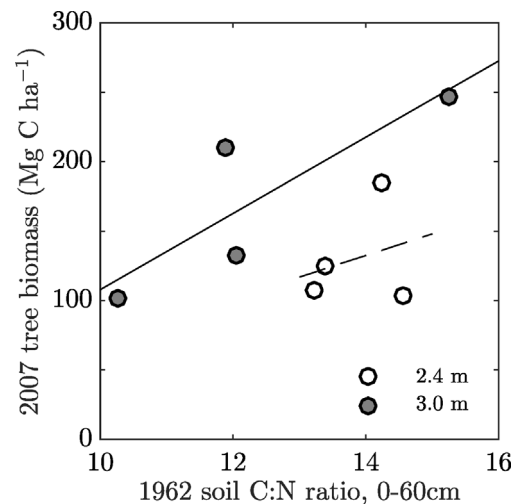


Fig. 8. Tree biomass at age 50 (2007) as a function of the legacy soil C:N ratio measured in 1962. Open circles correspond to 2.4 m tree spacing and closed circles to 3.0 m tree spacing. Regression results are $r^2 = 0.26$ and $p = 0.74$ for 2.4 m and $r^2 = 0.85$ and $p = 0.147$ for 3.0 m.

3.3. Confronting model results with empirical evidence

A remarkable feature of the observed Calhoun LTSE reforestation dynamics is the rapid growth to a peak tree C and N attained by 1991 (age 25) followed by a subsequent and rapid decline (Fig. 5; Table 2). The boom phase (1956–1991) is characterized by high accumulation rates of tree biomass, organic detritus, and mineralization and transfer of N from mineral-soil to biomass and detritus. At the end of the initial growth boom in 1991, peak average tree C was $130 \pm 4.4 \text{ Mg C ha}^{-1}$. Following the boom phase, tree biomass C decreased $54 \pm 8.7 \text{ Mg C ha}^{-1}$ between 1991 and 2007. During this bust phase, there was a substantial increase in tree mortality, resulting in the addition of $63 \pm 7.1 \text{ Mg C ha}^{-1}$ coarse woody debris to the forest floor (Mobley et al., 2013) at a rate over four times higher than mortality rates preceding 1991. The balance between observed mortality and tree C storage suggests reduced tree growth over time also contributed to the substantial tree C loss. Estimated as the sum of tree mortality rate (Mobley et al., 2013) and tree C accumulation rate (Mobley, 2011), the apparent tree growth rate decreased from an average $4.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ from age 0–26 to $0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ from age 35–51. Tree growth during the bust phase compensated for 15% of tree mortality. Therefore, the rapid decrease in live tree biomass during the bust phase resulted from a combination of both increased mortality and decreased growth.

The site history and data also support the model result that initial tree growth boom and subsequent N limitation can be amplified by initial soil conditions resulting from historical land use. Intensive land management during cotton production included N fertilization and tillage. Cultivation substantially altered soils, which were characterized by enriched soil N and an eroded surface organic soil horizon at the time of cotton field abandonment (i.e., reduced soil C:N ratio). The response of contemporary tree biomass (2007) to soil C:N just after the time of planting (1962) is shown in Fig. 8. For all plots, the contemporary 2007 tree C increases with the legacy 1962 soil C:N ratio, with more variation and a stronger dependence shown in the more densely planted plots. That is, plots with more initial soil N exhibited less contemporary tree biomass and, therefore, a larger “bust.” This observation is consistent with the reduced and extended model results for overdamped systems with a single overshoot, which are based on the assumed model structure and parameters. The Calhoun LTSE site history suggests initial soil conditions, resulting from prior agricultural practices, may have been

Table 2
Tree biomass overshoot observations for 2.4 m and 3.0 m tree spacings. The mean peak biomass and mean 2007 biomass are significantly different with $p = 0.00034$.

Spacing (m)	Plot No.	Peak year	Peak biomass (Mg ha ⁻¹)	2007 biomass (Mg ha ⁻¹)	Absolute change (Mg ha ⁻¹)	Relative change
2.4	I	1991	272.01	124.83	147.18	0.54
	II	1997	261.15	103.68	157.47	0.60
	III	1991	268.27	184.86	83.41	0.31
	IV	1991	286.58	107.59	178.99	0.62
3.0	I	1991	236.67	100.83	135.84	0.57
	II	1997	278.60	247.61	30.99	0.11
	III	1991	277.14	209.49	67.66	0.24
	IV	1991	252.74	133.09	119.65	0.47
		Average		266.6	151.5	115.2
	St. Dev.		16.1	55.5	50.3	0.19

a catalyst for boom and bust C-N reforestation dynamics in this ecosystem.

3.4. Other causes of tree biomass decline in secondary forests

Loss of standing live tree biomass is linked to a number of causes, including progressive N limitation, age-related mortality, and disturbance (Switzer and Nelson, 1972; Peet, 1981; Ryan et al., 1997; Luo et al., 2004; Johnson, 2006). Age-related biomass decline at the Calhoun LTSE was uniquely characterized by increased mortality (Mobley et al., 2013) and an 88% decrease in productivity over time that lead to over 40% decrease of C stored in live biomass between ages 35 and 51. In the most similar analog in the literature, Peet and Christensen (1987) previously identified a similar pattern of biomass decline in Loblolly Pine at Duke Forest, with biomass loss ranging from 0 to 20% across a gradient of increasing planting density (Fig. 1c) and site index. The authors hypothesized this negative biomass accumulation resulted from an imbalance between gap regeneration and canopy tree death. The present analysis of the Calhoun LTSE reforestation trajectory supplements this study by connecting biomass decline during reforestation to plant-soil C-N dynamics and the land use legacy using minimalist system models.

Loss of standing vegetation biomass over time was also related to slow changes in nutrient supply during soil development, a process designated 'retrogression' (Peltzer et al., 2010). The Calhoun LTSE reforestation dynamic is fundamentally different from ecosystem retrogression. While productivity and standing biomass at the Calhoun LTSE exhibited a decline with age, this decline was predicated by a large initial pool of labile N. Litter and soil C:N ratios were observed to increase over time (Richter et al., 2000; Mobley et al., 2013), an indication that trees actively redistributed soil N from a high bioavailability pool (i.e., fertilizer residues) to a low bioavailability pool (i.e., pine litter) (Richter et al., 2000). Indeed, loblolly pine is known for its low N requirements and low quality litter production (Aerts and Chapin, 2000). Therefore, Calhoun LTSE reforestation is characterized by a shift in resource, from agricultural legacy N to mineralized N from plant litter; whereas retrogression is characterized by a shift from N to phosphorus limitation throughout pedogenesis, as influenced by climate (Peltzer et al., 2010). Progressive resource limitation at the Calhoun LTSE was notably faster, on the order of decades, than the time-scale of ecosystem retrogression, observed on the order of 10^3 years.

A key question arising from the model-data analysis is whether internal plant-soil feedbacks or other candidate external disturbances are the dominant driver of observed plant turnover and the resulting plant-soil C-N trajectories. Reduced tree growth at Calhoun LTSE is clearly linked to decreased soil N availability, as the pine ecosystem exhibited acute N deficiency around the time of peak biomass, confirmed by observations of low foliar N% (Richter et al., 2000). In other ecosystems, it was suggested that such progressive N limitation might be punctuated by a decline in tree biomass (Switzer and Nelson, 1972; Christensen and Peet, 1984;

Ryan et al., 1997; Johnson, 2006). Increased mortality and biomass decline, on the other hand, likely results from external disturbances such as drought (Klos et al., 2009; Lowman and Barros, 2016), ice storms (McCarthy et al., 2006), and pest infestations (Kurz et al., 2008). Further, tree susceptibility to such disturbances is potentially mediated by internal ecosystem states or internally generated stresses, including age (Peet and Christensen, 1987), biomass (Ludwig et al., 1978), and resource availability (Hermes and Mattson, 1992). Uncertainty surrounding these interactions confounds the ability to discriminate between the roles of internal feedbacks and external disturbances on reforestation dynamics. However, some insights can be drawn from the model assumptions, now discussed.

3.5. Model assumptions and caveats

Models of forest plant-soil C-N cycles encompass a wide range of complexity, indicated by the number of state variables, non-linearity in flux parameterizations, and whether the system is forced by stochastic climate or disturbance (DeAngelis 1992; Agren and Bosatta, 1996; Porporato et al., 2003; Manzoni and Porporato, 2007; Strigul et al., 2008; Wang et al., 2014). Of several candidate models, the reduced model is the minimalist plant-soil N cycling model that produces overshoot behavior. The extended model is similarly presented as a minimalist model structure that couples the C and N cycles and reproduces observed fluctuations in ecosystem C and N pools at the Calhoun LTSE.

The reduced model assumes all outflows from the plant and soil N pools are linear, donor-controlled processes (i.e., turnover, uptake, and leaching). This assumption ignores potential non-linear dependences of the fluxes on the state variables (e.g., see DeAngelis 1992; Agren and Bosatta, 1996; Manzoni and Porporato, 2007); however, the model structure preserves pool connectivity and the directions of material flow in the ecosystem. The use of linear, donor-controlled fluxes limits the ability of the reduced model to make accurate predictions, but for such a simple model, this assumption does not substantially affect the qualitative behavior of model trajectories in the vicinity of the initial condition or steady state (e.g., Neubert and Caswell, 1997). The result that plant N overshoot depends on the relative values of the rate parameters and the initial soil N (Fig. 3) is robust to these model assumptions. Similar arguments can be made for the extended model structure (Figs. 6 and 7).

While both models assume a single linear and donor-controlled export from the mineral N pool only, other model parameterizations may more accurately represent N losses. Additional N losses are likely present, including leaching of dissolved organic N (Perakis and Hedin, 2002) or denitrification and volatilization (Cárdenas et al., 1993). Further, the processes driving N export have a non-linear dependence on environmental parameters and ecosystem state variables, such as soil moisture, temperature, and soil N availability (e.g., Cárdenas et al., 1993; Maggi et al., 2008). More complex

models are capable of a more realistic treatment of N export (Maggi et al., 2008); however, the dynamics of these models are much more difficult to interpret in terms of their structure and parameters.

In both the reduced and extended models, plant biomass overshoot is permitted because the dynamic equation for the plant N (or C) pool can be negative. That is, during “bust” phases, $\frac{dN_p}{dt} < 0$ and the production term is less than the turnover term. Alternating phases of positive (boom) and negative (bust) plant N accumulation are facilitated by a turnover (i.e., mortality) term that increases with the size of the plant biomass pool. While specific mortality factors, such as competition, age, or disturbance are not explicitly modeled by the linear, donor-controlled assumption, the functional form of this model is similar to others that simulate mortality as a sequence of random disturbances (Pacala et al., 1996; Moorcroft et al., 2001; Strigul et al., 2008). Further work is needed to study the impact of random external disturbances on reforestation dynamics (Liu et al., 2011) and is a logical topic for future work.

Finally, model parameters and external drivers are assumed constant here, whereas they may change over time. For example, the model does not consider variable decomposer N demand and decomposition rates (Manzoni et al., 2010), aerial N deposition (e.g., Templer et al., 2012), or climate and its impact on temperature, soil moisture, and productivity (e.g., Bernal et al., 2012; Lowman and Barros, 2016). As shown in equation (14) and Fig. 3, increases in external drivers tend to dampen the system and smooth dissipation of the initial conditions. Aerial deposition likely increased early in the experimental record (Templer et al., 2012) and then remained relatively constant from 1990 (NADP Site SC06, <http://nadp.sws.uiuc.edu/>) and, therefore, may have partially alleviated internally generated N stress. N input via biological N fixation may vary with productivity (Cleveland et al., 1999; Reed et al., 2011), which implies N input depends on the ecosystem state, whereas here it is assumed constant and independent of the ecosystem state. The assumption that fixation depends on productivity does not alter the structure of the models or the qualitative results presented here. Finally, with respect to climate, leaching is thought to be minimal in this ecosystem (Richter et al., 2000) and climatic conditions were not found to correspond directly with the boom and bust phases (data not shown).

4. Conclusion

Alternative reforestation trajectories in plant-soil systems were discussed in the context of the decades-long Calhoun LTSE, revealing possible conditions for boom and bust carbon-nitrogen dynamics. An analysis of soil N dynamics complemented by a minimal ecosystem C-N model supports the hypothesis that tree biomass loss during reforestation may result from plant-soil feedbacks set in motion by an agricultural legacy that elevated initial soil N availability. Both the extended and reduced models demonstrate tree biomass overshoot and its dependence on initial soil C and/or N conditions initial transient phases. The extended and reduced models exemplify cases of non-linear under-damped and linear over-damped dynamics (e.g., see Strogatz, 1994), respectively. While the reduced model was unable to reproduce the full dynamics of the observed system, it describes the overshoot phenomenon with a minimalist analytical link between external forcing, internal dynamics, and initial conditions.

The results discussed here offer one mechanistic explanation for previously hypothesized reforestation trajectories (Peet 1981) in terms of ecosystem C-N cycles. Evidence from models and a case study indicate an important role of biogeochemical cycles in determining successional dynamics. The reforestation trajectories studied here were modeled as initial transients with behavior that contrasts model dynamics near the steady state, emphasizing

the importance of analyzing the appropriate dynamical regime when interpreting ecological data with models (Hastings, 2004). In addition, both empirical and theoretical evidence link tree-soil oscillations in their trajectory to initial conditions that may be externally imposed, demonstrating the interplay between external and internal factors during reforestation. Recognition of such endogenous and self-generated complex dynamics in other ecosystems may improve understanding of successional dynamics and forecasts of ecosystem behavior under global change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.06.023>.

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