# Microbial drivers of woody plant encroachment in fire-maintained grasslands and savannas

**Short title**: Microbe impacts on woody encroachment

**Number of text boxes:** 0

**Number of figures:** 4

**Number of tables:** 1

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**Words in Main Text and Abstract:** 5299 (237 in abstract)

# Abstract

Woody plant encroachment into grasslands and savannas is a global phenomenon with wide-ranging consequences for people and nature, but we lack a comprehensive understanding of its drivers. Various factors can contribute to woody encroachment across ecosystems, but a notable commonality is that transitions from herbaceous to woody vegetation are spatially and temporally abrupt, suggesting that positive feedbacks play a role. Positive feedbacks are well-studied in the context of vegetation–fire dynamics, but growing evidence points to the potential importance of microbially mediated plant–soil feedbacks in woody plant encroachment. For example, ectomycorrhizal association, often associated with positive feedback, is especially common among woody plants known to encroach grass-dominated systems, while herbaceous plants tend to accumulate self-limiting microbial communities. To fill this gap, we developed a novel patch occupancy modeling framework for predicting microbial impacts on vegetation dynamics in fire-maintained grasslands, and parameterized this model with empirically derived estimates of plant–microbe interactions from global meta-analyses. We find that empirically measured microbial feedbacks can sharply constrain the fire regimes under which herbaceous communities are maintained. We also show that woody-favoring soil communities increase the duration of fire-based management necessary to recover grassland after encroachment and narrows the conditions under which such recovery is possible. In all, our model points to the overlooked yet consequential role of plant–soil feedbacks in driving changing vegetation patterns in fire-prone grass-dominated systems 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 is now affecting an estimated 500 billion 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 key 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 robust general framework of its key drivers (Archer *et al.* 2017; Deng *et al.* 2021). Part of the challenge is that both global and local processes likely contribute to this phenomenon. Global factors like increased atmospheric $CO_2$ have been hypothesized to favor woody plants with C3 photosynthesis systems in communities dominated by C4 grasses (Wang *et al.* (2011); Archer *et al.* (2017), but see Reich *et al.* (2018)). Similarly, altered climate patterns in which precipitation is concentrated among fewer but more intense rainfall events can contribute to woody plant dominance by increasing pools of deep soil water that are less accessible to shallow-rooting grasses than to woody plants (Kulmatiski & Beard 2013). However, global factors alone are insufficient to explain the considerable landscape-level heterogeneity in woody encroachment patterns (Archer *et al.* 2017; Van Auken 2009), which underscores the potential importance of local factors like herbivory and fire (Sankaran *et al.* 2005; Staver & Bond 2014). In less-arid ecosystems in particular, fire-related management practices likely play a key role in shaping variation in the rates and extent of woody plant encroachment

(Werner & Prior 2013). Frequent fires can act to exclude shrubs and trees from pyrophilic savanna communities 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, potentially becoming fire-insensitive (Baudena *et al.* 2009).

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 commonalities 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. One such process is a "fire-vegetation feedback", which can arise when woody-dominated plant communities that develop under fire-suppression are less fire-prone than herbaceous vegetation and thus suppress future fires (Nowacki & Abrams 2008; Tepley *et al.* 2018). Positive feedbacks can also arise due to woody plants' impacts on biotic and abiotic soil properties (Schlesinger *et al.* 1996). For example, woody plant establishment in drylands can give rise to "fertile islands" characterized by higher levels of soil moisture, nutrients, and organic matter (Ding & Eldridge 2020; Ochoa-Hueso *et al.* 2017; Schlesinger *et al.* 1996), which could subsequently impact plant germination and growth (Bonanomi *et al.* 2007). Woody plant encroachment can also alter the abundance and composition of microbial communities in the soil (Sha *et al.* 2025). These impacts could arise directly due to different soilborne symbionts of woody vs. herbaceous plants, and indirectly because woody encroachment alters abiotic soil properties such as texture and pH (Du *et al.* 2024). These changes to the soil could in turn affect the structure of the vegetation. Indeed, over the past several decades, an emerging paradigm in plant ecology positions soil microbes as the "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 that can favor coexistence and/or species replacement (Bever *et al.* 1997; Kandlikar *et al.* 2019).

Since their incorporation into plant community ecology in the 1990s (Bever *et al.* 1997; Putten *et al.* 1993), microbe-mediated plant–soil feedbacks have been shown to affect plant community diversity and functioning across a wide range of ecosystems (Crawford *et al.* 2019; Jiang *et al.* 2024). These feedbacks arise when plant species have differential impacts on the composition of the soil community, which in turn differentially impacts the growth of plant species in the community. Pairwise negative feedback, in which a conditioned soil microbe community benefits another plant species more than its host, can stabilize coexistence because the more common soil community provides a net benefit to the rarer plant species (Bever *et al.* 1997; Kandlikar 2024). Meanwhile, microbial feedbacks can promote monotypic plant stands, particularly if there are strong positive pairwise feedbacks between competitors (Kadowaki *et al.* 2018; Kandlikar 2024; Teste *et al.* 2017; Yan *et al.* 2022).

Although there has been virtually no experimental work on microbially-mediated plant–soil feedback in the context of woody plant encroachment, several lines of evidence point to the potential importance of these interactions. First, 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 difference is potentially driven by different functional traits of woody vs. non-woody species: at a global scale, herbaceous plants tend to be shorter and have higher specific leaf area and specific root length than woody plants (Díaz *et al.* 2015; Freschet *et al.* 2017) – traits associated with cultivating more self-limiting soil communities (Xi *et al.* 2021). Second, whereas most herbaceous species form mutualistic associations with arbuscular mycorrhizal fungi, some woody species associate with ectomycorrhizal fungi (Soudzilovskaia *et al.* 2020), which can directly protect plants against soilborne pathogens (Strobel & Sinclair 1992), and which tend to promote more positive feedback (Bennett *et al.* 2017). Moreover, ectomycorrhizal association is especially common among woody plants that are known to encroach herbaceous systems worldwide (Supplement S1), suggesting that these associations may contribute to their dominance.

In fire-maintained grasslands, the impacts of plant–soil feedback may be further mediated by changes to fire regimes, which can disrupt pairwise interactions between plants and soil microbes (Hewitt *et al.* 2022; Revillini *et al.* 2021). Fire can disrupt plant–microbe interactions directly by causing mortality among plants and soil microbes, and indirectly through changes to soil physical and chemical properties, potentially leading to a short-term “nullified” effect of soil microbes on plant growth (Kardol *et al.* 2022). Though more empirical studies are needed, available 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, high-severity wildfires can have persistent impacts on the diversity and composition of ectomycorrhizal fungi (Pulido-Chavez *et al.* 2021), which could disrupt woody plant-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 timing 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 use a patch occupancy modeling framework in which grasses and woody plants can occupy patches and, over time, condition those patches with a soil microbial community. Microbial communities then play a role in plant dynamics by modifying species' establishment rates into previously conditioned patches. We derive realistic estimates of woody plant self-facilitation and grass self-limitation from the empirical literature. We also evaluate how fires of varying frequencies and intensities alter predicted plant dynamics. 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) When is woody plant encroachment reversible?

## 2. Methods

Our approach builds on a patch occupancy model for plant-soil microbe dynamics introduced by Ke & Levine (2021), which we modified to evaluate the role of plant–soil feedback in driving woody plant encroachment 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 $\sigma$, 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 have no plant growing in it 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 $P$ values 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 (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 relative frequency of grasses and adult woody plants, 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 (reviewed in Ke *et al.* (2025), but see Dostál (2025) for evidence that microbes can also affect other demographic processes). The model also assumes that all dynamics take place at the landscape scale (there is no explicit spatial structuring), 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).

### 2.1. 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 ($\mu_i$), and is also affected by the decay rate of conditioned soil communities ( $d_j$). These dynamics are formalized as follows:

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

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

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

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.

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

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

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 nonreproductive woody plants on woody-conditioned soils ($P_{\sigma S}$) also decreases as these plants mature into reproductive adults, which in our model occurs at the same rate at which woody plants condition soils ($c_s$).

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

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

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

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.

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

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

## 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 (See Fig. 1B–D), and $P_{00}$ is increased correspondingly so all state variables sum to 1. Patches that experience plant mortality also lose any microbial conditioning, and 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; Loudermilk *et al.* 2012).

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 are 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 in surface fire systems like the Brazilian cerrado or longleaf pine savanna [Pausas *et al.* (2015); Martin and Sapsis 1991].

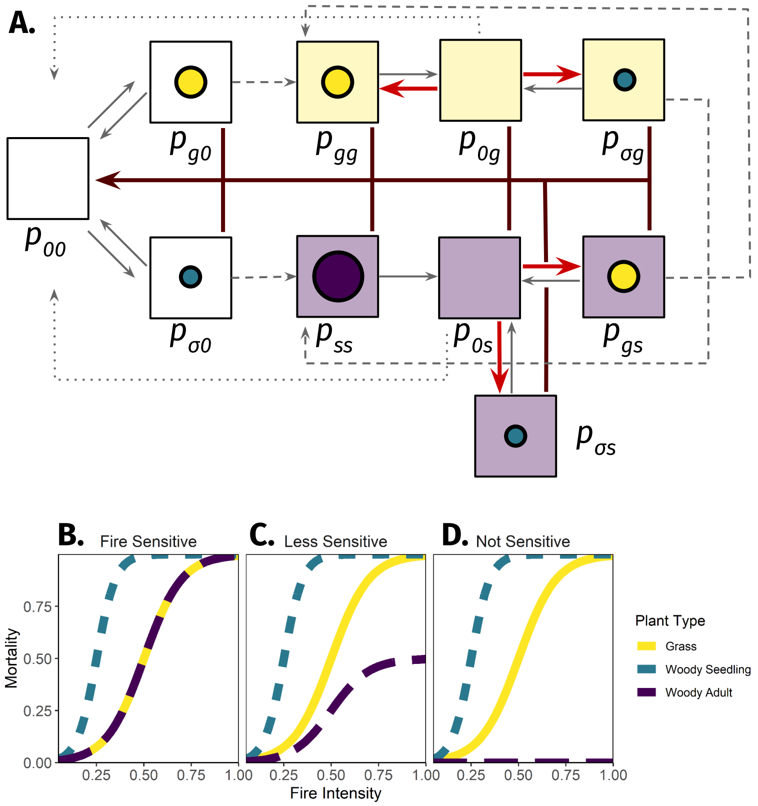

**Figure 1: Overview of model dynamics**. Panel **A** illustrates transitions between patch types, which are defined by plant status (no circle, yellow circle, small blue circle, or large purple circle, representing empty, grass, woody seedling, or woody adult presence) and soil microbial status (white, 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 lines indicate transitions caused by plant establishment or death, dashed arrows indicate transitions caused by microbial conditioning, and dotted arrows indicate transitions caused by the decay of conditioned soil microbes. 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).

### 2.3. Numerical simulations

We implemented this model and ran simulations in `Julia` (Bezanson *et al.* 2017) version 1.11.5. We used the packages `ParameterizedFunctions`, `DifferentialEquations`, and `DataFrames` (Bouchet-Valat & Kamiński 2023; Rackauckas & Nie 2017) to write the models, numerically solve each ODE problem, and retrieve the resulting time-series. 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.

## 3. Model Analysis and Results

### 3.1. Empirical estimates of model parameters

Wherever possible, we chose empirically validated estimates for model parameters. Specifically, we chose reasonable values for $m_{ss}$ and $m_{gg}$ parameters by identifying species in a global meta-analysis of woody plant encroachment (Ding & Eldridge 2024) that had also been included in a global meta-analysis of plant-soil feedback studies (Jiang *et al.* (2024); see Appendix S2 for details). This meta-analysis revealed that grass species that are being encroached by woody plants tend to experience self-limiting microbial feedbacks ($\widehat{m_{gg}} = 0.9$), while encroaching woody plant species tend to experience self-facilitating feedbacks ($\widehat{m_{ss}} = 1.1$). Thus, after exploring how variation in $m_{gg}$ and $m_{ss}$ terms impact model dynamics in our first analysis (Section 3.2), we explore the consequences of varying fire regime assuming soil-mediated self-limitation among grasses and self-facilitation among woody plants. Across all analyses, we assume neutral inter-specific feedback, i.e., $m_{sg} = m_{gs} = 1$. Finally, while timesteps in the model do not correspond to any particular timescale, we interpret each step as a year for simplicity. In this interpretation, our assumed microbial conditioning rate $c$ of 0.2 indicates that a patch becomes host-conditioned after 5 years, and our assumed decay rate $d$ of 0.25 indicates that microbial legacies in unoccupied patches decay over 4 years – estimates that are generally consistent with empirically measured rates of microbial conditioning and decay (Ke & Levine 2021; Magee *et al.* 2025). The historic fire frequency in grasslands and savannas can range from every 1-5 years to decadal intervals (Frost 1993; Stambaugh *et al.* 2011), so we consider high frequency fire in this model 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.

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**Table 1:** Model parameters and values used in simulations (unless otherwise indicated)

| **Parameter** | **Units** | **Value** | **Definition** |
|---|---|---|---|
| $r_g$ | time$^{-1}$ | 1.00 | Grass establishment rate |
| $r_s$ | time$^{-1}$ | 1.55 | Woody establishment rate |
| $\mu_g$ | time$^{-1}$ | 0.10 | Grass mortality rate |
| $\mu_s$ | time$^{-1}$ | 0.10 | Woody mortality rate |
| $d_g$ | time$^{-1}$ | 0.25 | Grass microbial decay rate |
| $d_s$ | time$^{-1}$ | 0.25 | Woody microbial decay rate |
| $c_g$ | time$^{-1}$ | 0.20 | Grass conditioning rate |
| $c_s$ | time$^{-1}$ | 1.55 | Woody conditioning rate |
| $m_{\text{gg}}$ | unitless | 0.90 | Impact of grass microbial community on grass establishment |
| $m_{\text{gs}}$ | unitless | 1.00 | Impact of woody microbial community on grass establishment |
| $m_{\text{sg}}$ | unitless | 1.00 | Impact of grass microbial community on woody establishment |
| $m_{\text{ss}}$ | unitless | 1.10 | Impact of woody microbial community on woody establishment |

## 3.2. Plant community dynamics in the absence of fire

Varying $m_{ii}$ values in the model lead 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. 2A), which generates a woody-dominated system. The time series in Fig. 2B and C show the dynamics of each of the ten patch types under different scenarios of microbial impacts on plant establishment. These are aggregated by plant species to generate grass and woody plant ending frequencies throughout the results.

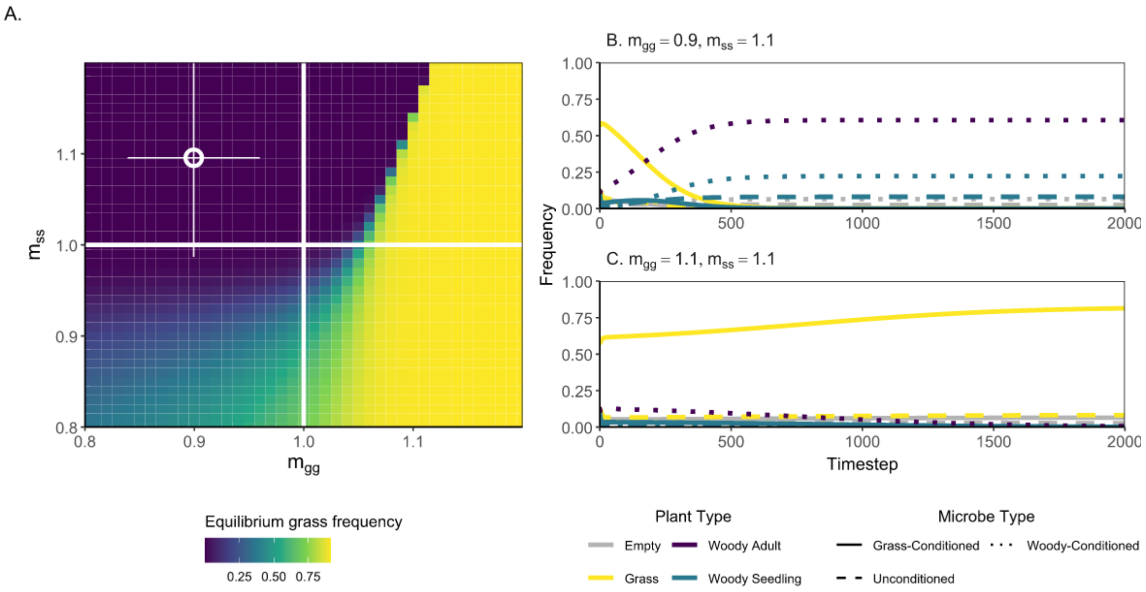

**Figure 2: Impacts of microbially mediated patch establishment on grass-woody plant dynamics.** Panel **A** shows the ending grass frequency across combinations of $m_{gg}$ and $m_{ss}$. The white point and standard errors show the results of a meta-analysis of $m_{ii}$ values from grass and woody plant species that have been observed 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 ending grass frequencies in panel A, the sum of the frequencies of each grass patch type ($m_{g0}$, $m_{gg}$, and $m_{gs}$) were averaged over the last 50 timesteps. These simulations show model dynamics for $r_g = 1$ and $r_s = 1.5$; values used for other parameters are provided in Table 1. See Supplement S3 for an exploration of $r$ values on model behavior. See Supplement S4 for an exploration of initial patch frequencies on model behavior when grass and woody microbes both self-facilitate as in Panel **C**.

## 3.3. Microbial mediation of fire impacts on plant communities

For our chosen parameter values (Table 1) and fire sensitivities (Fig. 1B–C), frequent and low-intensity fires are necessary to maintain grassy communities even in the absence of microbial feedbacks (top row of Fig. 3). As woody adults become less sensitive to fire across the three different fire sensivity scenarios we explore, 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 (Fig. 3A; see Supplement S5 for impacts of fire regime on woody plant frequency), and when woody plants are less prone to fire-induced mortality 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 Fig. 3) except when woody adults are totally insensitive to fire (rightmost column of panels; see Supplement S5).

Our empirically estimated measures of microbial impacts on plant performance indicate that microbial effects further reduce the fire regimes under which grass is maintained (bottom row of Fig. 3). 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 sensitive to fire than grasses (Fig. 3E–F), the fire intervals that maintain grassiness must be far more frequent under microbial mediation of plant dynamics.

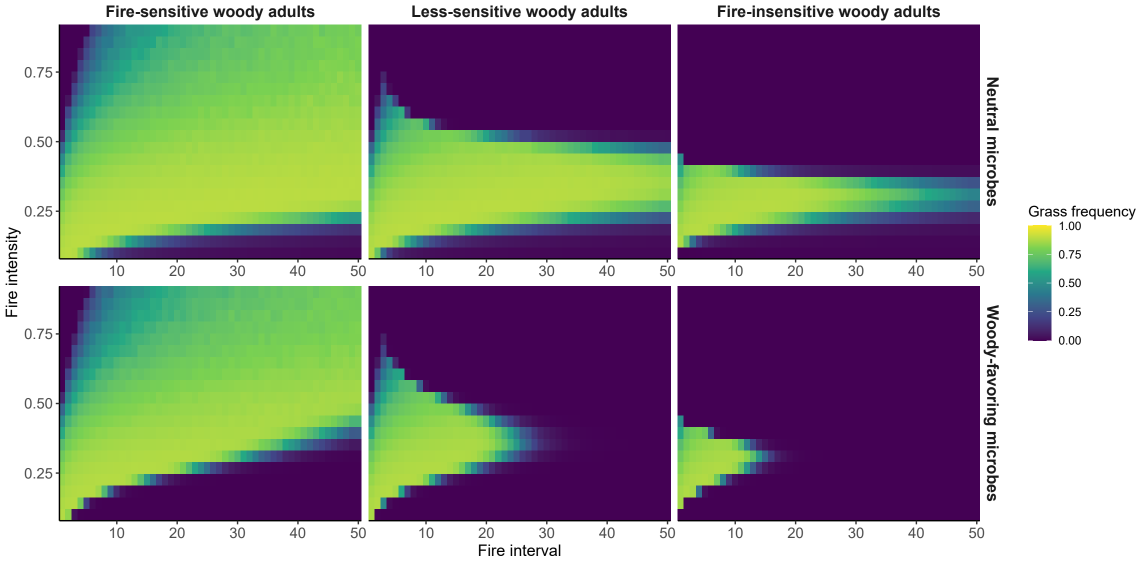

**Figure 3: Woody plant-facilitating microbial feedbacks restrict the fire regimes that permit grass persistence**. Each panel shows grass frequencies at 2000 timesteps under variable fire regimes (varying fire frequency and fire intensity within each panel) and under varying effects of fire on woody 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 bottom row show grass frequencies assuming that microbes generate positive feedbacks for woody plants and negative feedbacks for grasses, as indicated by our meta-analysis (Supplement S2, $m_{gg} = 0.9; m_{ss} = 1.1; m_{gs} = m_{sg} = 1$) In Panel **A**, mature woody plants are as susceptible to fire-induced mortality of a given intensity as grasses (as in Fig. 1B). In panel **B**, woody adults are half as susceptible to fire-induced mortality as grasses (as in Fig. 1C). In panel **C.** 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, indicating a high frequency of patches occupied by woody plants and with woody-conditioned soils), and evaluated the temporal dynamics of grass recovery under different low-intensity fire regimes (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 the top row of Fig. 4). Moreover, we find that woody-favoring microbial effects substantially constrain the fire regimes under which grassy restoration is possible, regardless of whether microbial feedbacks provide only provide a small benefit to woody plants ($m_{gg} = 0.9; m_{ss} = 1.1$, as indicated in our meta-analysis; Fig. 4B) or strongly benefit woody plants ($m_{gg} = 0.75; m_{ss} = 1.25$, Fig. 4C). In Figure 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 (shown in Supplement S6).

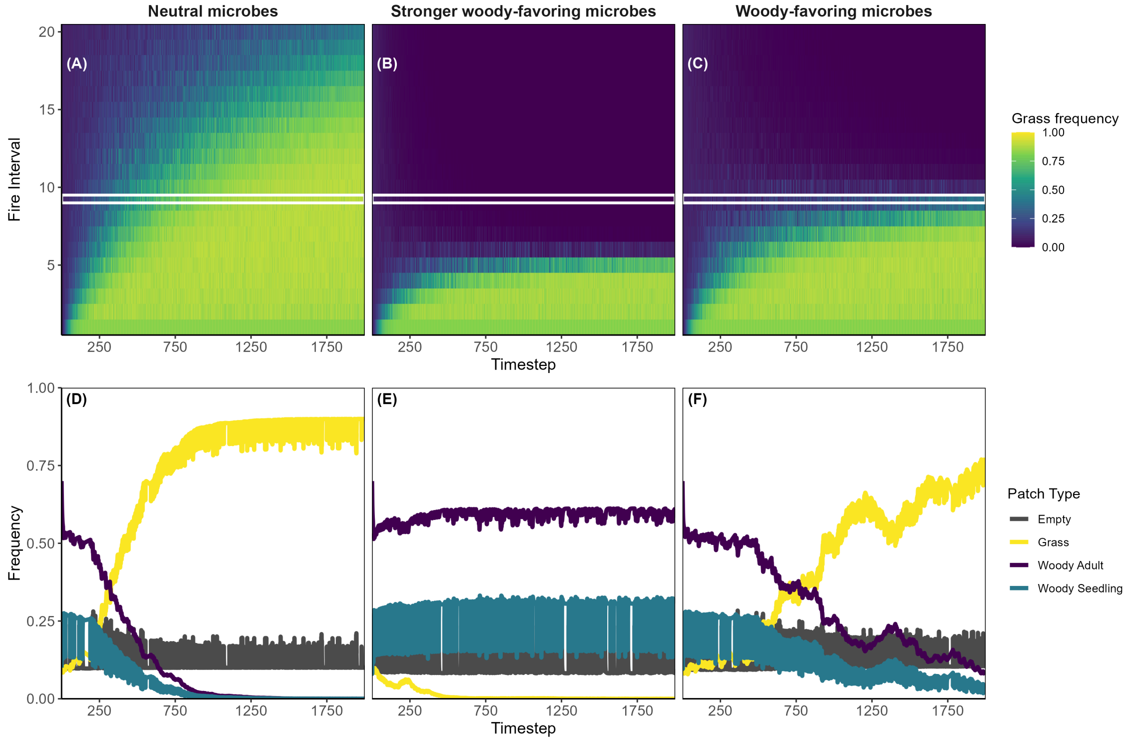

**Figure 4: Dynamics of grass recovery after woody encroachment under variable fire regimes and varying plant–microbe interactions.** Panels **A**–**C** show overall grass frequency over time (*x*-axis) under variable fire intervals (*y*-axis), assuming microbes give rise neutral or woody-favoring feedbacks. In Panel **A**, $m_{gg} = m_{ss} = 1$; in panel **B**, $m_{gg} = 0.75$ and $m_{ss} = 1.25$; Panel **C**, $m_{gg} = 0.9$ and $m_{ss} = 1.1$. Panels **D**-**F** illustrate time-series of grass and woody plant dynamics at a fire interval of 8 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 Supplement S6 for dynamics under other scenarios of woody adult sensitivity to fire.

## 4. Discussion

Woody plant encroachment is widespread in herbaceous communities worldwide, with important implications for biodiversity and ecosystem functioning. Here we developed a novel theoretical framework to evaluate the interactive roles of plant–microbe interactions and wildland fires in shaping the dynamics and reversibility of in woody encroachment. Our model, combined with realistic estimates of plant–microbe interactions derived from experimental studies, suggests that woody plant-favoring soil microbial feedbacks are common (Fig. 2), and can sharply constrain the fire regimes under which grassy communities are maintained (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. We therefore echo recent calls in the literature to better understand how plant communities are shaped by the interactive impacts of soil microbial feedbacks and of disturbances like fire (Kardol *et al.* 2022; De Long *et al.* 2018).

Previous models of savanna-forest transitions have emphasized the role of stochastic fire in maintaining a grassland state, particularly in less arid climates. These have mostly focused on vegetation-fire feedback, in which fire properties like frequency, intensity, or percolation depend on vegetation structure (Baudena *et al.* 2009; D'Odorico *et al.* 2006; Magnani *et al.* 2023). Our results suggest that qualitatively similar dynamics regarding the importance of fire for the maintenance of grassy vegetation can also arise due to plants' conditioning and responding to the soil environment. Although we center soil microbes as the primary drivers of this process, plant impacts on abiotic properties of the soil, including those that are commonly evaluated under the "fertile island" framework for woody plant encroachment (e.g., soil texture, nutrients, and hydrology; Schlesinger *et al.* (1996)), could in principle give rise to similar outcomes, 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 empirical observations of higher frequency fire regimes than the historic norm being necessary for grassland restoration in some cases (Case & Staver 2016).

Although we parameterized our model with estimates grounded in empirical data wherever possible, 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-prone 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-shrub interactions ($m_{gs}$ and $m_{sg}$ in our model). For example, out of 666 pairwise interactions in a recent meta-analysis of pairwise plant–soil feedback, only 26 directly evaluated feedbacks between an herbaceous and a woody plant species (Yan *et al.* (2022); See Supplement S2). Our analysis of grass recovery after woody encroachment suggests that the exact nature of these interactions in a given community of concern can sharply impact the success of fire in restoring grassy states. This underscores the value of explicitly measuring these interaction strengths, along with conditioning and decay rates.

Our results suggest several further avenues for future theoretical research that are likely to yield important insights. First, our numerical simulations assume 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; Govender & Van Wilgen 2006; Waldrop *et al.* 1992). 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. 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 strongly favor woody plants, sufficiently frequent fires can drive grassy dominance (Fig. 4c). Our framework can be readily extended to project the consequences of other exogenous, pulsed disturbances like tornados (Nagendra and Peterson 2016). In such systems, understanding rates of microbial conditioning and decay relative to the frequency of 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 saltwater intrusion and sea level rise on plant community shifts, where soil-mediated processes have been identified as potential contributors to shrubification (Ury *et al.* 2021).

Overall, the findings presented here have important implications for the study and management of woody plant encroachment. We show that woody-favoring soil microbial conditioning 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-prone 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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