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Resilience: nitrogen limitation, mycorrhiza and long-term palaeoecological plant–nutrient dynamics

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Ecosystem dynamics are driven by both biotic and abiotic processes, and perturbations can push ecosystems into novel dynamical regimes. Plant–plant, plant–soil and mycorrhizal associations all affect plant ecosystem dynamics; however, the direction and magnitude of these effects vary by context and their contribution to ecosystem resilience over long time periods remains unknown. Here, using a mathematical framework, we investigate the effects of plant feedbacks and mycorrhiza on plant–nutrient interactions. We show evidence for strong nutrient controlled feedbacks, moderation by mycorrhiza and influence on ecological resilience. We use this model to investigate the resilience of a longitudinal palaeoecological birch–δ^{15}N interaction to plant–soil feedbacks and mycorrhizal associations. The birch–δ^{15}N system demonstrated high levels of resilience. Mycorrhiza were predicted to increase resilience by supporting plant–nitrogen uptake and immobilizing excess nitrogen; in contrast, long-term enrichment in available nitrogen by plant–soil feedbacks is expected to decrease ecological resilience.

1. Introduction

Plants require soil nutrients for growth and actively influence nutrient cycles such as nitrogen. Such plant–soil feedbacks include the uptake and retention of nitrogen in plant tissues, release of nitrogen into leaf litter and woody debris, and support of ectomycorrhizal fungi (ECMs) that can influence plant access to multiple soil resources to support further plant growth. These plant–fungi associations have been shown to provide up to 80% of a plant's nitrogen requirements [1] and thus play a fundamental role in promoting resilience of populations and ecosystem functioning; however, in some cases, ECMs compete with plants for resources by immobilizing nitrogen in mycelia [2] and/or inhibiting plant access to nitrogen [3], thus modulating the availability and mineralization of nitrogen [4] to support plant growth and potentially destabilizing plant–nitrogen interactions. Whether ECMs support or suppress plant growth depends on the abundance of host plant species, type of microbial associations, life cycle stage of the plant, nitrogen availability in the ecosystem and other environmental conditions [2,5]. Furthermore, the relative importance of plant–plant interactions and plant–soil feedbacks in determining plant dynamics [6] and the potential mitigating effect of mycorrhiza [7] remains a contemporary research topic (e.g. [5]). Such complexity challenges efforts to predict the stability and resilience of plant–nitrogen interactions over periods of environmental change. Palaeoecological proxy data on plant biomass and terrestrial nitrogen availability provide unique and valuable long-term observations required to assess the resilience of ecological interactions subject to environmental perturbations operating over centuries and/or millennia [8].

Here, we hypothesize that mycorrhizal associations contribute to ecosystem resilience by modifying interactions between plants and available nutrients. We use a mathematical framework, built upon previous work [9–12], to investigate the contribution of mycorrhiza to plant–nitrogen dynamics and ultimately ecological resilience. We then fit this model to a palaeoecological birch–nitrogen time series to assess the resilience of a natural system to alterations in plant–nutrient abundances and interactions with mycorrhiza.

2. Material and methods

2.1. Mathematical model

To investigate how the presence of mycorrhiza affect plant (P)–nitrogen (N) dynamics, and more broadly ecological resilience, we construct a mathematical model of plant and nitrogen dynamics. The model builds on those used to interrogate plant–nitrogen interactions from palaeoecological data [8–11]. Population growth is dependent on available nitrogen and plants influence ecosystem-scale nitrogen availability through the release of decaying tissues. ECMs can affect plant growth by moderating nitrogen uptake and/or competing for nitrogen [5] immobilizing plant-available nitrogen [13]. Mycorrhiza affect nitrogen loss rates from the system and/or help recycle organic forms of nitrogen that can be used by plants [4]. Given this, we focus on the effects of ECMs on plant nitrogen uptake and immobilization. Our model framework is of the form:

$$\frac{dN}{dt} = \lambda - f(N, P) - j(N, M) - \mu_n N + g(P) \qquad (2.1)$$

and

$$\frac{dP}{dt} = rf(N, P) - h(P)P - \mu_p P, \qquad (2.2)$$

where, in equation (2.1) describing the nutrient (N) dynamics, λ is the allochthonous input rate of nitrogen into the system, $f(N, P)$ is a function describing nitrogen uptake by plants (see below). $j(N, M)$ is the immobilization of nitrogen by mycorrhiza (M). This is not independent of other factors (such as carbon–nitrogen feedbacks or competition between mycorrhiza and other microbes) and to capture this breadth of outcomes we define $j(N, M) = \pm \gamma N M$, (where γ is the rate of immobilization). μ_n is the loss of nitrogen from the system through volatilization, dentrification or leaching, and $g(P)$ is a function describing the recycling of nitrogen from decaying plant biomass (see below).

In equation (2.2) describing the plant dynamics, r is the plant population growth rate, as noted above $f(N, P)$ is the uptake of nitrogen by the population for plant growth, $h(P)$ is a density-dependent plant feedback term ($h(P) = \nu P^\beta$) and μ_p is the (instantaneous) plant death rate.

Uptake rate. The uptake rate of nitrogen by plants is described by:

$$f(N, P) = (\alpha' NP), \qquad (2.3)$$

where α' is the uptake coefficient describing the use of available nitrogen to support plant population growth. Nitrogen uptake is modulated by mycorrhiza according to $\alpha' = \alpha(1 + bM)$, where $b \in [-1, 1]$, such that mycorrhiza can behave mutualistically and increase (+) or parasitically and inhibit (−) plant access to sources of available nitrogen.

Nitrogen release rate. Nitrogen can be released back into the system as a function of plant biomass losses. We describe this process as a delayed response to plant biomass with:

$$g(P) = \mu_p \eta P(t - \tau), \qquad (2.4)$$

where μ_p is the instantaneous death rate of the population, η is the proportion of plant biomass returned as available nitrogen and τ is

the time lag between the release of plant biomass and transformation into available nitrogen. Given that nitrogen availability is structured through the soil profile (e.g. [5]), this time delay captures the release of nitrogen from decaying plant biomass before it can be used by the plant or modulated by the mycorrhiza.

2.2. Analysis

The model analysis proceeds by addressing three questions (i) how does nitrogen uptake affect plant population growth, (ii) how do mycorrhiza moderate plant nitrogen uptake and ecosystem-scale nitrogen availability and (iii) how is resilience of plant–nitrogen dynamics affected by plant–soil feedbacks, density-dependent population growth and modulation of soil resources by mycorrhiza. We use analytical (e.g. local stability analysis) and numerical (e.g. numerical integration) methods for model analysis (see electronic supplementary material for fuller details). We then fit models to a long-term palaeoecological birch–δ^{15}N dataset and assess ecological resilience.

3. Results

3.1. Nutrient effects on plant dynamics

The effect of nitrogen uptake on plant population growth $((1/P)(dP)/(dt))$ is estimated by:

$$\frac{1}{P}\frac{dP}{dt} = r[\alpha' N] - \nu P^\beta - \mu_p. \qquad (3.1)$$

From this, positive plant population growth (fitness) occurs when $r[\alpha' N] > (\nu P^\beta + \mu_p)$. This inequality can be investigated further when plant populations are at equilibrial levels. This is $P^* = [(r\alpha' N - \mu_p)/\nu]^{(1/\beta)}$. At equilibrium, a baseline amount of nitrogen is required for positive plant population growth to occur (i.e. plant birth rate exceeds plant death rate). As mycorrhiza can act mutualistically (increase) or parasitically (inhibit) to affect plant nitrogen uptake ($\alpha' = \alpha(1 \pm M)$), this influences plant population growth.

3.1.1. Dynamics

To explore the specific mechanisms by which nitrogen availability affects plant dynamics, a limiting case of the full model can be derived.

If in the absence of plant density dependence, the nitrogen uptake rate exceeds background losses (e.g. by denitrification) and/or immobilization of nitrogen by mycorrhiza ($\alpha P \gg (\mu_n + \gamma M)$), then the nitrogen–plant dynamics can be represented by:

$$\frac{dN}{dt} = \lambda - \alpha' NP + \mu_p \eta P(t - \tau) \qquad (3.2)$$

and

$$\frac{dP}{dt} = r\alpha' NP - \mu_p P. \qquad (3.3)$$

If these nutrient dynamics act on a faster timescale than the plant dynamics then the steady state nutrient dynamics ($\overline{N}$) are:

$$\overline{N} = \frac{\lambda + \mu_p \eta P(t - \tau)}{\alpha' P}. \qquad (3.4)$$

So the plant dynamics can then be approximated by:

$$\frac{dP}{dt} = r(\lambda + \mu_p \eta P(t - \tau)) - \mu_p P. \qquad (3.5)$$

For small time delays $\tau \to 0$ then the solution to this expression for the plant dynamics at time T is:

$$P(T) = \frac{r\lambda}{\mu_p(r\eta - 1)}(\exp(t\mu_p(r\eta - 1)) - 1). \quad (3.6)$$

Provided $\eta < 1$ then the plant dynamics will asymptote and equilibrate at $(r\lambda)/(\mu_p(r\eta - 1))$. This equation shows that with greater allochthonous inputs of nitrogen (λ) or slower releases of nitrogen from decaying plant matter ($\mu_p(r\eta - 1)$), there will be a higher equilibrium plant population level ($P(T)$). This introduces nutrient-driven (*donor-controlled*) feedback mechanisms that can stabilize the plant dynamics.

For a given rate of external inputs of nitrogen (λ), the rate at which nitrogen is recycled from decaying plant biomass (η) has a strong effect on plant population dynamics (electronic supplementary material, figure S1). High rates of release of plant-derived nitrogen destabilize the dynamics (leading to exponential plant population increases); increasing the background availability of nitrogen (λ) exacerbates the rate of this exponential increase (electronic supplementary material, figure S1a). Lower rates of nitrogen release from decaying biomass stabilize plant population dynamics while increases in background supplies of nitrogen raise the realized equilibrium population level (electronic supplementary material, figure S1b).

3.2. Mycorrhiza influence nutrient–plant dynamics

Given the plant–nutrient dynamics (equations (2.1)–(2.2)), the steady-state level of available nitrogen (N^*) is given:

$$N^* = \frac{\lambda + \mu_p \eta P^*}{\alpha' P^* + \gamma M + \mu_n}. \quad (3.7)$$

As might be expected, increases in uptake by plants ($\alpha' P^*$), immobilization by mycorrhiza (γM) or loss of nitrogen (μ_n) will all lead to lower steady-state levels of nitrogen. In contrast, increases in the allochthonous inputs of nitrogen (λ) and/or releases of nitrogen from decaying plant matter ($\mu_p \eta P^*$) will lead to higher steady-state levels of nitrogen.

Mutualistic mycorrhiza or parasitic mycorrhiza interact with plant–nutrient dynamics to affect levels of available nitrogen and nitrogen limitation of plant population growth (electronic supplementary material, figure S2). In general, mutualistic mycorrhiza (when $\alpha' = \alpha(1 + M)$) favour stable plant–nutrient interactions (electronic supplementary material, figure S2a). When mycorrhizae behave mutualistically, rising plant biomass and low levels of mycorrhizal biomass lead to asymptotic increases in available nitrogen. In contrast, parasitic mycorrhiza (when $\alpha' = \alpha(1 - M)$, reducing plant nitrogen uptake) can destabilize plant–nutrient dynamics (electronic supplementary material, figure S2b). In this situation, increasing mycorrhizal biomass results in unregulated increases in available nitrogen (electronic supplementary material, figure S2b) and destabilizes the dynamics (electronic supplementary material, figure S3).

3.3. Effect of biotic feedbacks on resilience of plant–nitrogen interactions

To determine the resilience of the plant–nitrogen system we use local stability analysis. We define resilience as the decay rate of perturbations back to the steady states and this rate is determined from the real part of the dominant eigenvalue associated with the local stability matrix (see electronic supplementary material). We use this approach to determine how resilience is affected by biotic feedbacks from plants and mycorrhiza.

The resilience of plant–nutrient dynamics is dependent on interactions with mutualistic mycorrhiza (when $\alpha' = \alpha(1 + M)$) (figure 1). Increases in the proportion of plant biomass recycled as available nitrogen (η) decreases the resilience of the system (figure 1), such that any perturbation will grow over time, moving the system away from its current state. However this plant–soil feedback can be moderated by other biotic factors such as the rate of immobilization (γ). At low levels of plant–nitrogen recycling, higher rates of immobilization by mutualistic mycorrhiza leads to greater system resilience (figure 1a,c); however, there is a threshold point in the amount of plant-derived nitrogen beyond which increases in mycorrhizal immobilization results in lower resilience.

Incorporating plant density-dependent plant dynamics ($h(P) = \nu P^\beta$) alters the shape of the resilience curve and the relative effect of immobilization at low levels of plant-derived nitrogen feedback (η) (figure 1c). Yet, the threshold point at which plant release rates lead to low resilience is the same for both the density-dependent and density-independent models (figure 1c).

When mycorrhiza behave parasitically (when $\alpha' = \alpha(1 - M)$), the plant–nitrogen system is never resilient (i.e. resilience <0) (figure 1b,d). In this situation, higher rates of mycorrhizal immobilization lead to lower system resilience in all circumstances.

3.4. Model–data comparison

To investigate the role of mycorrhiza on the resilience of plant–nutrient systems, we fit the model (equations (2.1)–(2.2)) to a 5000 year palaeoecological proxy time series of plant biomass (based on pollen accumulation rates) and nitrogen availability from Dubh-Lochan (Great Glen, Scotland) [11,14] using a Bayesian state space approach (see electronic supplementary material). The series spans the early to mid-Holocene period (10 700 to 5200 cal. yrs BP) and shows long-term declines in both birch and nitrogen availability after the first 2000 years (see electronic supplementary material).

Comparing stochastic plant density-independent and density-dependent dynamic models to the data suggests that a plant density-independent model together with mutualistic mycorrhizal effects provides the most parsimonious description of the birch–nitrogen dynamics at Dubh-Lochan (electronic supplementary material, figure S4; $\chi^2_{\text{diff}} = 0.159$ on 2 d.f., $p = 0.924$).

Using the parametrized density-independent plant–nutrient model (and observed relative abundances of birch and nitrogen), changes in predicted resilience of the plant–nutrient interaction at Dubh-Lochan can be determined from the local stability matrix (used for the model analysis—see electronic supplementary material). Figure 2 shows predicted resilience for the long-term birch–nitrogen system for four key parameters: rate of resource uptake (α), estimated mycorrhizal biomass (M), biomass release rate (η) and mycorrhizal immobilization rate (γ). Credible intervals from key posterior parameter distributions at each time
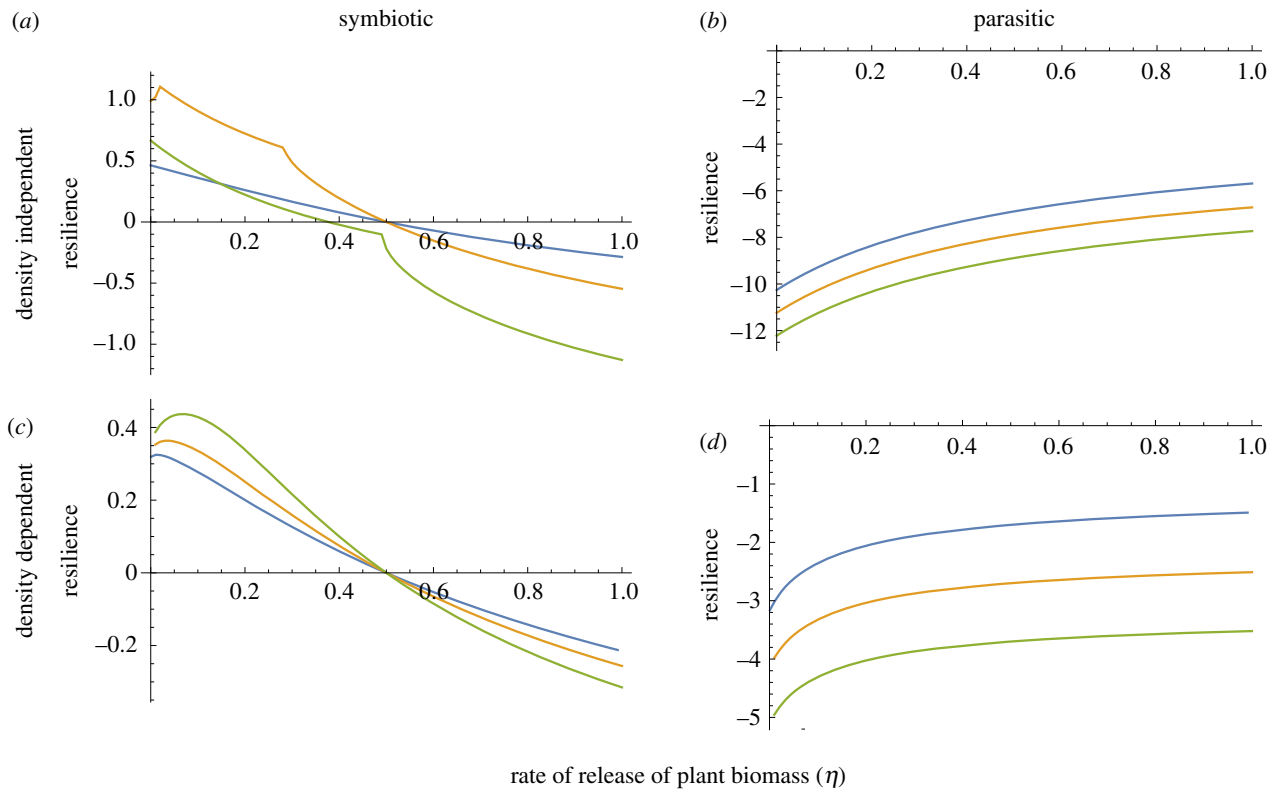
Figure 1. Resilience (decay rate of perturbations, see electronic supplementary material) of the plant–nutrient system to interactions with mycorrhiza under (*a,b*) density-independent or (*c,d*) density-dependent plant dynamics. With mutualistic mycorrhiza (*a,c*) increases in the rate at which plant biomass releases nitrogen can destablize the system and decreases resilience. Changes in the rate of immobilization (blue line to orange line to green line) on resilience depends on the plant population dynamics and biotic interactions. Parasitic mycorrhiza (*b,d*) always destabilize and make plant–nutrient systems less resilient.
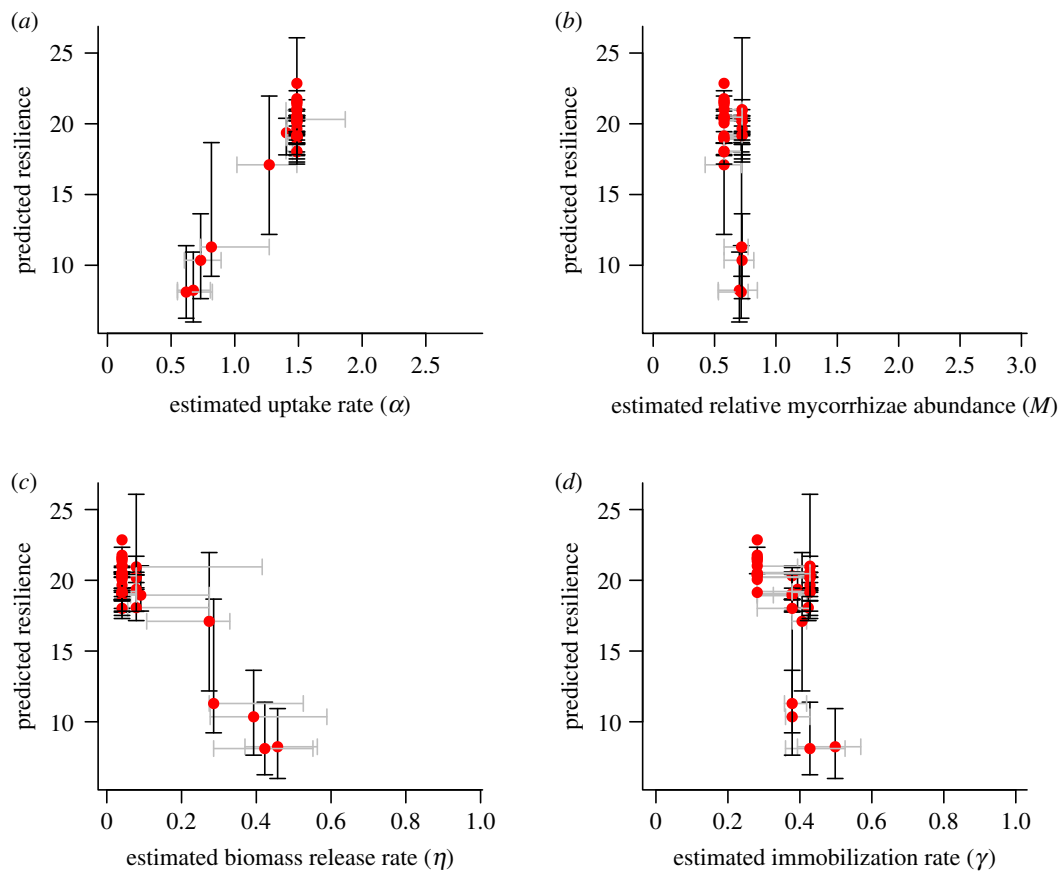

Figure 2. Predicted resilience of the birch–nitrogen system at Dubh-Lochan for a range of model parameter values: (*a*) the predicted plant nutrient uptake rate (α), (*b*) the predicted mycorrhizal biomass (*M*), (*c*) the plant biomass release rate (η) and (*d*) the mycorrhizal nutrient immobilization rate (γ). Parameter estimates are updated through time using a sequential Monte Carlo approach. Grey bars represent parameter credible intervals (estimated from the Bayesian state space) at a particular time point. Black bars are the range of predicted resilience levels (for a parameter at a particular time point).

point reveal how variation in parameters influences predicted resilience of the overall system. Increases in nutrient uptake rate (α) increase system resilience (i.e. small perturbations will decay away, figure 2a); however, increasing plant-derived available nitrogen (η) reduced resilience (i.e. any perturbation will grow over time, figure 2c). In general, greater biomass of mycorrhiza (M) further increases resilience (figure 2b). The predicted immobilization rate (γ) varied over a narrow range of parameter values and the system remained resilient across all of them (figure 2d).

4. Discussion

Here, we have investigated the role of biotic interactions on the dynamics and resilience of plant–nutrient interactions. We show that nutrient-controlled (*donor-controlled*) feedbacks can determine plant population dynamics and equilibrium states (equations (3.5) and (3.6)). How nutrients flow through the system, their availability and their immobilization determine plant population levels (electronic supplementary material, figure S1a,b). Our model predictions show that high levels of plant-derived nitrogen enrichment can destabilize coupled plant–nitrogen dynamics. Immobilization of nitrogen by mycorrhizal associations can offset this effect (i.e. via the microbial bottleneck, *sensu* [15]) and improve resilience, but only at low levels of plant-derived nitrogen inputs. When nutrients increase beyond a threshold point, immobilization of nitrogen by mycorrhiza was predicted to reduced resilience. Similarly, direct interference in plant nitrogen uptake by mycorrhiza (i.e. parasitism) led to reduced resilience in all circumstances. Thus biotic interactions can strongly influence nutrient cycling [16] and plant performance [6] by dampening or exacerbating feedback effects.

How important are these processes in real ecosystems? Our model–data comparison with palaeoecological birch–δ^{15}N data showed evidence for donor-controlled plant–nitrogen dynamics and mutualistic interactions with mycorrhizal fungi. Increasing plant nitrogen uptake had a positive effect on system resilience (figure 2a). Mycorrhiza were also associated with greater resilience (figure 2b), likely by promoting and regulating access to alternative available nitrogen sources (e.g. [17]). Our results conform with observations from modern ecosystems that although mycorrhizae have the potential to behave parasitically, mutualistic behaviour is more likely [18], especially in nitrogen poor environments [19].

Predicted immobilization rates, like mycorrhizal biomass, varied over a narrow range of values and—contrary to our model results—always led to greater system resilience (figure 2d). ECMs can immobilize nitrogen in relatively recalcitrant hyphae, which become part of the soil organic matter after they die, thus promoting nitrogen retention and regulating the rate of recycling of organic nitrogen [19]. This mechanism is predicted to improve resilience of birch–nitrogen interactions, likely by offsetting the negative effects of plant-driven feedbacks (figure 2c). That nitrogen immobilization has a prevalent role in birch–ECM dominated forests and plant dynamics are heavily influenced by nitrogen–carbon–microbe interactions [5] highlights that alternative sources of (organic) nitrogen (e.g. amino acids—[17]) may be highly influential in these ecosystem dynamics [4]. Together with long palaeo ecological records, the dynamics of ECMs and the sources of nitrogen availability in forest ecosystem resilience warrants much more in-depth scrutiny.

This is—to our knowledge—the first attempt to incorporate the role of mycorrhizal association into a plant–nitrogen dynamic model fitted to long-term palaeoecological data and used to assess ecosystem resilience. The results support the important role of biotic controls in nutrient cycling (e.g. [4,9]) and driving ecosystem resilience. A key limitation however is the current lack of continuous palaeoecological records of mycorrhizal biomass concurrent with other proxies [20]. Future work should focus on linking carbon–nitrogen–microbe dynamics to plant–nutrient interactions, dynamics and resilience. These caveats notwithstanding we show that knowledge of the type, direction and magnitude of biotic interactions is critically important in determining the dynamics, stability and resilience of these ecological systems.

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6

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