



Plant-soil feedback in the ‘real world’: how does fire fit into all of this?

P. Kardol · T. Yang · D. N. Arroyo · F. P. Teste

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Abstract

Aims Plant–soil feedback (PSF) is an important mechanism controlling plant growth, vegetation dynamics, and longer-term and larger-scale patterns of plant community diversity. We know that feedback between plants and soil biota depends on several external factors, such as nutrient and water availability, and interactions with neighbouring plants. We argue that in the ‘real world’, PSF are not working in isolation but instead proceed within a complex context of multiple interacting factors. Fire is one of those complex external factors which could greatly

alter PSF by re-setting or re-directing plant-soil biota interactions.

Methods We reviewed key literature on the effects of fire on soil biota and soil physicochemical properties with soil depth, to generate predictions on the complex effects of fire on PSF.

Results We highlight that fire has strong potential to directly and indirectly affect the strength of PSF. To what extent this influences longer-term plant community trajectories depends on the interactions between fire characteristics and ecosystem type. Here, we conceptualized these effects of fire on soil properties and biota, and then discuss the main pathways through which fire should alter PSF.

Conclusions We think that PSF processes should be nullified under and after fire. Average neutral PSF responses are expected to be more common in the short-term or within the timeframe required for major soil microbial players to regain their pre-fire abundances and diversity. We conclude by providing directions for future research and possible methods to study fire effects on PSF both in the field and under controlled conditions.

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P. Kardol
Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden

T. Yang · F. P. Teste (✉)
Swift Current Research & Development Centre,
Agriculture and Agri-Food Canada (AAFC),
Swift Current, SK, Canada
e-mail: francois.teste@agr.gc.ca

D. N. Arroyo
Instituto Nacional de Tecnología Agropecuaria (INTA),
Estación Experimental Agropecuaria (EEA) San Luis,
Villa Mercedes, Argentina

F. P. Teste
Instituto de Matemática Aplicada de San Luis (IMASL),
CONICET, Universidad Nacional de San Luis, San Luis,
Argentina

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Introduction

Plant-soil feedback (PSF) is a mechanism in which plants modify their surrounding soil, which then feeds back to affect plant growth (van der Putten et al. 2013). Particularly well studied, is how individual plant species change the composition of their root- and litter-associated soil biota and how this in turn affects plant growth (Bever 1994; Bever et al. 1997): biotic PSF. These biotic PSF play a role in temporal trajectories of plant community composition, and are important for the spatial structure and maintenance of plant diversity (Bennett et al. 2017; Teste et al. 2017; van der Putten 2017). We do, however, still know little about how external factors influence PSF (De Long et al. 2019; Gundale and Kardol 2021).

Fire has long been one of the main abiotic disturbances of arid to sub-humid ecosystems (Kunst et al. 2014; Tálamo and Caziani 2003). With an increase in frequency and intensity of fires and a longer ‘fire season’, as forecasted by climate change models and observational evidence (Boer et al. 2020; Covington and Pyne 2020; Goss et al. 2020; Jolly et al. 2015; Rogers et al. 2020), a better understanding of its interactive roles with soil-driven processes is in high demand. This is particularly relevant, because fire now also occurs in biomes where fire used to be rare, such as the Arctic tundra and Amazonian forests (Covington and Pyne 2020). We know that fire typically triggers shifts in plant communities and that fire in the short-term promotes plant diversity (Kelly et al. 2020). We also know that at larger spatio-temporal scales, fire creates landscape heterogeneity: pyrodiversity (Jones and Tingley 2022; Martin and Sapsis 1992) (Fig. 1). However, we still lag far behind in our understanding of how fire affects soil biota involved in PSF, and there are very few studies on the impact of fire on PSF in any ecosystem (De Long et al. 2019). Hence, burning questions remain. For example, can we predict how shifts in soil microbial and faunal communities due to transient, but drastic increases in soil temperatures modify the strength or direction of PSF? And, in which ecosystems do fire effects on soil biota play out the strongest?

A large variety of direct and indirect effects of fire can alter the functions of soil microbial and faunal communities, particularly those associated with surface litter and those living in the upper layer of the soil, including soil organisms associated with plant

roots. Fire can directly kill soil biota by flames, or excessive heat or smoke. Direct effects of fire can also result from habitat loss. Indirect effects of fire on soil biota are practically endless, yet are typically caused by changes in soil physicochemical and biological properties. However, our aim in this Opinion paper is not to review the complex and variable effects of fire on soil biota as recently done by Certini et al. (2021), Barreiro and Díaz-Raviña (2021), and Köster et al. (2021) but to focus on certain well-documented effects that can reverberate themselves on PSF processes. In particular, we propose a framework that helps understanding how the short (i.e. < one year) and long-term (i.e. > 5 years) effects of fire reach out further by altering PSF. We discuss how the characteristics of fires within a given ecosystem, notably the intensity and frequency, are paramount to altering PSF processes. We then outline how we think fire-induced shifts in soil properties and soil microbial and faunal communities can lead to potentially long-lasting shifts in PSF. Finally, we suggest a way forward to explicitly include fire in future PSF studies.

Direct effects of fire on soil biota

Flames and high soil temperatures induced by fire can directly damage cell structure, and hence, kill soil biota (Certini et al. 2021; Pressler et al. 2019) (Fig. 2). This is particularly obvious for organisms living in the litter layer, which is often entirely consumed by fire. Yet, fire can also increase temperatures at the soil surface and sometimes at deeper soil depth to levels lethal for organisms (Fig. 2). Temperature thresholds are under debate (Pingree and Kobziar 2019), but some studies have shown that lethal soil temperatures for soil microbes can be as low 60 °C for about one minute (DeBano et al. 1998). Regardless, fire can massively reduce microbial biomass in the upper soil layers, and to a lesser extent in deeper layers (Certini et al. 2021). For example, in Mediterranean forest ecosystems, fire can instantly consume up to 65% of the soil organic matter (Granged et al. 2011). These direct effects of fire on soil biota are, however, stronger for some groups than for others. Here, we can adopt knowledge from studies on climate extremes which have shown that plants and different groups of soil biota vary in their temperature

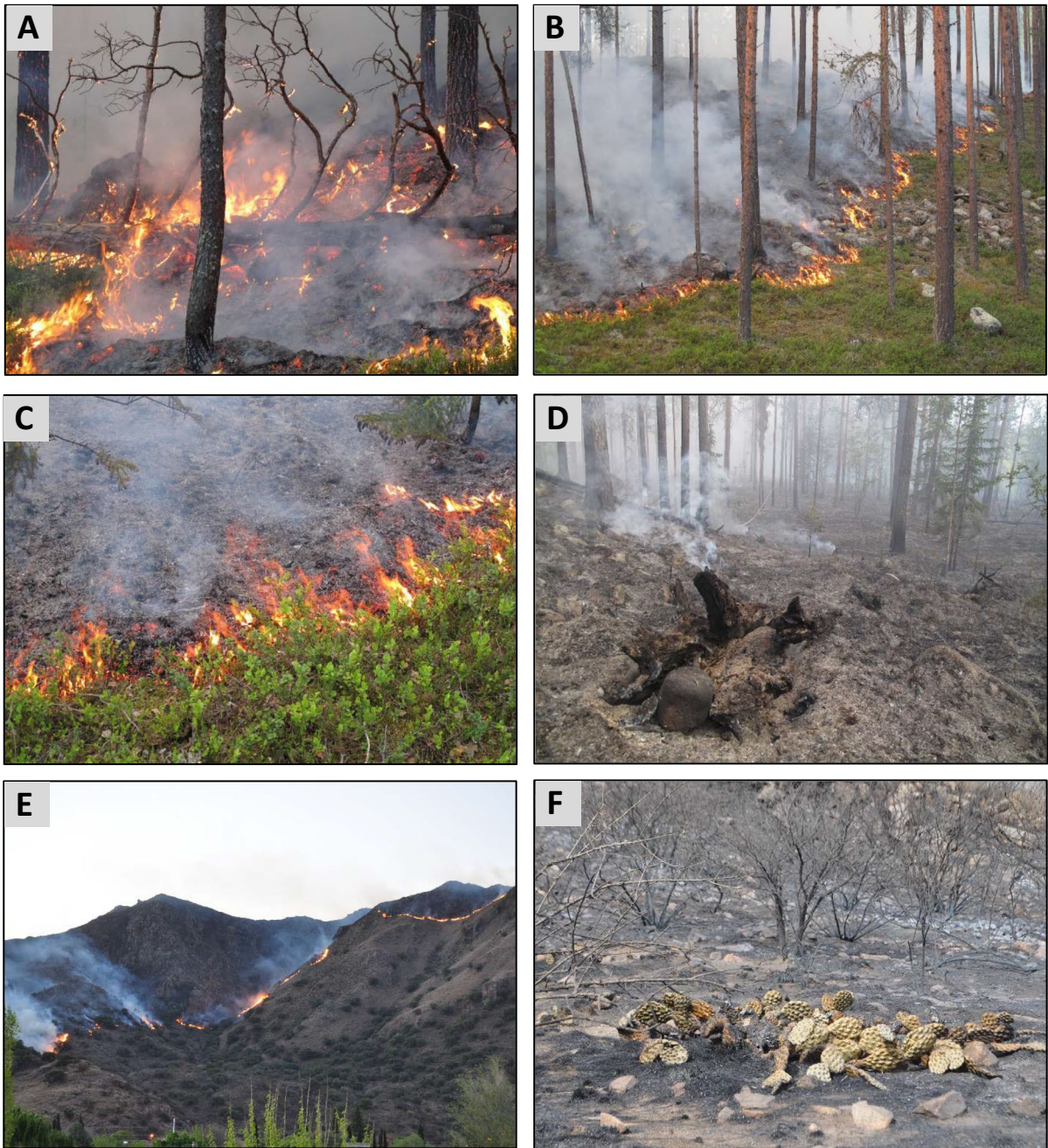


Fig. 1 Examples of natural and prescribed fires. Panels A to D: Prescribed fire in a boreal forest at ‘Ecopark’ Kåringberget, northern Sweden ($64^{\circ}06'11''\text{N}$, $18^{\circ}39'05''\text{E}$). The low-intensity fire consumed coarse woody debris, the understory vegetation, and parts of the litter and organic layer but not the overstory trees. Panels E to F: Natural fire in a dry grassland transition to dry Chaco forest near San Luis, Argentina ($33^{\circ}16'25''\text{S}$, $66^{\circ}15'54''\text{W}$). This fast-moving fire only consumed the fine understory components (i.e., woody debris, litter, and small

plants). Most plant species survived even though the fire killed most of their aerial parts, except relatively tall shrubs and trees. Recovery rates for soil biota can vary greatly. For example in boreal forest (A) or oak-pine humid forest, recovery can be very slow lasting up to 14 years, while in highland grasslands (E) or dry forest (F) recovery is expected within a year (Barreiro and Díaz-Raviña, 2021; Köster et al. 2021). Photos: Paul Kardol and François P. Teste

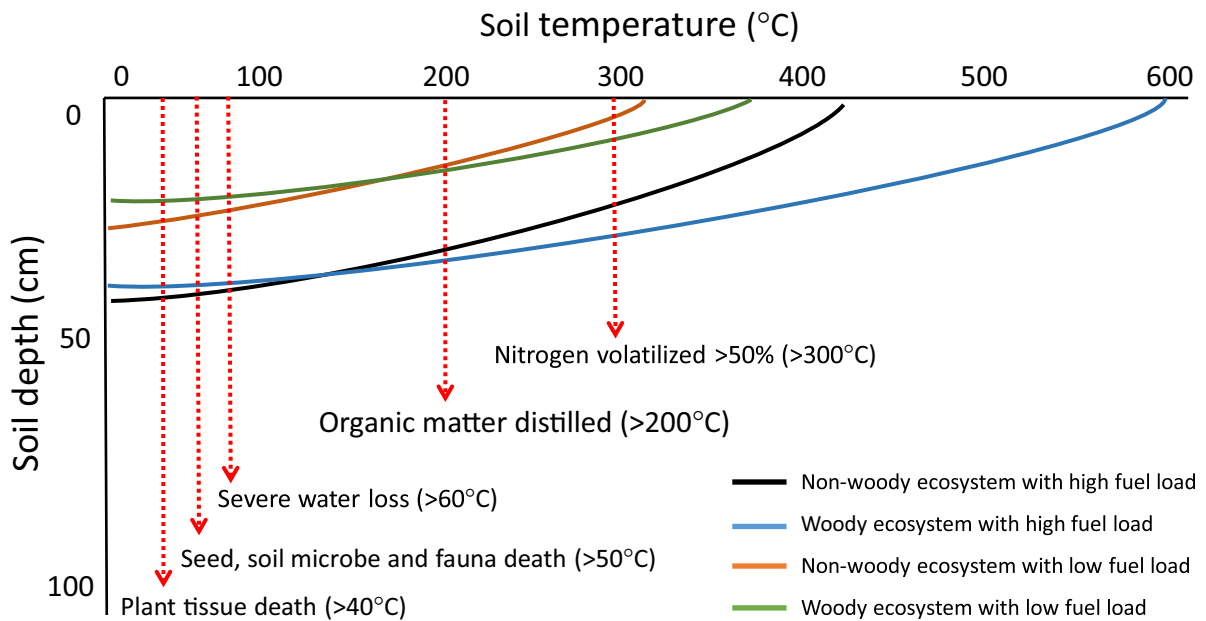


Fig. 2 Hypothesized direct effects of fire on soil temperature in relation to soil depth for contrasting types of ecosystems based on previous studies (Benscoter et al. 2011; Campbell et al. 1995; Carrington 2010; Hungerford et al. 1991; Stoof et al. 2013). Vertical red-dotted arrows indicate threshold temperatures for some of the main drivers and components of PSF: organism responses and soil properties. We generalized these

findings to outline that large soil temperature changes can happen with fire effects on soil biotic and abiotic properties being most prominent in the upper soil layer (≈ 0 –25 cm; depending on the type of ecosystem) with less severe impacts at lower soil depth since heat transfer attenuates sharply with soil depth (Fairbanks et al. 2020; Qin and Liu 2021)

tolerance and sensitivity (Thakur et al. 2022) – fire can be seen as an extreme case of a climate extreme.

It has been suggested that soil bacteria are typically less affected by high soil temperatures than soil fungi, and that fire has particularly negative effects on mycorrhizal fungi (Bowd et al. 2022b; Pattinson et al. 1999; Treseder et al. 2004). However, it remains a challenge to draw general conclusions from these patterns since there are heat-resistant fungi (Day et al. 2020) and some mycorrhizal fungi may survive fire through resting spores or compacted hyphae (e.g. sclerotia). Furthermore, some fungi position their mycelial network deep in soil away from fire effects or can extend into unburnt patches, or in intact plant roots (also see *Indirect effects* below) (Hewitt et al. 2017). Direct effects of fire on soil fauna are also typically negative but strongly depend on where they live (e.g., litter or deeper soil layers), their mobility, and the fire season (e.g., during their reproductive or dormant phase) (DeBano et al., 1998; Mantoni et al. 2020; Pingree and Kobziar 2019). Litter-dwelling fauna are (obviously) most likely to be affected. In

summary, the direct effects of fire on soil biota can influence the strength and direction of PSF through: i) changes in microbial and faunal biomass (population size), and ii) shifts in soil microbial and faunal community composition (Fig. 3).

Indirect effects of fire on soil biota

Fire can also indirectly affect soil biota (Bowd et al. 2022a, b; Certini et al. 2021; Pressler et al. 2019; Qin and Liu 2021; Singh et al. 2021; Terzano et al. 2021), and hence, PSF (Fig. 3). Arguably the most important indirect effects of fire on soil properties are the loss of litter and transformation of soil organic matter, shifts in pH, nutrient availability, moisture retention, and soil texture (DeBano et al. 1998; Pereira et al. 2019). Here, fire-derived charcoal further influences abiotic soil properties, such the absorption of phenolic compounds (Hart and Luckai 2013; Makoto et al. 2011; Zackrisson et al. 1996). We know these abiotic soil properties are all important drivers of

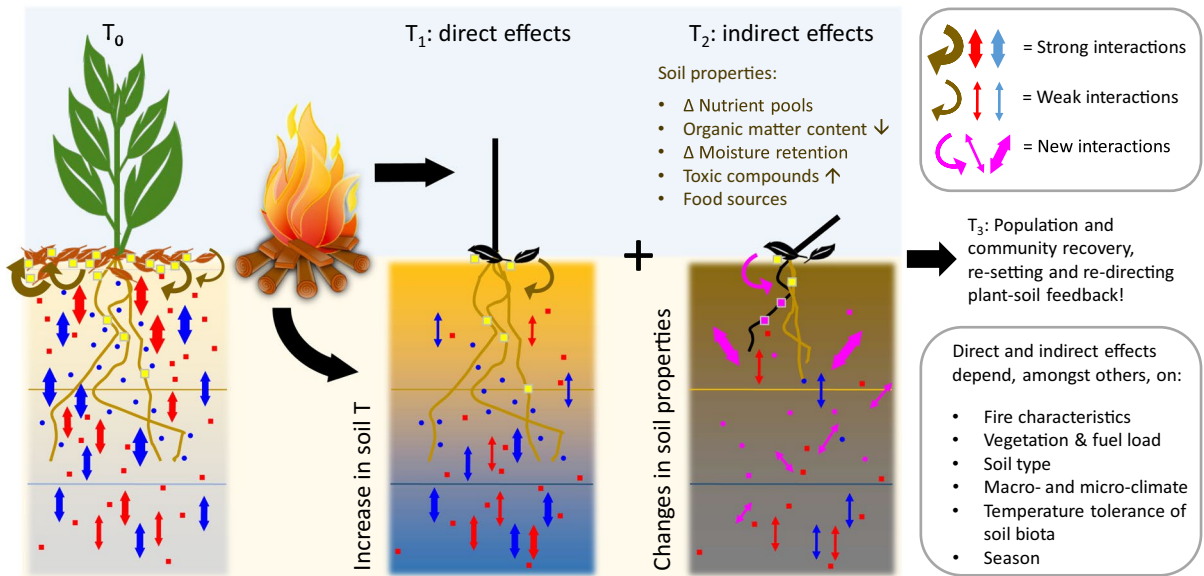


Fig. 3 Conceptual diagram showing multiple pathways of how fire can affect plant-soil feedback (PSF). Direct and indirect effects of fire together alter plant-soil biota interactions with consequences for PSF. Reductions in biomass and population sizes of soil biota (indicated by red squares and blue dots) and litter-associated biota (indicated by yellow squares) resulting from flames and increase in soil temperature weaken positive and negative rhizosphere-mediated feedback interactions (indi-

cated by blue and red arrows) as well as litter-mediated feedback interactions (indicated by brown arrows). Indirect effects through changes in soil properties alter feedback by shifting the composition of soil communities (indicated by magenta dots and squares), leading to new interactions between plants and soil biota (magenta arrows). Changes in soil properties include, amongst others, shifts in soil chemistry, micro-climate, and food sources

soil communities. For root-associated soil biota, fire effects on their host plants (e.g., survival, post-fire re-sprouting) are likely even more important (Nearby et al. 1999). In many (or most) cases, fire does not kill all plants, particularly not in ecosystems that are adapted to regular fire events. Some plants protect their meristems by thick bark, gemmiferous roots, or subterranean organs like tubercles in woody plants and scales in semi-buried shoot buds in grasses (Kauffmann, 1990; Steuter and McPherson, 1995; Stephan et al., 2010). Plants may also re-sprout from roots at deeper soil layers that would be less or not at all affected by fire (Kauffmann, 1990). These plant traits and post-fire processes often leave a residual pool of root-associated soil biota in the rhizosphere soil shortly after fire (Dahlberg 2002).

These indirect effects of fire through changes in soil abiotic properties and host plant performance can outweigh the direct effects of fire on soil biota, in particular on the longer-term. This is likely the case since the list of potential indirect effects of fire on soil biota is virtually endless. Here, we just mention

a few of these indirect effects that we think are well documented and that are likely to alter PSF. For example, elevated temperatures lead to higher water evaporation rates from the soil surface and this can increase soil water repellency (Arcenegui et al. 2008). Fire-induced changes like this will have major effects on the abundance and composition of the soil biota of which many rely on organic matter as food source and on water for survival and movement. However, it is not easy to generalize the effects of fire on these key soil properties (e.g., soil moisture content). What remains to be shown is which of these effects of fire on soil properties are strong enough to modify PSF strength and direction, and when these effects matter most.

Follow-through effects on plant-soil feedback

For effects of fire on PSF, we can first consider the ‘immediate’ effects resulting from selective reduction in abundance and biomass of associated groups of soil

microbes and soil fauna, i.e., the direct effects of fire on soil biota. These immediate effects would reduce the pool size of soil biota and, hence, would reduce the *strength* of both positive and negative feedback effects (Fig. 4), for the plants that survived the fire (e.g., trees not affected by a ground fire, or perennial herbs re-sprouting from unaffected rhizomes, tuberous roots, or bulbs) as well as for plants that quickly colonize after fire through dispersal or through germination of seeds from the seed bank (e.g., species that require fire for their seeds to germinate). How much the direct effects of fire on PSF reduce the strength of PSF, will depend on the net balance of fire effects on positive vs. negative feedback effects (Fig. 4). Still,

fire can also have longer-term effects on PSF, particularly intense fires, resulting from prompt changes in soil properties, i.e., the indirect effects (Fig. 4). Here, things get more complex as these indirect effects would not only alter the strength of PSF but could also *re-set* and *re-direct* PSF as taxa or groups of soil microbes and soil fauna differ in their recovery tactics and rates after fire (Fig. 4). This partly also depends on how and how fast the plant community recovers after fire. So, the challenge inherent to PSF research of who-drives-who also applies here.

Soil microbes and fauna exhibit great variation in their reproductive cycles. As such, it has been argued that bacterial communities recover rapidly

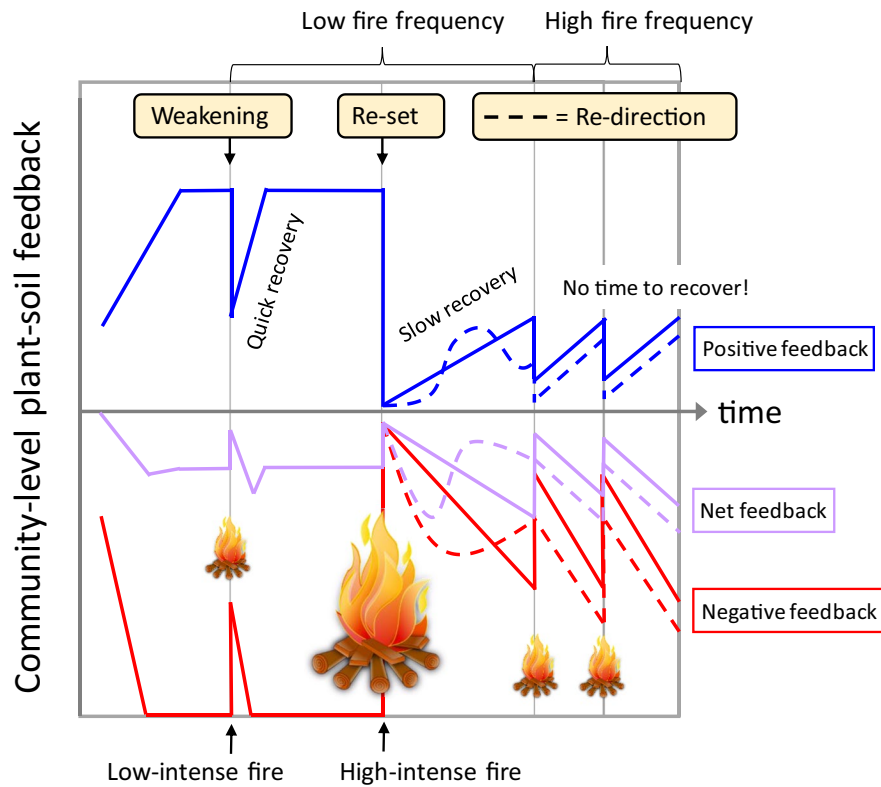


Fig. 4 A hypothetical scenario illustrating the longer-term consequences of effects of fire on plant-soil feedback (PSF). Starting from scratch (e.g., in case of primary succession), positive and negative feedbacks build up, often resulting in net negative feedback at the plant community level, maintaining community diversity (De Long et al. in this Special Issue). Here, net feedback is the result of additive effects of positive and negative feedbacks. Low-intense fire weakens PSF but may have little consequences on the longer term as communities can quickly recover. High-intense fires, on the other hand, can

drastically influence the role of PSF in plant community structure by re-setting feedbacks to (almost) zero, with slow rates of recovery. After a re-set, it is also possible that PSF will be re-directed as new plant-soil biota interactions establish under altered micro-climatic and soil conditions. High fire frequency, as predicted under future climate, would not allow PSF to recover to initial values. If soil pathogens recover faster than soil mutualists, then this could lead to more negative new feedback. Other scenarios are possible

after fire. For example, some bacteria produce resistant endospores that can tolerate and survive high soil temperatures (Lucas-Borja et al. 2019). Also, shifts in the composition of rhizosphere bacteria, including Firmicutes and Acidobacteria, have been linked to PSF effects in *Panax notoginseng* (Luo et al. 2019). These rhizosphere bacteria appeared to have strong antagonistic effects on soil-borne pathogens; thus reducing the strength of negative PSF, compared to when these bacteria were not abundant. The recovery of many other groups of soil microbes and soil fauna depends on the post-fire abiotic soil properties (which are sometimes very different from the conditions before fire; see above), and their motility and dispersal rates. Here, the differential recovery of microbial and faunal taxa can influence the performance of the plants colonizing after fire, and hence, re-direct PSF; in which case the soil biota are the drivers. However, there are also scenarios where plants take the driver's seat in steering PSF after fire. For example, root-associated biota, such as mycorrhizal fungi, depend on plant development and specialized saprotrophs involved in litter-mediated PSF (as in the case of home-field advantage effects (Veen et al. 2019) depend on specific plant litter input; in those cases the plants are the drivers. Here, it is interesting to imagine how soil biota recolonize from nearby unburnt patches (hyphal growth) or by active or passive dispersal from local pools. In this context, it has been suggested that saprotrophs need less time to recover after fire compared to mycorrhizal fungi (Holden et al. 2016; Treseder et al. 2004). Notably, Senior et al. (2018) showed that fire weakened the positive PSF for *Eucalyptus* trees, possibly because of disruption of associations with arbuscular mycorrhizal and ectomycorrhizal fungi. As for soil-borne pathogens, their diversity is considerably knocked-back after fire (Beals et al. 2022). However, a study in a pyrodiverse dry-sclerophyll forest found that pathogens are relatively more abundant shortly after fire compared to other soil microbial groups (Bowd et al. 2022b). The speed of recovery and built-up of pathogen propagules after fire remains poorly documented, thus a gap to fill to better understand and predict how fire can delay the return of negative PSF.

So far, how fire influences PSF, on the short term and on the long term, remains mostly untested. Scarce data on the impact of fire on PSF leads to a potentially biased view of the role of PSF in the 'real world' that

will burn more often and more intensely, yet only until fuel loads are high enough to maintain intense fires. Accordingly, it is also important to understand how other disturbances (i.e. grazing) interact with fire regulating the role of fuel accumulation that affects both fire intensity and frequency. In ecosystems that burn more intensely or more frequently, PSF processes may be re-set every now and then (Fig. 4), and hence, only play a modest role in structuring plant communities on the long term and a weak role in maintaining plant community diversity (Teste et al. 2017). On the other hand, in 'slow' systems, such as boreal forests, it may take many years or decades for some soil biota to fully recover from intense fires (Bokhorst et al. 2017); therefore, strong shifts in PSF strength and direction are also possible. Given what is currently known about the effects of fire on soil biota, we predict that fire, particularly intense fires, will cause sudden and large shifts in the direction and strength of PSF in ecosystems dominated by woody plants. We expect a near-complete reversal of the direction of PSF in ecosystems that host fire-adapted mutualistic microbes (e.g., N_2 -fixing bacteria) coupled with a considerable reduction in soil-borne pathogens, as seen in temperate deciduous forests of the USA (Beals et al. 2022). As for litter-mediated PSF, we would expect minor changes since dominant bacterial groups involved in decomposition and nutrient-cycling processes are not severely affected by fire. On the other hand, major changes could result if fire is intense enough to burn off humus and organic layers of the soil. Furthermore, the magnitude of PSF strength could be affected when fungal saprophytic communities are less diverse after fire (Beals et al. 2022), while in drier forests, saprophytic fungi tend to be promoted (Bowd et al. 2022b). The many interacting components underlying PSF responses under and after fire, does nevertheless point to a nullified effect, that is overall and average neutral PSF in the short term or within the timeframe required for major soil microbial players to regain their pre-fire abundances and diversity (Fig. 4). Cycles of returning microbial communities would be relatively quick in pyrodiverse dry vegetation (e.g., Australian *Eucalyptus* or Chaco forest) compared to wetter, less commonly fire-disturbed forests (e.g., coastal temperate forest of the Americas).

To what extent fire affects PSF and how this influences longer-term plant community dynamics and

patterns of plant diversity depends on a large number of factors, i.e., context-dependency. This makes drawing generalization difficult. We now discuss two of the main factors to provide guidance in how to further explore this area of research: vegetation or ecosystem type and fire characteristics (frequency, intensity, and duration). First, how heat transfer affects the downward propagation of combustion, and if and how fire increases soil temperature, strongly depends on soil properties. Here, soil organic matter content, soil texture, and moisture content are all important drivers (Benscoter et al. 2011). For example, soil temperature could easily exceed over 400 °C within the first 120 min after fire ignition, especially in top 10 cm layer of organic soils (Benscoter et al. 2011). Comparatively, mineral soils are poor conductors of heat. The soil texture before a fire also influences the temperatures that the soil reaches at different depths (level and rate of warming). For example, very sandy soils have a higher heat transfer capacity, thus soil temperature in top layers during the first hours of fire can be much higher compared to clay or silty soils (Akter et al. 2015); this also implies that sandy soils can reach higher soil temperatures in a shorter period of time (Akter et al. 2015). Further, while water conducts heat very well (much better than air), considerable thermal energy is lost through evaporation; hence, effects of fire on soil biota are expected to be greatest in dry soils. Together, this suggests fire most strongly re-sets or re-directs PSF when fire hits ecosystems with thick organic layers on sandy soils after extended periods of drought. A good example is the Västmanland wildfire in east-central Sweden on 31 July 2014 that burned down a large area of boreal forest (Gustafsson et al. 2019; Ibanez et al. 2022). Here, Ibanez et al. (2022) showed that detrimental effects of severe fire on soil biota may negatively affect the post-fire regeneration of conifer seedlings, but not of broadleaf seedlings. Differential effects on post-fire seedling performance through disruption of plant-soil biota interaction may have long-term consequences for trajectories of forest development.

Looking into the future, what are the different scenarios? For this, we should weigh up how vegetation type interacts with fire characteristics and how climatic changes play into this. Here, we would need to project fuel loads under future climatic conditions. Ecosystems with multi-layered vegetation and mixed plant communities including moss, herbs,

shrubs, and trees more readily develop high fire intensity because they have varying proportions of fuels: fine fuels (diameters < 0.5 cm) that start fires by burning rapidly, and medium and coarse fuels (diameters > 0.5 cm) that burn for a considerable time after passing the main fire front. These medium and coarse fuels are responsible for the strongest impacts (Bradstock et al. 2010; Keeley 2009; Keeley and Syphard 2019) leading to higher soil temperature reaching deeper into the soil profile (Daigneault 2014), and hence, stronger impacts on PSF. As fires become more frequent and more intense (Keeley and Syphard 2019), we expect greater impact on the relevance of neutral PSF in a greater number of ecosystems. As such, ecological scenarios that combine high fuel load in fire-prone ecosystems (e.g., due to human fire suppression or greater local inter-annual climate variability) will most severely re-set PSF processes. For example, a diverse plant community that historically would have exhibited strong negative PSF effects for most of its plant species (Klironomos 2002; Reinhart 2012), may now tend to produce more neutral or positive PSF if fire intensity reduces soil-borne pathogens (D'Ascoli et al. 2005; Hart et al. 2005; Holden et al. 2016). On the other hand, increased fire frequency as predicted under global change scenarios may constrain the build-up of fuel and thus result in lower fire intensity. We thus expect that in the medium- to long-term, negative PSF may become once again more prominent (Fig. 4).

Towards a deeper understanding of the role of PSF in the 'real world'

In better understanding PSF under "real-world" abiotic disturbances such as fire, we need well-designed field experiments based on how fire influences natural ecosystems. This will lay the foundation to a more comprehensive understanding of the role of PSF after fire in structuring and maintaining plant community composition and diversity. We provide what we think remains to be tested in the field and which type of studies are needed to address current research gaps. We also suggest in which regions such studies and associated treatments could be applied successfully. Here, we give step-wise directions to guide future research in this area.

- 1) Pre-fire: for a range of coexisting species, quantify PSF responses in the field under realistic natural conditions by maintaining experimental units in the field that are not cross-contaminated by soil biota from neighbouring units or the surrounding. This can be done by treatments restricting exchange of soil biota (e.g., mesh barriers); these will need to be fire and heat resistant or be deployed long before the fire event and then re-used if resisted fire damage, or again installed immediately after the fire. Characterize the soil biota involved in these PSF.
- 2) Post-fire, wildfire or experimental fire treatments: repeat step 1. Where possible, measure fire effects on soil temperature and quantify fire-induced changes in soil chemistry. Experimental fires would make it possible to precisely compare effects of different fire intensities and fire frequency in a statistically robust manner, and directly link changes in soil properties to fire characteristics. On the other hand, testing PSF responses after wildfire would allow including more of the natural variation in the spatial patterns of fire (e.g., patchiness) in the experimental design. Steps 1 and 2 would be particularly suitable in grasslands, savannahs, or dry forest regions where prescribed fires could be applied and controlled relatively easily.
- 3) Compare how the strength and direction of PSF differs pre- and post-fire. Here, areas or treatments with varying levels of fire intensity and duration, and hence, differential effects on plant-associated and free-living soil biota are informative.
- 4) Monitor post-fire soil community recovery (comparing to pre-fire communities) and repeat step 3 at regular time intervals such as every year for several consecutive years or until pre-fire vegetation has mostly returned. This is much work but would nicely integrate fire and PSF in longer-term projections of plant community diversity.
- 5) Determine the relative importance of PSF for plant performance in the presence of neighbouring species. Here, for example, root-exclusion treatments can tease out the relative importance of heterospecific root competition and mycorrhizal-fungal hyphae-mediated facilitation on PSF responses. This step would only be feasible in regions with well-developed soil layers or where

rock content does not hinder the installations of the root treatments.

- 6) Test all of the above across a wide variety of globally important ecosystem types and biogeographic areas, taking into account the above-mentioned limitations. This informs about where and when interactions between fire and PSF matter most.

Slightly more complex field and glasshouse experiments including controlled fire treatments allow us to begin to determine the impact of direct vs. indirect fire effects on PSF. Here, glasshouse and lab experiments can further inform on indirect effects due to soil nutrient fluxes after a burn and elevated soil temperature. More precise temperature shifts with soil depth and its impact on soil communities involved in negative PSF responses could be tested in carefully designed field experiments with controlled burns applied to small research plots. Finally, and possibly more importantly is the need to predict the long(er)-term effects of the interaction of fire and PSF on plant species diversity. Here, simulation models can further inform if they are constructed and calibrated using the data gathered from field experiments (steps 1, 2 and 6 above). These simulation models could be used to predict long-term effects of the interaction of fire and PSF on plant community species richness and diversity (Mangan et al. 2010; Teste et al. 2017), ultimately providing the answers to long-term effects of these interactions on biodiversity.

Concluding remarks

Most of our current theoretical and applied knowledge about PSF points to its relevance in driving patterns of plant diversity in ecosystems such as grasslands, shrublands, and forests under relatively stable conditions (Mariotte et al. 2018; Gundale and Kardol 2021). However, when fire wipes out key soil microbes or all of the players in PSF processes, and transforms the abiotic environment, then all we know about how PSF structures patterns of plant community development is temporarily irrelevant. Fire will disrupt PSF by altering the composition, structure, and diversity of soil microbial and faunal communities. As fire becomes the leading natural disturbance in many types of terrestrial ecosystems, including

those ecosystems who did not or only rarely experienced fire before, there is a clear need to determine its potentially far-reaching impacts on how PSF drives long-term community dynamics. However, where should we start? Here, we made a case to go beyond simply determining the effects of fire on soil abiotic and biotic properties, but to determine how fire *interacts* with PSF. We provided several predictions of how fire can interact with PSF and how empirical research could test these predictions. Results gained from research on fire effects on PSF should increase our understanding of the speed, trajectory, and diversity of plant communities recovering after fire. Finally, these results from research on fire effects on PSF have valuable applied applications; such as to better inform the sustainable and climate-smart management of rangelands including dry forests and associated semiarid fire-prone grasslands.

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Author Contributions All authors contributed to the study conception and design. The first draft of the manuscript was written by François P. Teste and Paul Kardol and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability This work does not have any dataset.

Declarations

Conflict of interest We declare no potential conflict of interest.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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