Long–term consequences of plant–soil feedback in fire-maintained grasslands and savannas

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Abstract

Woody encroachment into grasslands and savannas is widespread and has wide-ranging consequences. Past work suggests that positive feedbacks are a common feature of woody encroachment, and emerging evidence points to the importance of soil microbes in this process. For example, many encroaching plants associate with N-fixing bacteria or ectomycorrhizal fungi, while herbaceous plants often accumulate self-limiting microbes. However, projecting the long-term consequences of plant-soil feedbacks in natural systems that are simultaneously shaped by disturbances like fire remains a challenge. We developed a mathematical framework for predicting microbial impacts on vegetation dynamics in fire-maintained grasslands and parameterized this model with data from a meta-analysis. We find that plant-soil feedbacks necessitate especially frequent fire to maintain grassy communities and restrict the recovery of grass after woody encroachment. In all, our model points to the importance of belowground processes in driving woody encroachment and the urgent need for empirical data testing this process.

1. Introduction

Expansion of woody vegetation into grasslands and savannas has been widespread and consistent over the last several decades and now affects an estimated 500 million hectares globally (Archer *et al.* 2017; Deng *et al.* 2021; Ding & Eldridge 2024; Sala & Maestre 2014; Venter *et al.* 2018). Woody plant encroachment has been documented in grassy biomes on every continent besides Antarctica, including desert grasslands, semiarid and mesic savannas, and alpine and Arctic tundra (Aguirre *et al.* 2021; Van Auken 2000; Bond & Midgley 2012; Britz & Ward 2007; Peng *et al.* 2013; Robinson *et al.* 2008; Romero Ovalle *et al.* 2021; Silapaswan *et al.* 2001; Tormo *et al.* 2020), and it has far-reaching consequences. Increases in woody plant abundance are not only associated with reduced herbaceous plant diversity (Ratajczak *et al.* 2012; Wieczorkowski & Lehmann 2022), but can also restructure mammalian and herpetofaunal diversity, especially in less productive ecosystems (Stanton *et al.* 2017). Woody encroachment also impacts ecosystem function (Eldridge *et al.* 2011; Sala & Maestre 2014). In Patagonian rangelands, for example, vegetation structure (e.g., grass vs. shrub cover) has as strong of an impact as climatic drivers on variation in ecosystem functions like net primary productivity and precipitation-use efficiency (Gaitán *et al.* 2014). Finally, woody plant encroachment can impact human wellbeing, particularly among pastoralist communities who rely on rangelands for subsistence and income (Ding & Eldridge 2024; Skhosana *et al.* 2025). In all, understanding and managing woody plant encroachment represents a central challenge for 21st century ecologists.

Despite considerable interest in understanding the processes giving rise to woody plant encroachment, its global extent has precluded the development of a comprehensive framework of its drivers (Archer *et al.* 2017; Deng *et al.* 2021). Part of the challenge is that both global and local processes – including increased atmospheric CO_2, altered precipitation regimes, and changing land use patterns – likely contribute to this phenomenon (Archer *et al.* 2017; Van Auken 2009; Sankaran *et al.* 2005; Staver & Bond 2014; Wang *et al.* 2011). Although multiple processes likely play a role in woody plant encroachment, one commonality across systems is that transitions from herbaceous to woody vegetation tend to be spatially and temporally abrupt (D'Odorico *et al.* 2011), and often, encroachment is not reversible by woody plant removal (Ding & Eldridge 2022). These features suggest that positive feedbacks likely contribute to the development and persistence of woody plant encroachment (Nowacki & Abrams 2008; Ratajczak *et al.* 2011; Wilson & Agnew 1992).

Positive feedbacks in communities experiencing woody plant encroachment could arise through various processes. In mesic grasslands especially, frequent fires can favor grasses due to higher susceptibilities of woody plants' seedlings and saplings to fire, while long periods of fire suppression allow woody plants to establish and reach maturity, preventing the spread of future fire ("vegetation–fire feedback") (Baudena *et al.* 2009; N'Dri *et al.* 2018; Werner & Prior 2013). As such, prescribed fire is a common management strategy for the maintenance of grassy systems (Archer *et al.* 2017; Govender & Van Wilgen 2006). However, burgeoning evidence suggests that positive feedbacks could also arise because many encroaching woody plants associate with distinct fungal and bacterial symbionts (Sha *et al.* 2025), which could in turn affect vegetation dynamics. Indeed, over the past several decades, an emerging paradigm in plant ecology positions soil microbes as an "unseen majority" that drives a variety of plant community outcomes (Bever *et al.* 2010; Van Der Heijden *et al.* 2007; Reynolds *et al.* 2003), including by driving feedback loops in plant population dynamics (Bever *et al.* 1997; Kandlikar 2024).

Several lines of evidence point to the potential importance of plant–soil feedback in driving woody plant encroachment. First, many woody species known to drive grassland conversion, such as *Acacia*, *Prosopis*, *Vachellia*, *Ceanothus*, or *Alnus* species, associate with nitrogen-fixing bacteria. In African savannas, for example, >90% of sites experiencing woody encroachment feature woody species with nitrogen-fixing capacity (Stevens *et al.* 2017). Second, unlike grasses, some woody species associate with ectomycorrhizal fungi (Soudzilovskaia *et al.* 2020), which can protect plants against soilborne pathogens (Strobel & Sinclair 1992), and which tend to promote positive feedback (Bennett *et al.* 2017; Song *et al.* 2026; Teste *et al.* 2017). In fact, ectomycorrhizal association is over four times more common among woody plants that are specifically known to encroach grassy systems (χ^2 = 58.8, p = 1.04e-12; Supplement S1), suggesting that these associations may contribute to their dominance. Third, global meta-analyses have revealed that, unlike woody plants, grasses and forbs tend to cultivate soil communities that suppress conspecific plant growth (Jiang *et al.* 2024; Kulmatiski *et al.* 2008). This process of differential conditioning and response can alter plant community composition by providing woody plants a competitive advantage and enabling their encroachment into grassland systems (Bever *et al.* 1997; Crawford *et al.* 2019; Kandlikar 2024).

In fire-prone communities, the impacts of plant–soil feedback may be further mediated by fire (Hewitt *et al.* 2022; Revillini *et al.* 2021). Fire can disrupt plant–microbe interactions directly by causing plant and/or microbial mortality and indirectly through changes to abiotic soil properties.

Though more empirical studies are needed (Kardol *et al.* 2022), emerging evidence suggests that fire can weaken plant–soil feedbacks (Senior *et al.* 2018; Warneke *et al.* 2023), including neutralizing microbial self-limitation in grasses (Hopkins & Bennet 2024). On the other hand, severe wildfires can have long-lasting impacts on ectomycorrhizal fungal communities (Pulido-Chavez *et al.* 2021), which could disrupt woody-favoring positive feedbacks. Further, recent theoretical and empirical advances have shown that plant–soil feedbacks strengthen over a host plant's lifetime and that microbial legacies can persist for years after host death (Ke *et al.* 2025; Magee *et al.* 2025). As a result, variation in the frequency and intensity of fires relative to the rates of conditioning and decay of microbial feedbacks could impact the development and consequences of plant–soil feedback in grasslands experiencing woody encroachment.

Here, we seek to systematically explore how soil microbes could impact woody plant encroachment. To do so, we develop a mathematical model for microbially mediated vegetation dynamics in fire-prone systems and parameterize the model with realistic estimates of intraspecific feedback for grasses and woody plants that we derive through a meta-analysis of experimental data. With this framework, we answer the following questions: (1) Under what scenarios of microbial effects can grasses and woody plants both persist? (2) What impact do plant-soil microbial feedbacks have on the fire regimes that can maintain grassy systems? (3) How do soil microbes alter the conditions under which woody plant encroachment can be reversed with fire-based management?

2. Methods

2.1. Empirical patterns of woody plant encroachment

To establish an empirical basis for microbial contributions to woody plant encroachment, we built on Ding & Eldridge (2022)'s global meta-analysis, for which the authors had identified the most dominant encroaching woody plant species in 243 studies of woody encroachment. We began by expanding this database to include additional woody and grass species identified in the original studies. We then paired this expanded database of woody encroachment with another global database of plant–soil feedback studies that included nearly 6,000 estimates of plant growth in self-conditioned versus non-self-conditioned soil (Jiang *et al.* 2024). We then conducted a meta-regression to quantify the degree to which soil microbes generate positive or negative feedback among the identified woody species and grasses. This Bayesian mixed-effects model included growth form as a fixed effect, and a random intercept for study with species nested within. The model was fit with weakly informative priors in `brms` (see Supplement S2 for details and model diagnostics). We then projected the long–term dynamical consequences of these empirical estimates of intraspecific feedback using a patch occupancy model, described below.

2.2. Modeling approach

Our approach builds on a patch occupancy model for plant-soil feedback (Ke & Levine 2021), which we modified to evaluate the role of soil microbes in shaping plant community dynamics in fire-prone grassland systems (Fig. 1A) . This framework assumes that the landscape can be characterized as comprising an infinite number of patches, each of which can be occupied by one plant (here, either a grass or woody plant). Reflecting empirical evidence that woody species vary in their reproductive capacity and fire sensitivity across life stages (Hoffmann *et al.* 2019; Sankaran *et al.* 2005; Werner & Prior 2013), and consistent with past models of tree-grass dynamics in savannas (Baudena *et al.* 2009), we model the dynamics of woody species with a two-stage life history (nonreproductive seedlings, denoted σ, and reproductive adults, denoted s). Grasses are not assumed to have stage structure. Each patch also hosts a soil microbial community, which is either in a "background" state, or which represents the conditioning effect of a grass or a woody plant. We use the notation P_{ij} to refer to the proportion of patches that are occupied by plant i ($i = g, \sigma, s$, indicating grass, woody seedling, or woody adult) and harbor soil microbial community j ($j = g, s$, indicating grass-conditioned or woody-conditioned soils). i and j can also be 0, representing patches that are empty or that have a baseline (unconditioned) soil community, respectively. As the system of equations describes the dynamics of each patch type in terms of its proportion, the sum of all P_{ij} at each timestep is always 1.

Our framework assumes that plants can only establish into patches that are currently unoccupied, i.e., plants cannot displace established individuals from their patches. This assumption is consistent with empirical evidence that in savannas and grasslands, established grasses tend to limit the survival and growth of woody plant seedlings (Hoffmann *et al.* 2009; Riginos 2009), and conversely, that grass establishment is suppressed near woody plants (Köchy & Wilson 2000; Peters 2002). Rates of establishment into empty patches are determined by the frequency of grasses and woody adults, as well as by the soil microbial status of the patch. In other words, our model assumes that soil microbes primarily impact plants by altering the establishment process (which encompasses both germination and growth immediately after germination), rather than by affecting adult survival or reproduction. This assumption is consistent with the broader field of plant–soil feedback, which has traditionally focused on microbial effects on biomass accumulation rates of young plants (Ke *et al.* 2025). The model also assumes that there is no explicit spatial structuring within the landscape, and that each individual of a given species and stage is equally likely to experience mortality or contribute to establishment in other patches (there is no genetic variation).

2.2.1. Model dynamics in the absence of fire

Patches that are unoccupied and have a unconditioned (or baseline) soil community (i.e., P_{00}, Eqn. 1) can become occupied by either a grass or woody plant at a species-specific establishment rate r_i, proportional to the prevalence of reproductive individuals and of unoccupied patches. In patches that are currently unoccupied but whose soils have the microbial legacy of a previous plant resident (i.e., P_{0g} and P_{0s}, Eqns. 2-3), establishment rates r_i are further modified by the soil community j ($m_{ij} > 1$ indicating that microbial community j increases plant i's establishment rate relative to its establishment in unconditioned soils, and vice-versa for $m_{ij} < 1$). The prevalence of unoccupied patches increases with plant mortality (μ_i), and is also affected by the decay rate of conditioned soils (d_j). These dynamics are formalized as follows:

$$\frac{dP_{00}}{dt} = -\overbrace{r_s P_{00}(P_{ss})}^{\substack{\text{woody}\\ \text{establishment}}} - \overbrace{r_g P_{00}\big(P_{g0+}P_{gg} + P_{gs}\big)}^{\text{grass establishment}} + \overbrace{\mu_g P_{g0} + \mu_\sigma P_{\sigma 0}}^{\substack{\text{mortality in}\\ \text{unconditioned patch}}} + \overbrace{d_g P_{0g} + d_s P_{0s}}^{\substack{\text{microbial decay in}\\ \text{unoccupied patch}}} \tag{1}$$

$$\frac{dP_{0g}}{dt} = -\overbrace{r_g m_{gg} P_{0g}\big(P_{g0} + P_{gg} + P_{gs}\big)}^{\text{grass establishment}} - \overbrace{r_s m_{sg} P_{0g}(P_{ss})}^{\substack{\text{woody}\\ \text{establishment}}} + \overbrace{\mu_g P_{gg} + \mu_\sigma P_{\sigma g}}^{\substack{\text{mortality in}\\ \text{grass-conditioned patch}}} - \overbrace{d_g P_{0g}}^{\substack{\text{microbial}\\ \text{decay}}} \tag{2}$$

$$\begin{aligned} \frac{dP_{0s}}{dt} = &- \overbrace{r_s m_{ss} P_{0s}(P_{ss})}^{\text{woody establishment}} - \overbrace{r_g m_{gs} P_{0s}\big(P_{g0} + P_{gg} + P_{gs}\big)}^{\text{grass establishment}} + \\ &\overbrace{\mu_s P_{ss} + \mu_\sigma P_{\sigma s} + \mu_g P_{gs}}^{\substack{\text{mortality in}\\ \text{woody-conditioned patch}}} - \overbrace{d_s P_{0s}}^{\substack{\text{microbial}\\ \text{decay}}} \end{aligned} \tag{3}$$

Patches with a grass or a woody plant present but that have an unconditioned soil community (i.e., P_{g0}, $P_{\sigma 0}$, Eqns. 4-5) arise when the corresponding plant species establishes into an unconditioned patch. Mortality in these patches returns them to P_{00}, while plant conditioning (or in the case of woody plants, conditioning and growth), which occurs at a rate c_i, alters the microbial status of the patch.

$$\frac{dP_{g0}}{dt} = \overbrace{r_g P_{00}\big(P_{g0} + P_{gg} + P_{gs}\big)}^{\substack{\text{grass establishment in}\\ \text{unconditioned patch}}} - \overbrace{\mu_g P_{g0}}^{\substack{\text{grass}\\ \text{mortality}}} - \overbrace{c_g P_{g0}}^{\substack{\text{grass}\\ \text{conditioning}}} \tag{4}$$

$$\frac{dP_{\sigma 0}}{dt} = \overbrace{r_s P_{00}(P_{ss})}^{\substack{\text{woody establishment in}\\ \text{unconditioned patch}}} - \overbrace{\mu_\sigma P_{\sigma 0}}^{\substack{\text{woody}\\ \text{mortality}}} - \overbrace{c_s P_{\sigma 0}}^{\substack{\text{woody}\\ \text{conditioning}}} \tag{5}$$

The prevalence of patches occupied by a grass or a woody plant and with a corresponding grass- or woody-conditioned soil microbial community (i.e., P_{gg}, $P_{\sigma s}$, and P_{ss}, Eqns. 6–8) grows due to plant establishment in to previously conditioned patches or due to plant conditioning of baseline soil, and declines due to plant mortality. The prevalence of woody seedlings on woody-conditioned soils ($P_{\sigma s}$) also decreases as these plants mature into reproductive adults, which we assume occurs at the same rate at which woody plants condition soils (c_s).

$$\frac{dP_{gg}}{dt} = \overbrace{r_g m_{gg} P_{0g}\left(P_{g0} + P_{gg} + P_{gs}\right)}^{\substack{\text{grass establishment in}\\ \text{grass-conditioned patch}}} + \overbrace{c_g\left(P_{g0} + P_{gs}\right)}^{\text{conditioning}} - \overbrace{\mu_g P_{gg}}^{\text{mortality}} \tag{6}$$

$$\frac{dP_{\sigma s}}{dt} = \overbrace{r_s m_{ss} P_{0s} P_{ss}}^{\substack{\text{woody establishment in}\\ \text{woody-conditioned patch}}} - \overbrace{c_s P_{\sigma s}}^{\substack{\text{growth into}\\ \text{adult stage}}} - \overbrace{\mu_\sigma P_{\sigma s}}^{\text{mortality}} \tag{7}$$

$$\frac{dP_{ss}}{dt} = \overbrace{c_s\left(P_{\sigma 0} + P_{\sigma g}\right)}^{\substack{\text{conditioning by and growth of}\\ \text{woody seedlings}}} + \overbrace{c_s\left(P_{\sigma s}\right)}^{\substack{\text{growth of}\\ \text{woody seedlings}}} - \overbrace{\mu_s P_{ss}}^{\text{mortality}} \tag{8}$$

Finally, the prevalence of patches occupied by a grass or a woody plant but that have the soil community of the other species (i.e., P_{gs} or $P_{\sigma g}$, Eqns. 9–10) grows due to plant establishment into conditioned patches and decreases due to plant conditioning and mortality.

$$\frac{dP_{gs}}{dt} = \overbrace{r_g m_{gs} P_{0s}\left(P_{g0} + P_{gg} + P_{gs}\right)}^{\substack{\text{grass establishment in}\\ \text{woody-conditioned patch}}} - \overbrace{\mu_g P_{gs}}^{\text{mortality}} - \overbrace{c_g P_{gs}}^{\text{conditioning}} \tag{9}$$

$$\frac{dP_{\sigma g}}{dt} = \overbrace{r_s m_{sg} P_{0g}(P_{ss})}^{\substack{\text{woody establishment in}\\ \text{grass-conditioned patch}}} - \overbrace{\mu_\sigma P_{\sigma g}}^{\text{mortality}} - \overbrace{c_s P_{\sigma g}}^{\text{conditioning}} \tag{10}$$

Model parameters used in simulations are provided in Table 1.

2.2.2. Impacts of fire

We model fires as discrete events that alter the relative frequencies of patches. Broadly, plant and microbial mortality due to fire of intensity f follows a logistic distribution (Fig. 1B–D), reflecting that many plants in fire-maintained ecosystems may lose their aboveground biomass ("topkill") but resprout after a low-intensity fire (Hoffmann *et al.* 2009; Pausas *et al.* 2015). Patches that experience plant mortality also lose any microbial conditioning, such that these patches return to P_{00}. Soils in unoccupied patches with a legacy-conditioned effect also decay to P_{00}, with both following a logistic distribution. In this spatially implicit implementation, a low intensity fire could represent a low temperature fire that causes little mortality or a heterogeneous fire that only burns some areas (Fill & Crandall 2023). We directly impose a fire frequency and intensity to isolate potential microbial impacts on vegetation structure in a fire-prone system. This approach has the additional benefit of emulating management with prescribed fire.

Within this framework, we evaluate the role of microbes in shaping plant community dynamics under three scenarios that capture variation in woody adults' fire sensitivities. In all scenarios, the logistic function relating fire intensity to plant mortality is parameterized such that a fire of intensity 0.5 causes 50% mortality of the grass, and woody seedlings are more sensitive to fire than are grasses (50% mortality at a fire intensity of 0.25). The fire sensitivity of woody adults varies across the three scenarios, each reflecting empirical trends.

In the first scenario, woody adults experience mortality due to fire at the same rate that grasses do (Fig. 1B). This case corresponds to dwarf shrubs and semi-shrubs like *Vaccinium* spp. in the Arctic and *Sarcopoterium spinosum* in the Mediterranean steppe, which can be susceptible to fire even as adults (Henkin *et al.* 1999; Narita *et al.* 2015). In the second scenario, woody adults are half as sensitive to fire as grasses (Fig. 1C). This case corresponds to shrubs or small trees that may partially escape fire as adults, such as *Vachellia drepanolobium* in eastern African woodlands and savannas (LaMalfa *et al.* 2019). In the third scenario, woody adults are totally insensitive to fire, experiencing zero mortality (Fig. 1D). This corresponds to trees that escape the "fire trap" through vertical growth, self-pruning, and/or thick bark, especially in surface fire systems like the Brazilian cerrado and longleaf pine savanna (Hoffmann *et al.* 2019).

2.2.3. Numerical simulations

We ran simulations in `Julia` (Bezanson *et al.* 2017) version 1.11.5, using the packages `ParameterizedFunctions`, `DifferentialEquations`, and `DataFrames` (Bouchet-Valat & Kamiński 2023; Rackauckas & Nie 2017). Numerical solutions were generated using `Tsit5()`, an efficient fifth-order Runge-Kutta method (Tsitouras 2011). Fires were implemented with a preset time callback function, which allows for changes to state variables at specified instances. Fire years were randomly sampled over the given timespan based on the specified fire frequency. We used `JuliaCall` (Li 2019) in `R` version 4.4.2 to execute the Julia code, running each simulation with fire 100 times for 2000 timesteps.

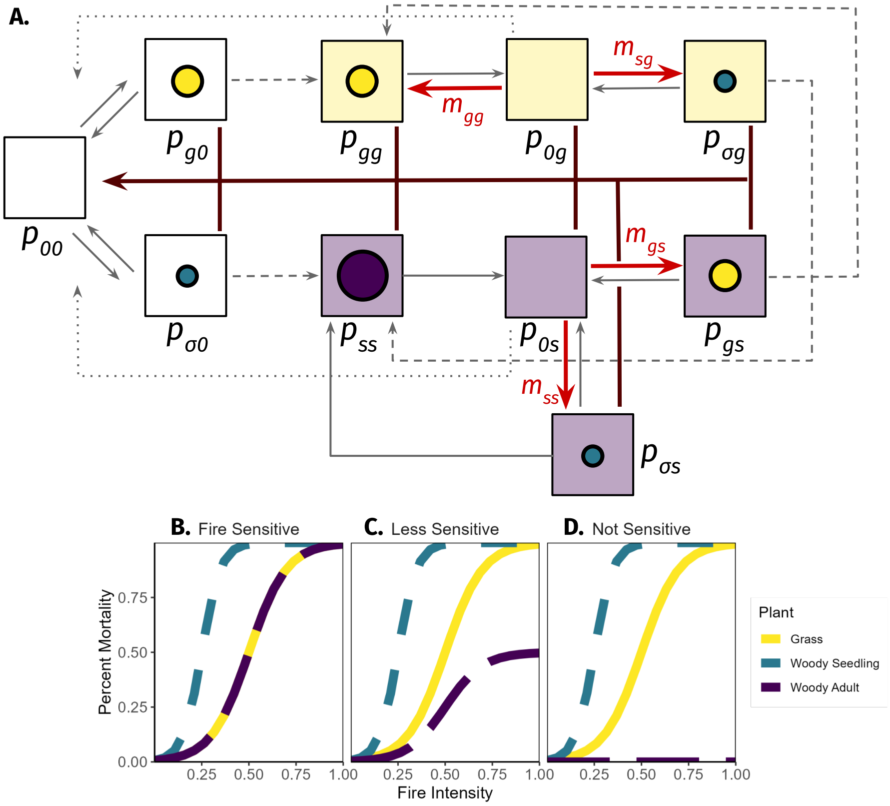

Figure 1: Overview of model dynamics. Panel **A** illustrates transitions between patch types, which are defined by plant status (no circle, yellow circle, small blue circle, or large purple circle, representing empty, grass, woody seedling, or woody adult presence) and soil microbial status (white, yellow, or purple backgrounds, representing unconditioned, grass-conditioned, or woody-conditioned soils respectively). Soil microbial conditioning affects establishment rates of plants (transitions indicated with red arrows). Solid gray lines indicate transitions caused by plant establishment or death, dashed gray arrows indicate transitions caused by microbial conditioning, and dotted gray arrows indicate transitions caused by the decay of conditioned soil microbes. Solid brown arrows indicate transitions caused by fire. Panels **B–D** illustrate three scenarios of varying fire sensitivity of grasses (solid yellow line), woody seedlings (blue dashed line), or woody adults (purple dashed line). Grass and woody seedlings' fire sensitivities are the same across all scenarios, but woody adults are either equally sensitive to fire as grasses (Panel B), half as fire-sensitive as grasses (C), or are fire insensitive (D).

Table 1: Model parameters and values used in simulations (unless otherwise indicated). We explore three sets of values for m_{gg} and m_{ss} ($m_{gg} = m_{ss} = 1$; $m_{gg} = 0.87, m_{ss} = 1$; or $m_{gg} = 0.87, m_{ss} = 1.12$), as explained in Section 3.1.

Parameter	**Units**	**Value**	**Definition**
r_g	year^{-1}	1.00	Grass establishment rate
r_s	year^{-1}	1.55	Woody establishment rate
μ_g	year^{-1}	0.10	Grass mortality rate
μ_s	year^{-1}	0.10	Woody adult mortality rate
μ_σ	year^{-1}	0.10	Woody seedling mortality rate
d_g	year^{-1}	0.25	Grass microbial decay rate
d_s	year^{-1}	0.25	Woody microbial decay rate
c_g	year^{-1}	0.20	Grass conditioning rate
c_s	year^{-1}	1.55	Woody conditioning rate and growth rate of woody seedlings
m_{gs}	unitless	1.00	Impact of woody microbial community on grass establishment
m_{sg}	unitless	1.00	Impact of grass microbial community on woody establishment

3. Model Analysis and Results

3.1. Empirical estimates of model parameters

Our meta-analysis revealed that grass species that are being encroached tend to experience self-limiting microbial feedbacks (lnRR = −0.14, crI = −0.28 − 0.00, corresponding to $\widetilde{m_{gg}} = 0.87$). Encroaching woody plant species tend to experience self-facilitating feedbacks (lnRR = 0.11, crI = −0.15 − 0.37, corresponding to $\widetilde{m_{ss}} = 1.12$; Table 2), but there was more uncertainty in this estimate. Thus, after exploring how variation in m_{gg} and m_{ss} terms impact model dynamics in our first analysis (Fig. 2A), we explore the consequences of varying fire regime assuming soil-mediated self-limitation among grasses ($m_{gg} = 0.87$). Reflecting broader uncertainty in the strength of conspecific feedback among woody plants, we explore both neutral and self-facilitating microbial effects on their establishment ($m_{ss} = 1$ or $m_{ss} = 1.12$). Given limited empirical estimates for microbially mediated grass-woody interaction coefficients (Supplement S2), we assume neutral inter-specific feedback, i.e., $m_{sg} = m_{gs} = 1$.

We assume that patches become host-conditioned after 5 years and that microbial legacies in unoccupied patches decay over 4 years, estimates that fall within the range of empirically measurements of these processes (Ke & Levine 2021; Magee *et al.* 2025). Finally, the historic fire frequency in grasslands and savannas can range from every 1–5 years to decadal intervals (Frost 1993; Govender & Van Wilgen 2006), so we consider high frequency fire to be every 2 timesteps and low frequency fire to be every 50 timesteps. All parameter values used in our analyses are presented in Table 1.

Table 2: Model estimates for intraspecific feedback of grasses and woody plants. For each, the model estimate and credible interval is provided, first as the original log response ratio and then in the exponentiated forms corresponding to m_{gg} and m_{ss}. The number of unique studies and species in the meta-analysis for each plant type is also shown.

Growth form	Effect size (LRR)	Exponentiated effect size	Studies	Species
Grass	−0.14 (-0.285 – 0.002)	0.87 (0.75 – 1)	318	26
Woody	0.11 (-0.149 – 0.374)	1.12 (0.86 – 1.45)	47	12

3.2. Plant community dynamics in the absence of fire

Variation in microbial impacts on host plant growth (m_{ii}) leads to qualitatively different outcomes in terms of grass and woody plant persistence. Grass generally dominates when $m_{gg} > 1$ (yellow region in Fig. 2A), and microbial effects stabilize coexistence when both m_{gg} and m_{ss} are less than 1. However, the average empirically observed impact of the conspecifically conditioned microbial community is self-facilitating for woody plants and self-limiting for grasses (white point in Fig. 1A), which generates a woody-dominated system. The time series in Fig. 1B–C show the dynamics of each of the ten patch types; these are aggregated by plant species to generate grass and woody plant frequencies throughout the results.

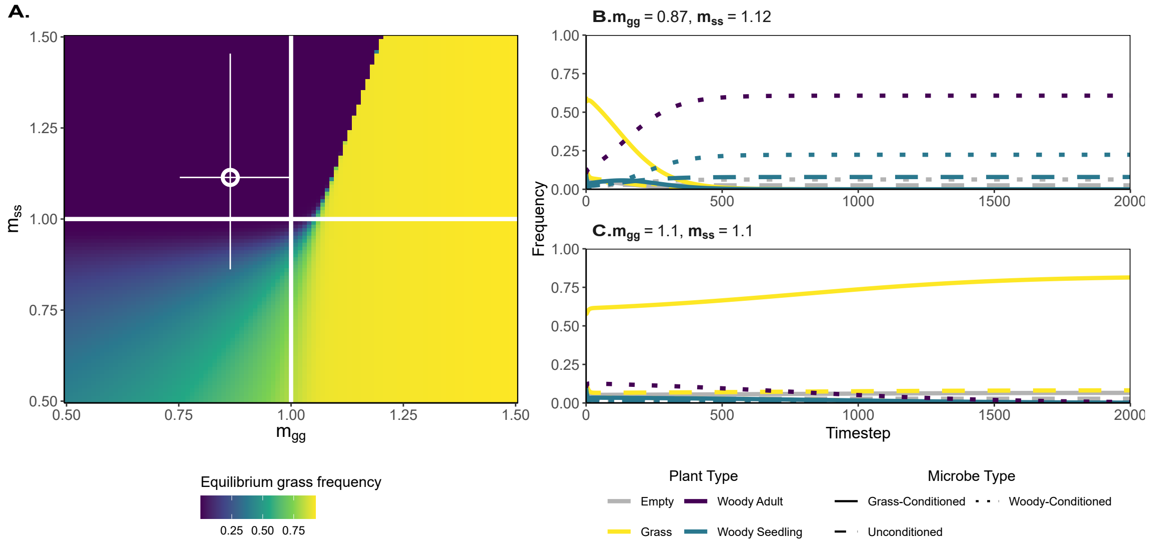

Figure 2: Impacts of microbially mediated patch establishment on grass-woody plant dynamics in the absence of fire. Panel **A** shows the equilibrium grass frequency across combinations of m_{gg} and m_{ss}. The white point and standard errors show the results of a meta-analysis of m_{ii} values from resident grass and encroaching woody plant species that have been identified in studies of woody plant encroachment (see Supplement S2). Panels **B** and **C** show patch dynamics over time for two combinations of m_{gg} and m_{ss}. To generate frequencies in panel A, the sum of the frequencies of each grass patch type (p_{g0}, p_{gg}, and p_{gs}) were averaged over the last 50 timesteps. These simulations show model dynamics for baseline grass establishment rate (i.e., in unconditioned soil) of $r_g = 1$ and baseline woody plant establishment rate of $r_s = 1.55$; values used for other parameters are provided in Table 1. See Fig. S1 for an exploration of r impacts on model behavior. Bistability emerges when both grasses and shrubs condition self-facilitating soils; see Figs. S2 and S3 for details.

3.3. Microbial mediation of fire impacts on plant communities

For our chosen parameter values (Table 1) and fire sensitivities (Fig. 1B–D), frequent and low-intensity fires are necessary to maintain grassy communities even in the absence of microbial feedbacks (Fig. 3A–C). As woody adults become less sensitive to fire, the set of fire regimes that maintain grassy plant communities become increasingly constrained. Irrespective of their fire sensitivity, woody plants dominate in systems with infrequent, low-intensity fires (narrow purple strip at the bottom of Fig. 3A–C; see also Fig. S4). When woody adults are less fire-sensitive than grasses, they also dominate under infrequent, high-intensity fires (Fig. 3B–C). Neither grasses nor woody plants persist under frequent and high intensity fires (top-left corner of each panel in Figs. 3 and S4) except when woody adults are totally insensitive to fire (Fig. S4C).

Accounting for grass microbial feedbacks further reduces the fire regimes under which grass is maintained (Fig. 3D–F). Specifically, when woody adults are fire-sensitive, microbial feedbacks increase the minimum fire intensities required to maintain grassy plant communities for a given fire interval. Additionally, when woody adults are less fire-sensitive than grasses (Fig. 3E–F), the fire intervals must be far more frequent under microbial mediation of grass dynamics to maintain grassiness. Further accounting for self-facilitating woody microbial feedbacks (Fig. 3G–I) additionally constrains which fire regimes maintain grassy communities, requiring even higher-intensity fires for a given interval when woody plants are fire-sensitive and even more frequent fires when they are less sensitive than grasses.

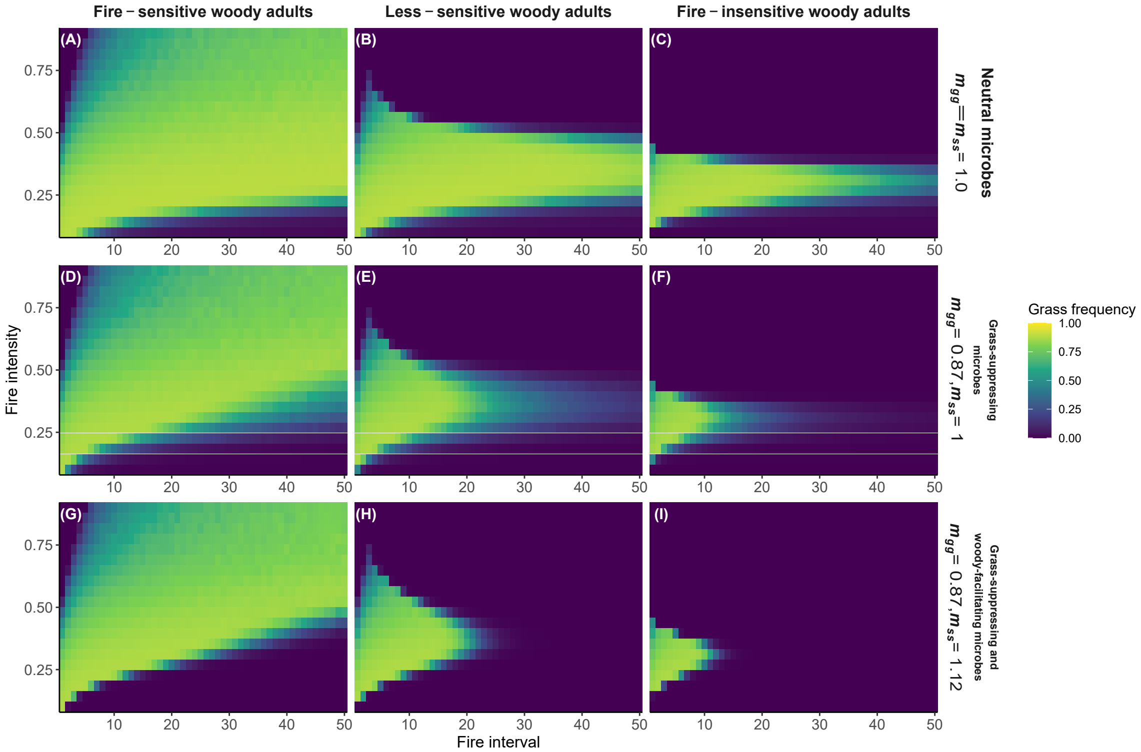

Figure 3: Woody plant-facilitating microbial feedbacks restrict the fire regimes that permit grass persistence. Each panel shows grass frequencies at 2000 timesteps under variable fire regimes (varying fire frequency and fire intensity within each panel) and under varying effects of fire on woody adult mortality (across different columns). Plots in the the top row shows grass frequencies assuming no microbial feedbacks (i.e., all m terms equal to 1); plots in the middle row show grass frequencies assuming that microbes generate negative intraspecific feedbacks for grasses and have neutral impacts on woody plants; plots in the bottom row show grass frequencies assuming microbes generate both negative intraspecific feedbacks for grasses and have positive intraspecific feedbacks for woody plants, as indicated by our meta-analysis (Supplement S2, $m_{gg} = 0.87; m_{ss} = 1.12; m_{gs} = m_{sg} = 1$). In Panels **A, D, and G**, mature woody plants are as fire-sensitive as grasses (as in Fig. 1B). In panels **B, E, and H**, woody adults are half as fire-sensitive as grasses (as in Fig. 1C). In panels **C, F, and I** woody adults are insensitive to fire (as in Fig. 1D).

3.4. Impacts of microbes on grassland restoration

We next evaluated how microbial feedbacks modify the fire frequencies necessary to recover grass-dominated communities after woody plant encroachment has occurred. To do so, we conducted simulations in which the initial conditions of the community represented a woody-dominated system (p_{ss} = 0.7), and evaluated the temporal dynamics of grass recovery under different fire frequencies (intensity = 0.25). Generally, we find that more frequent application of low-intensity fires leads to more rapid grass recovery (more rapid transitions from purple to yellow in Fig. 4A–C). Moreover, we find that self-limiting grass microbial effects substantially constrain the set of fire frequencies under which grassy restoration is possible, regardless of whether microbial feedbacks are neutral ($m_{gg} = 0.87; m_{ss} = 1.0$; Fig. 4B) or positive ($m_{gg} = 0.87; m_{ss} = 1.12$, as indicated by our meta-analysis; Fig. 4C) for woody plants In Fig. 4, we assume that adult woody plants are fire-insensitive, but we verified that microbes consistently constrain the conditions for grass restoration regardless of woody adult fire sensitivities (Fig. S5).

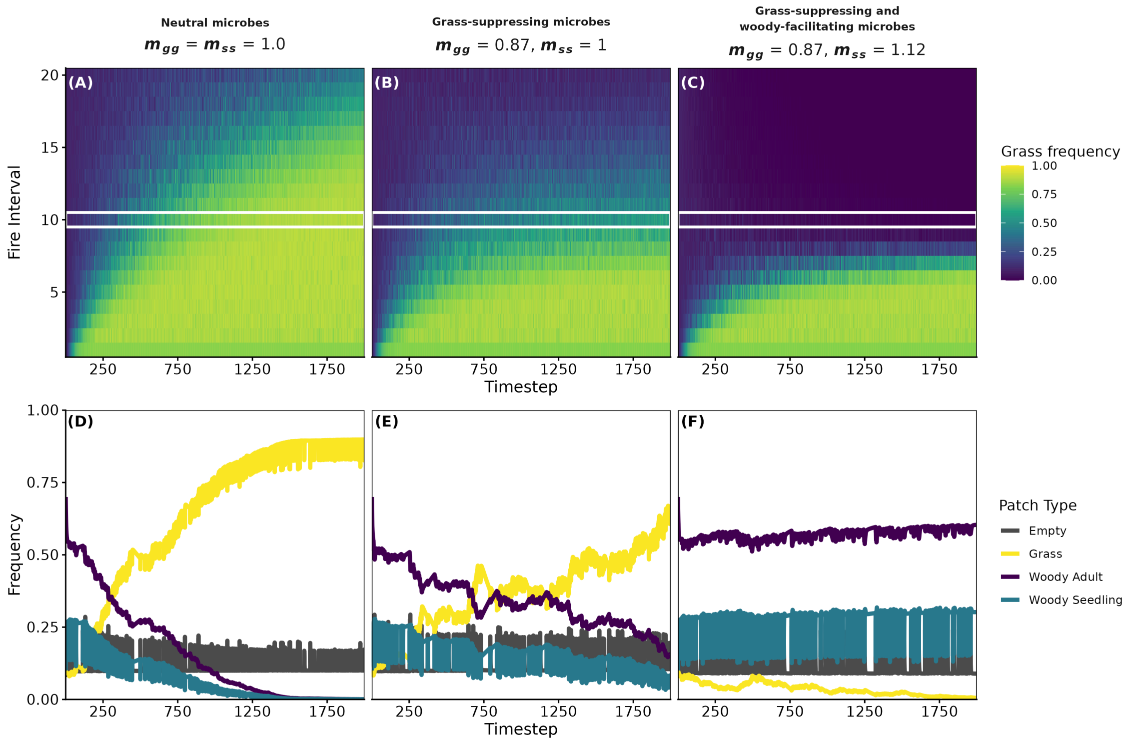

Figure 4: Dynamics of grass recovery after woody encroachment under variable fire regimes and varying plant–microbe interactions. Panels **A**–**C** show overall grass frequency over time (*x*-axis) under variable fire intervals (*y*-axis), assuming microbes give rise neutral or woody-favoring feedbacks. In Panel **A**, $m_{gg} = m_{ss} = 1$; in Panel **B**, $m_{gg} = 0.87$ and $m_{ss} = 1$; in Panel **C**, $m_{gg} = 0.87$ and $m_{ss} = 1.11$, as indicated in our meta-analysis. Panels **D**-**F** illustrate time series of grass and woody plant dynamics at a fire interval of 10 timesteps under three corresponding scenarios of microbial impacts (white horizontal rectangles in Panels **A**–**C**). In all scenarios shown here, woody adults are insensitive to fire; see Fig. S5 for dynamics under other scenarios of woody adult sensitivity to fire.

4. Discussion

Woody plant encroachment is widespread in grassy biomes worldwide, with important implications for biodiversity and ecosystem functioning. Here we evaluate the interactive roles of plant–soil feedback and managed fire regimes in shaping the dynamics and reversibility of woody encroachment. By combining theory and data, we find that soil microbial feedbacks commonly limit grass growth and favor woody plants (Fig. 2), and can sharply constrain which fire regimes maintain grassy communities (Fig. 3). This pattern was consistent across a range of potential woody adult fire responses, each chosen for their ecological relevance. This consistency suggests that microbe-mediated feedbacks could have important implications for many fire-prone systems, including both savannas with fire-escaping trees and grasslands with smaller-statured shrubs. Further, we find that strong microbial feedbacks can impede restoration of already encroached systems, requiring more frequent fire to recover grassy states. Even when grass recovery is possible, stronger woody-favoring microbial feedbacks require more successive fires for conversion back to a grassy state, meaning recovery is slowed (Fig. 4). In all, our work points to the potentially transformative role of soil microbial feedbacks in shaping vegetation dynamics in fire-prone biomes experiencing woody plant encroachment.

Previous models of savanna-forest transitions have emphasized the role of periodic fire in maintaining a grassland state, particularly in less arid climates. These have mostly focused on vegetation-fire feedback, in which vegetation structure both depends on and alters fire properties like frequency, intensity, or percolation (Baudena *et al.* 2009; D'Odorico *et al.* 2006; Magnani *et al.* 2023). Our results suggest that qualitatively similar outcomes regarding the importance of fire for the maintenance of grassy vegetation can also arise due to plants' conditioning and responding to the soil environment. The distinct soil microbial associations of grasses vs. woody plants suggest a key role for the soil microbiome in this process, but plant impacts on abiotic soil properties, including those that are commonly evaluated under the "fertile island" framework (Schlesinger *et al.* 1996), could in principle give rise to similar dynamics, provided that grasses and woody plants respond differently to these soil changes. Regardless of the mechanism driving the feedback, fires appear to increase the range of conditions in which both grasses and woody plants coexist. Our model also corroborates frequent empirical observations of higher frequency fire regimes than the historic norm being necessary for grassland restoration (Case & Staver 2016).

Although we parameterized our model with estimates grounded in empirical data, this work underscores the need for further experimentation on plant–soil feedbacks in fire-prone systems, particularly between grasses and woody plants. While most studies of plant–soil feedbacks have taken place in grasslands (Kulmatiski *et al.* 2008), including in fire-maintained systems like the North American prairie, they have focused on interactions within the same plant functional type. We know comparably little about microbially mediated grass–woody plant interactions (m_{gs} and m_{sg} in our model). For example, out of 1036 pairwise interactions in a recent meta-analysis of pairwise plant–soil feedback, only 49 directly evaluated feedbacks between an herbaceous and a woody plant species (Yan *et al.* 2022) (Supplement S2). In the absence of strong empirical data, we assumed neutral microbially mediated grass–woody interactions in our analyses, but other theoretical work on plant–soil feedback has shown that interspecific interactions play an important role in determining microbially mediated species coexistence dynamics (Kandlikar 2024). This suggests that empirically quantifying microbial mediation of both intra- and interspecific interactions in communities of concern will provide vital insights into microbial impacts on woody encroachment and the success of fire-based restoration.

Our results suggest several further avenues for future theoretical research that are likely to yield important insights. First, our analysis assumes that the frequency and intensity of fire are independent of the vegetation structure – an assumption that more closely reflects fire dynamics in systems actively managed with fire (e.g., periodic lower-intensity prescribed burns) than in plant communities where fires arise and are allowed to proceed naturally (Boer *et al.* 2009; Fill & Crandall 2023; Govender & Van Wilgen 2006). In such ecosystems, higher flammability of grasses could result in more frequent and contiguous fires in grass-dominated communities that eliminate self-suppressing microbial communities of grasses more efficiently than in our model. Conversely, lower shrub or tree flammability could result in woody-favoring microbes persisting more through fire than in our model (Magnani *et al.* 2023; Pausas *et al.* 2016), thus compounding woody dominance in systems that have already undergone encroachment. Developing a unified model of vegetation–soil–fire feedbacks that integrates both sets of processes might reveal important dynamical properties that address outstanding uncertainties about where, why, and how fast woody plant encroachment is predicted to occur. A second promising advancement would be to model fire-mediated plant–microbe interactions among multispecies plant communities comprising grasses, forbs, shrubs, and trees that vary in their sensitivity to fire and strength of microbial feedback. This would enable predictions not only regarding the relative frequencies of grasses and woody plants in the system but also other important system properties such as abundance distributions and functional diversity, which are important regulators of ecosystem function (Van Der Plas 2019). Finally, there is growing evidence that fungal species can vary in their sensitivities to fire and in their dynamics post-fire (Fox *et al.* 2022), suggesting that future modeling work that incorporates the possibility of varying microbial fire sensitivities could yield more robust predictions of microbe-mediated plant dynamics in fire-prone systems.

In addition to their relevance for understanding woody plant encroachment, our results also point to important directions for future research to understand how plant–soil feedback shapes vegetation dynamics in the "real world" (De Long *et al.* 2018). A growing number of studies find mismatches between predictions of microbe-mediated plant community dynamics based on interaction strengths measured in controlled conditions and observed dynamics in field settings (e.g., (Forero *et al.* 2019)). Our model suggests that exogenous events like fires could help explain such discrepancies — for example, even when microbes favor woody plants, sufficiently frequent fires can drive grassy dominance (Fig. 4B–C). Our framework can be readily extended to project the consequences of other exogenous, pulsed disturbances like tornadoes (Nagendra & Peterson 2015). In such systems, understanding rates of microbial conditioning and decay relative to the disturbance regime will provide crucial insight into the potential impact of soil-mediated plant interactions. Further modifications to our theoretical framework could also shed light onto the impacts of press disturbances like rising CO_2 on plant community shifts (Archer *et al.* 2017).

Overall, our findings have important implications for the study and management of woody plant encroachment. We show that plant–soil feedback can narrow the fire intervals under which grassland recovery is possible and, in those scenarios of possible recovery, increase the duration of fire-based management necessary to recover. This is crucial information because woody plant encroachment is a consistent and global phenomenon that is of increasing concern for management goals related to grassland-associated biodiversity and maintenance of rangeland economies. Uncertainties persist in identifying the most critical aspects of fire-maintained ecosystems, with efforts largely focused on climate, plant flammability, and plant fire response (Magnani *et al.* 2023; Williams & Abatzoglou 2016). Our model points to the overlooked yet potentially transformative role of the host plant-conditioned soil microbiome in driving changing vegetation patterns in these systems and the urgent need for empirical data testing this process.

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