

Arctic tundra ecosystems under fire—Alternative ecosystem states in a changing climate?

Ramona Julia Heim^{1,2}  | Adrian V. Rocha³  | Vitalii Zemlianskii¹  | Kirsten Barrett⁴ |
 Helga Bültmann² | Amy Breen⁵ | Gerald Verner Frost⁶  |
 Teresa Nettleton Hollingsworth^{7,8} | Randi Jandt⁵ | Maria Kozlova⁹ | Anastasiya Kurka¹⁰ |
 Mark Torre Jorgenson¹¹ | Simon M. Landhäuser¹² | Michael Mark Loranty¹³  |
 Eric A. Miller¹⁴ | Kenji Narita¹⁵ | Evgeniya Prvdolyubova¹⁶ | Norbert Hölzel² |
 Gabriela Schaeppman-Strub¹

Correspondence

Ramona Julia Heim
Email: ramona.heim@posteo.de

Funding information

U.S. National Aeronautics and Space Administration (NASA), Grant/Award Number: 80NSSC22K1256

Handling Editor: Robert G. Björk

Abstract

1. Climate change is expected to induce shifts in the composition, structure and functioning of Arctic tundra ecosystems. Increases in the frequency and severity of tundra fires have the potential to catalyse vegetation transitions with far-reaching local, regional and global consequences.
2. We propose that post-fire tundra recovery, coupled with climate change, may not necessarily lead to pre-fire conditions. Our hypothesis, based on surveys and literature, suggests two climate–fire driven trajectories. One trajectory results in increased woody vegetation under low fire frequency; the other results in grass dominance under high frequency.
3. Future research should address uncertainties regarding possible tundra ecosystem shifts linked to fires, using methods that encompass greater temporal and spatial scales than previously addressed. More case studies, especially in under-represented regions and ecosystem types, are essential to broaden the empirical basis for forecasts and potential fire management strategies.
4. **Synthesis.** Our review synthesises current knowledge on post-fire vegetation trajectories in Arctic tundra ecosystems, highlighting potential transitions and alternative ecosystem states and their implications. We discuss challenges in defining and predicting these trajectories as well as future directions.

KEY WORDS

climate change, disturbance, fire frequency, grasses, lichens, mosses, permafrost, plant functional types, recovery, shrubs

For affiliations refer to page 1051.

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1 | ARCTIC TUNDRA IN THE FACE OF CLIMATE CHANGE

In the face of climate change and related increases in fire occurrence, the state of the Arctic tundra biome is being re-evaluated (Armstrong McKay et al., 2022; Callaghan et al., 2022). The Arctic tundra has been a relatively stable biome, capable of withstanding perturbations during the last millennia, since reaching its current ecological state at the end of the last glacial period (Bliss et al., 1973; Dunbar, 1973). However, this is no longer the case; the Arctic is warming four times faster than the globe on average (Chylek et al., 2022; Niittynen et al., 2020; Rantanen et al., 2022). Its hydrologic cycle has intensified, with increased atmospheric moisture, precipitation, and river discharge rates (Bintanja et al., 2020; Box et al., 2019; Rawlins & Karmalkar, 2023). Increased precipitation does not always mean that Arctic ecosystems become wetter. In some regions, climate change is also leading to the drying of the ecosystem due to increased evaporation that exceeds precipitation, or due to permafrost (perennially frozen ground) thaw (Liljedahl et al., 2016; Zhang et al., 2009). Climate change impacts on Arctic tundra ecosystems thus drive permafrost degradation (Schuur & Mack, 2018), changes in vegetation productivity (Jia et al., 2003), and intensifying fire regimes (Chen, Romps, et al., 2021).

1.1 | Changes in tundra vegetation

Climate change-induced increases in temperature, moisture levels and nutrient availability may enhance tundra vegetation productivity, which is typically constrained by environmental factors (Martin et al., 2017; Mekonnen et al., 2018). These changes can also impact other processes related to the carbon cycle (Jeong et al., 2018). Under climate warming, increased shrub abundance is considered a primary factor driving enhanced productivity and vegetation community changes, especially in mesic and wet tundra habitats (Elmendorf et al., 2012). This highlights the potential for interactions among temperature, water and nutrient availability to drive shifts in plant community composition (Chapin III et al., 1995). These environmental changes resulting from climate warming are also predicted to advance the treeline from the boreal forest into the tundra (Harsch et al., 2009; Kruse et al., 2019, 2023).

Significant vegetation shifts on a local scale have wide-ranging impacts on biodiversity (Wallace & Baltzer, 2020), habitat structure (Ims et al., 2019), and ecosystem services (Mauclet et al., 2022), while also contributing to climate tipping points through altered energy (Oehri et al., 2022; Swann et al., 2010) and carbon fluxes (Clemmensen et al., 2021). When permafrost thaws, changes in vegetation and soil release substantial greenhouse gases (Olefeldt et al., 2016; Schuur et al., 2015), although increased vegetation could potentially offset some of these emissions by enhancing carbon storage (McGuire et al., 2018; Mekonnen et al., 2021).

1.2 | Consequences of fire on Arctic tundra ecosystems

Compared with the direct effects of gradual climate warming on Arctic plant communities, fires can have more abrupt consequences on tundra ecosystems. Understanding these impacts is especially important as observed increases in fire occurrence are expected to continue into the future (Chen, Romps, et al., 2021; Hu et al., 2015). The drivers of increased fire activity and severity include rising temperatures, longer growing seasons and increased lightning activity (He et al., 2022), as well as land-use changes, such as the expansion of infrastructure (Povoroznyuk et al., 2022). Post-fire vegetation successional trajectories are strongly related to the fire regime (i.e. the frequency, severity, season and extent of a fire), the abiotic conditions (edaphic and climatic conditions) and the life-history traits of the plants, including their disturbance legacy within a vegetation community (Davis et al., 2018; Johnstone et al., 2016; Figure 1). Consequently, post-fire recovery exhibits high variability across tundra locations, reflecting not only diverse fire characteristics but also local ecosystem differences such as ground ice regimes (Foster et al., 2022).

The effect of fire on above- and below-ground biomass and soil organic matter depends on fire severity (Bowman et al., 2020). At one extreme, vegetation affected by low-severity fires can recover within 1–2 growing seasons, whereas at the other extreme, high-severity fires can consume all biomass and soil organic matter, leaving behind only bare mineral soil. The period between fires defines the time span in which vegetation can recover through resprouting and colonisation. Increased fire frequency favours fast-growing species (e.g. ruderal herbs and graminoids) at the expense of slower-growing species (evergreen shrubs and lichens) that require more time to recover (Hollingsworth et al., 2021). Changes in the fire regime can thus lead to shifts in the abundance of different plant functional types (PFTs) with impacts on the environment and ecosystem functioning.

Fires can also affect vegetation indirectly through changes to the soil. These indirect effects are particularly strong in permafrost regions, as the combustion of vegetation and the soil organic layer leads to a decline in thermal insulation, and charred surfaces have lower albedo, resulting in higher soil temperatures (Chambers et al., 2005; Jiang et al., 2015; Rocha & Shaver, 2011). Higher soil temperatures, in turn, accelerate permafrost thaw, increase soil microbial activity and organic matter decomposition (Gibson et al., 2018; Jansson & Hofmockel, 2020), which can lead to shifts in vegetation (Ogden et al., 2023). Tundra fires can also alter soil moisture dynamics, increasing or decreasing moisture supply depending on microtopography, soil temperature and thermokarst development (Chen, Lara, et al., 2021; Pegoraro et al., 2021; Rodenhizer et al., 2023). Soil moisture can, for example, decline after fire because of increased permafrost thaw and a thinner organic layer, while rapid subsidence can lead to localised water saturation (He et al., 2021; Rodenhizer et al., 2023). These changes in permafrost and soil processes have feedbacks on

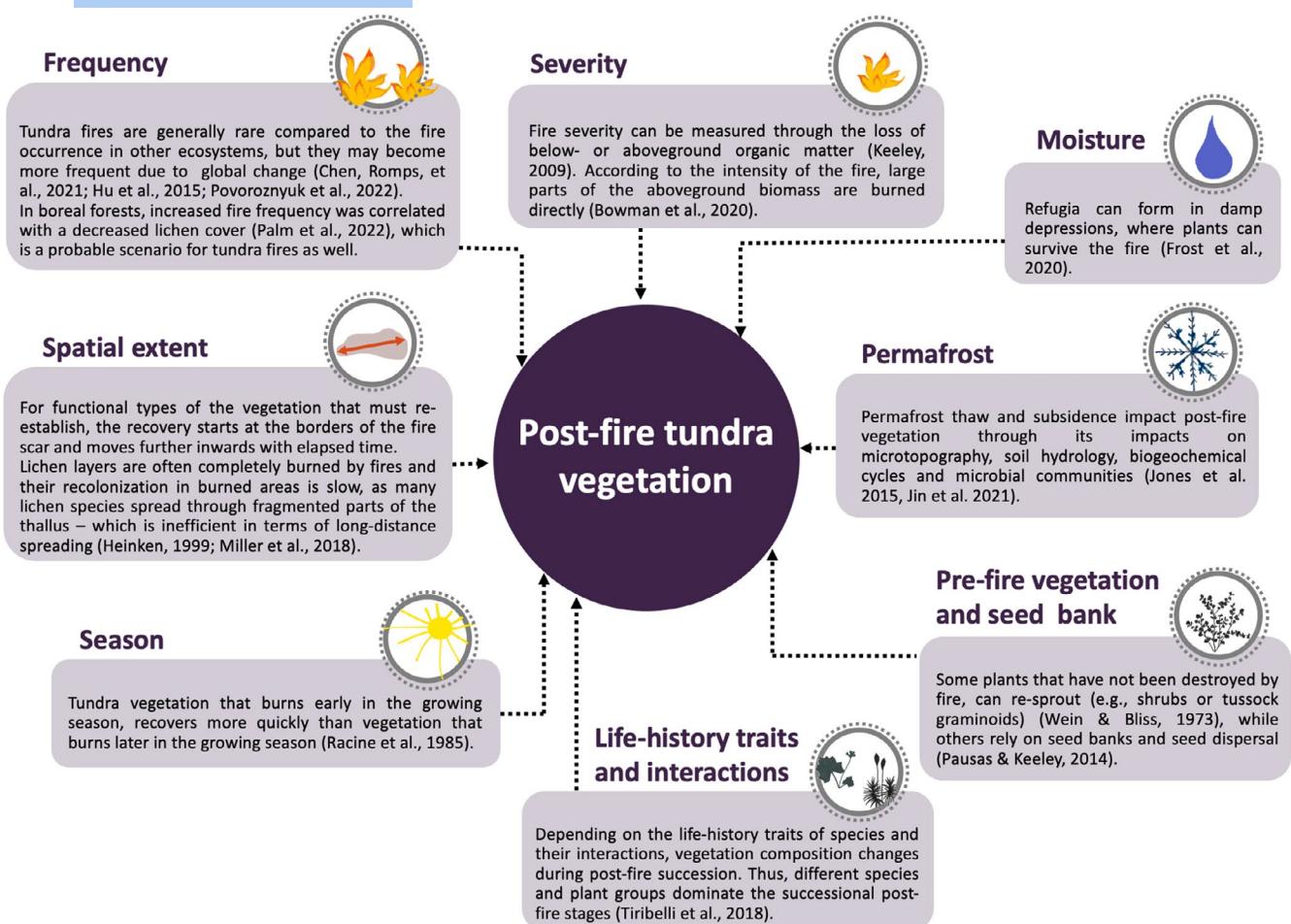


FIGURE 1 Factors that influence post-fire Arctic tundra vegetation.

vegetation through changes in hydrology and nutrient availability (Jin et al., 2021).

Fires initially reduce nutrients, especially nitrogen, through combustion (Heim et al., 2022; Mack et al., 2011). However, over time, fires can increase nitrogen levels due to enhanced mineralisation (Aerts, 2006; Jiang et al., 2015; Salmon et al., 2016). Fire also increases mineral phosphorus supply through pyromineralisation (Klupar et al., 2021). The impact of fire on nutrient availability and plant growth varies based on soil temperature, moisture and acidity (Hobbie & Gough, 2004). Post-fire deepening of the seasonally thawed active layer allows plants to access previously frozen nutrients, benefiting vascular plants with deeper roots and more resources (Blume-Werry et al., 2019; Wang et al., 2017).

Fires are relatively rare in the Arctic compared with other biomes (Wein, 1976), and fire frequency is highly variable (Racine et al., 1985). The time between fires spans an order of magnitude from 424 to 4374 years in southern versus northern Arctic Alaska (Rocha et al., 2012). In Siberia, the transition zone between the tundra and boreal forest biome (Payette et al., 2001) has a fire return interval of 792 years (Berner et al., 2012). However, these estimates are highly variable and uncertain because fires are so infrequent in the Arctic, and observational records are relatively short.

Paleorecords indicate that wildfires occurred more frequently in ancient shrub tundra ecosystems, with an average fire return interval of 144 years—a frequency comparable to that of modern boreal forests (Higuera et al., 2008). In recent decades, the annual burnt area has approximately tripled in the Siberian Arctic (Kharuk et al., 2022) and on the North Slope of Alaska (Miller, Jones, et al., 2023).

Fire also strongly interacts with other disturbance processes in Arctic landscapes. Fires are, for example, strongly linked to drought stress, and they also drive cryoturbation and ice-wedge degradation (Foster et al., 2022). These interactions between disturbances are complex and not well understood, but most Arctic disturbance regimes are expected to intensify with continued warming, so interactions between disturbances will likely intensify as well (Foster et al., 2022).

2 | A META-ANALYSIS OF FIRE EFFECTS ON TUNDRA VEGETATION COVER

Although relatively scarce across the circumpolar region, existing field studies provide information on long-term post-fire vegetation trajectories. We performed a meta-analysis across 15 studies to

elucidate trends in post-fire succession of low Arctic vegetation for five PFTs (lichens, bryophytes, herbs, graminoids, shrubs) across more than seven decades (Figure 2; detailed methods described in *Supporting Information*, Material). The studies comprise different ecosystem types, including forest–tundra, defined as the transition zone between the tundra and forest biome (Payette et al., 2001), lichen-dominated upland tundra, dwarf-shrub tundra, tussock tundra and sedge wet meadow tundra. It is important to note that, because this meta-analysis spans several decades, it likely captures interactive effects between fire and climate change that cannot be disentangled. These confounding factors may influence the observed recovery patterns, potentially altering traditional post-fire succession trajectories. In this section, we present the results of our meta-analysis, focusing on the observed post-fire recovery patterns of the different PFTs. Our aim here is to report the data-driven findings without introducing speculative elements.

2.1 | No clear post-fire pattern for bryophyte and herbaceous cover

Across all studies, we did not find a clear post-fire pattern for bryophyte and herb PFTs (Figure 2b,c). Short-term increases in certain herbaceous species, such as fireweed (*Chamaenerion angustifolium* or its synonym *Epilobium angustifolium*; Onagraceae), are frequently observed following a burn (Landhäuser & Wein, 1993). However, the long-term effects on herbaceous cover are less clear.

The lack of a pattern for bryophytes and herbaceous species can be attributed to the large differences between studies. Bryophytes, for example, can increase after fire (Frost et al., 2020; Heim et al., 2021; Racine et al., 1987) or decrease (Barrett et al., 2012; Jones et al., 2013; Narita et al., 2015). Differences in the recovery pattern of bryophytes can be linked to the pre-fire vegetation type, soil moisture, permafrost condition or microtopography. These impacts can obscure broader trends, making it challenging to identify generalised patterns.

2.2 | Lichen cover does not recover to pre-fire levels

Even many decades post-fire, ground lichen cover was lower compared with the pre-fire abundance (Figure 2a). Lichens are extremely slow-growing (Abdulmanova & Ektova, 2015) and their dispersal distances by thallus fragments (Heinken, 1999) or spores are relatively short. Additionally, they are vulnerable to competition for light from taller, faster-growing vegetation.

2.3 | Rapid recovery of graminoid cover

Graminoid (grasses and sedges) cover exceeded pre-fire levels in the first few decades post-fire, but then declined to below pre-fire

levels by four decades post-fire (Figure 2d). True grasses (Poaceae) and sedges (Cyperaceae) have different post-fire recovery dynamics. While sedges can dominate unburnt tundra, grass cover is usually low. Sedges like tussock cottongrass are fire resistant because their growth form protects root-stocks, allowing them to dominate early successional stages (Bliss & Wein, 1972; Curasi et al., 2023; Wein & Bliss, 1973). Grasses also become abundant shortly after fire due to resprouting from below-ground organs, germination from seedbanks (Racine et al., 1987), wind-disseminated propagules (Rowe, 1983), and their ability to efficiently adapt their root structures to acquire nutrients (Wang et al., 2017).

2.4 | Strong increase in shrub cover after several decades

Shrub cover (including tall shrubs, dwarf or deciduous and evergreen shrubs) was lower compared with control levels in the first years after fire (Figure 2e). In contrast to lichens, shrub cover eventually increased and typically exceeded pre-fire levels within four decades (e.g. Frost et al., 2020). This pattern can be related to the ability of shrubs, like the dwarf birch (*Betula nana* s.l.; Betulaceae), to resprout from organs protected from the fire, such as the root collar, rhizomes and roots (Racine et al., 1987). In addition, shrubs respond positively to many climate change impacts, such as increased active layer depth, extended growing season, or increased summer temperatures (Myers-Smith et al., 2015). Established shrubs, particularly deciduous ones, can create self-reinforcing cycles. By increasing vegetation turnover time, they enhance long-term nutrient availability, further promoting their own growth and expansion (Parker et al., 2015, 2021).

3 | POSSIBLE VEGETATION TRAJECTORIES IN THE ARCTIC TUNDRA UNDER CLIMATE CHANGE AND FIRES

Fires are globally powerful agents of ecosystem change, capable of inducing ecosystem shifts that persist over ecologically significant timescales, often lasting decades, centuries, or even millennia (Fletcher et al., 2014; Tiribelli et al., 2018). Fires can accelerate vegetation transitions caused by climate change, especially when environmental conditions exceed the limits that once allowed existing plant communities to naturally replenish themselves (Hansen & Turner, 2019; Johnstone et al., 2016). In addition, fires can trigger ecosystem shifts between various states under the same climatic conditions, and are capable of propelling changes in either direction (Pausas, 2015). The concept of alternative ecosystem states (AES) suggests that a single set of external factors can lead to various possible ecosystem states. This idea is rooted in the mathematical principle of multiple stable states, where a system can exhibit more than one stable condition based on the same parameters (Petraitis, 2013). Disturbances, particularly fires, play a crucial role

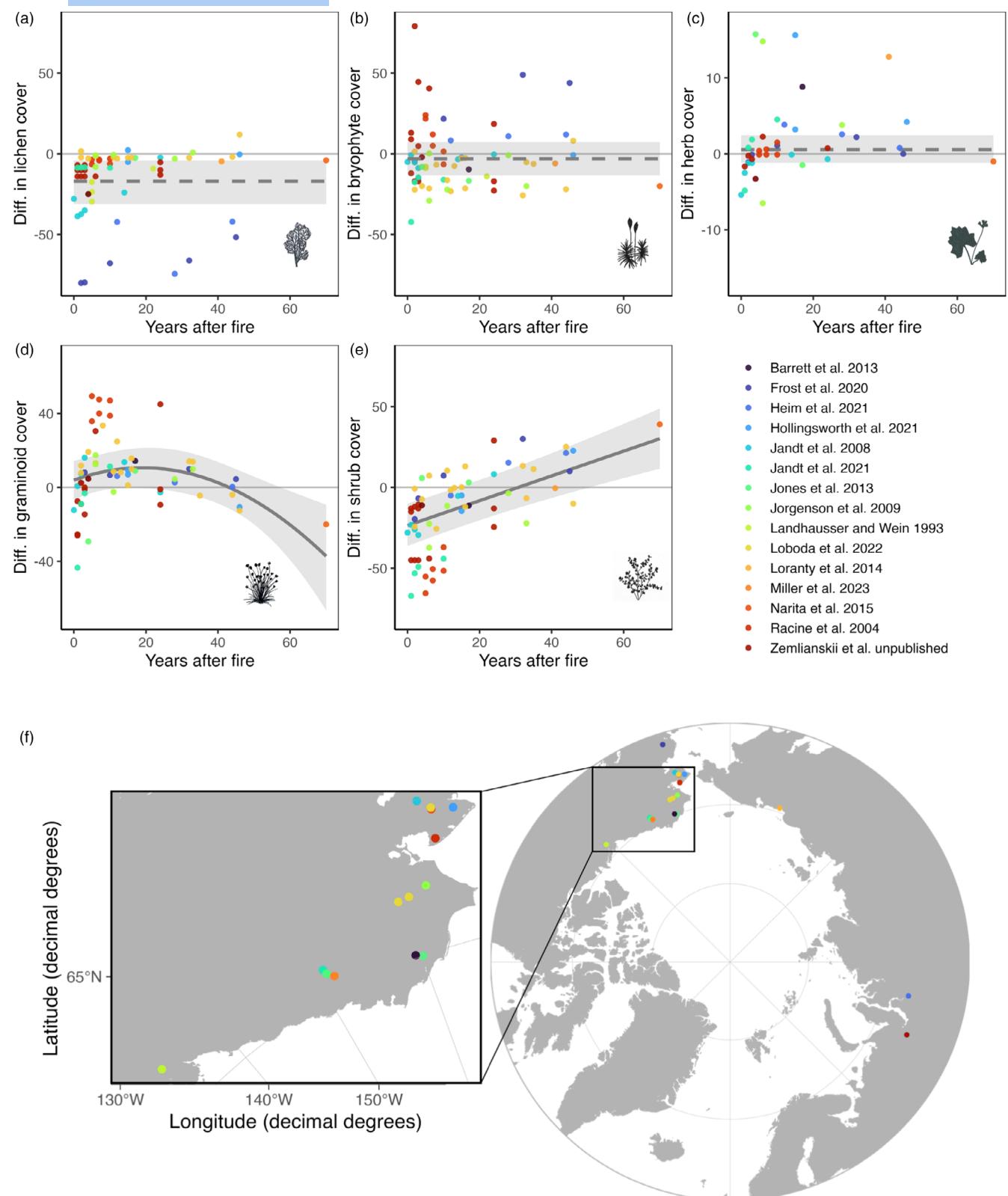


FIGURE 2 Trends in the long-term development of vegetation cover of five plant functional types after tundra fires with (a) lichens ($R^2_{\text{marg}} = 0$, $R^2_{\text{cond}} = 0.89$), (b) bryophytes ($R^2_{\text{marg}} = 0$, $R^2_{\text{cond}} = 0.31$), (c) herbs ($R^2_{\text{marg}} = 0$, $R^2_{\text{cond}} = 0.05$), (d) graminoids ($R^2_{\text{marg}} = 0.13$, $R^2_{\text{cond}} = 0.56$), (e) shrubs ($R^2_{\text{marg}} = 0.26$, $R^2_{\text{cond}} = 0.73$). Coloured dots are data from the 15 datasets (see f for location) included in the meta-analysis. Thin horizontal lines indicate zero difference and thus maintain the pre-fire (control) state. Grey lines show predicted means for the best model (null model, years after fire or with the quadratic term of years after fire). Solid lines indicate a significant impact of years after fire on the cover values, while dashed lines indicate a non-significant impact of years after fire on cover. The shaded area is the 95% credible Interval (Crl). If the 95% Crl does not include the zero line (see lichens), it means that there is at no point in time a predicted recovery of the cover to pre-fire levels. Bayesian R^2 is reported for all models in Table S2. Please find the results of the same analysis without imputed values in Figure S1.

in forming AES through impacts on vegetation communities globally (Pausas & Bond, 2020). Changes in fire return intervals can induce stable state shifts, potentially driving ecosystems towards distinct states that persist (Landesmann et al., 2021; Tiribelli et al., 2018) even under constant climate conditions (Pausas, 2015).

Alternative states are not a new concept for tundra ecosystems, as evidenced by previous studies exploring state shifts in Arctic tundra vegetation due to grazing pressures, including the role of reindeer in mitigating climate-induced shifts from grass to shrub dominance, and hypotheses about shifts from lichen to graminoid-dominated states under varying levels of grazing intensity (Bråthen et al., 2017; Egelkraut et al., 2018; Van der Wal, 2006).

As we discuss both fire and climate change effects, it is important to distinguish between AES and climate-driven transitions. AES refers to two different ecosystems occurring under the same environmental and climatic conditions, while climate-driven transitions represent changes occurring due to changing environmental factors. Our intention is not to provide conclusive evidence of the existence of transitions and AES in tundra ecosystems, but rather to identify potential mechanisms and hypotheses related to possible divergent trajectories. We aim to develop concepts that catalyse future research in this area, recognising that definitively proving these transitions and states will remain a significant challenge in the future. This difficulty is exemplified by the recent work of Higgins et al. (2024), which highlights the complexities of identifying AES even in well-studied savanna-forest systems. In the next three sections, climate change becomes a central theme as we discuss how recovery patterns might evolve under changing environmental conditions and how fire, climate change, and vegetation are anticipated to interact.

3.1 | Hypothetical post-fire trajectory to increased shrub abundance

Paleorecords from the Arctic indicate that prehistoric shrub-dominated tundra had a higher fire frequency than today and remained stable for millennia (Higuera et al., 2008). Tundra shrubs generally thrive under warmer climatic conditions, exhibiting increased growth (Iturrate-Garcia et al., 2017; Myers-Smith et al., 2011). If shrub cover expands after a fire event (see Figure 2e), a warmer climate could sustain this elevated shrub cover state compared with pre-fire levels (Figure 3a). Examples of this post-fire trajectory, related to a climate-change induced ecosystem transition, can already be observed in the recovery patterns of very old tundra fires on the North Slope of Alaska that have remained shrub-dominated for more than 100 years after a fire (Jones et al., 2013; Miller, Jones, et al., 2023).

One potential trajectory related to climate change is therefore the dominance of woody plants after a fire event. This can occur due to shrubs' ability to rapidly recover from underground organs, surviving plant parts, or seed banks. Once established, these woody species remain dominant due to warmer climatic conditions that

alter environmental factors such as soil temperature (Landhäusser & Wein, 1993). In this scenario, other functional groups such as lichens would not recover to pre-fire levels because of interactions between climate warming and fire that individually and jointly decrease Arctic lichen cover and give woody species a competitive advantage (Joly et al., 2009).

3.2 | Hypothetical post-fire trajectory to increased grass abundance

While our meta-analysis did not directly examine fire frequency, we can infer potential shifts towards a grass-dominated vegetation based on the combined results of our analysis and literature review. Our meta-analysis reveals a significant increase in graminoid vegetation within two decades post-fire, while shrubs fail to recover during this period. This finding suggests that if tundra fires occur at intervals less than 25 years, a transition towards increased grass abundance is feasible in tundra ecosystems. Tundra grasses demonstrate rapid recovery and colonisation following fire events, thriving under conditions of increased fire frequency (Hollingsworth et al., 2021). Climate warming and increased fire occurrence have the potential to transform previously fire-resistant landscapes into more fire-prone environments, as observed in Alaska's Noatak Valley (Gaglioti et al., 2021). As grasses become dominant after fire events, vegetation flammability increases, creating a positive feedback loop that further increases fire susceptibility (Landesmann et al., 2021; Tiribelli et al., 2018).

3.3 | Hypothetical shifts between shrub and grass dominance under climate change

The persistence of fire-driven AES depends on an interplay of fire and vegetation adaptations (Baudena et al., 2020; Magnani et al., 2023; Pausas, 2015; Staver et al., 2011). Strong feedbacks between vegetation and fire are crucial for maintaining a fire-driven stable state (Pausas & Keeley, 2014). Tundra shrubs have a lower flammability compared with grasses (Sylvester & Wein, 1981). In addition, they transform the surrounding environment and outcompete other species for resources such as light and nutrients (Mekonnen et al., 2018; Myers-Smith et al., 2011; Pajunen et al., 2011). These feedback mechanisms lead to the maintenance of a woody-dominated state by reinforcing shrub dominance and mitigating frequent fires. Dead grass leaves are the most flammable among tundra plants, rendering them more prone to ignition than shrubs (Sylvester & Wein, 1981). The quick buildup of dry leaf litter in graminoid tundra types significantly increases their flammability compared with shrub-dominated areas. Grasses possess several competitive advantages in post-fire environments, including rapid regeneration from rhizomes or seedling establishment (Racine et al., 1987) to quickly extend roots into newly accessible, nutrient-rich soil layers that were previously frozen (Wang et al., 2017).

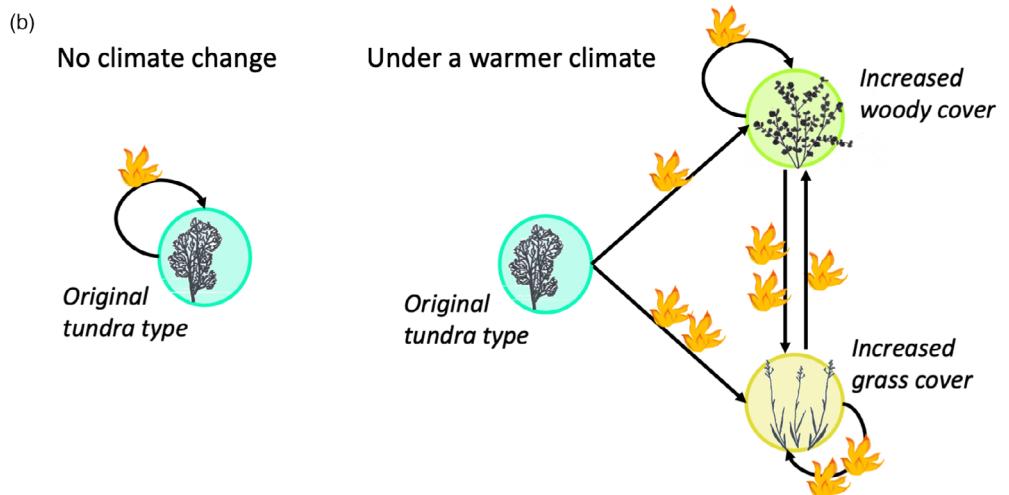
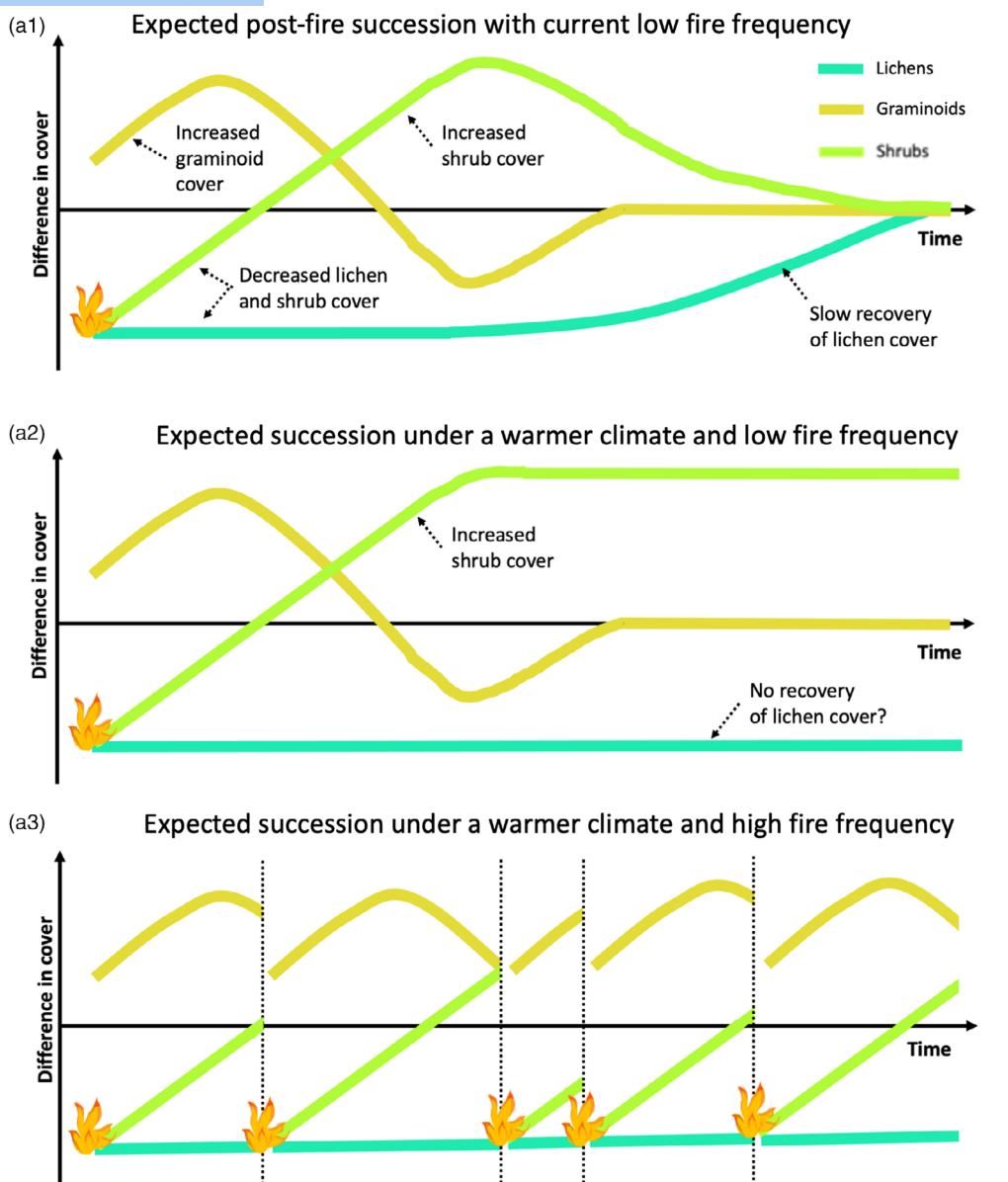


FIGURE 3 (a1-a3) The post-fire trajectory of tundra vegetation cover back to the original state (a1) and of two possible trajectories under climate change (a2, a3). The y-axis displays the difference in cover between control and fire plots. The black x-axis is the at $y=0$. If the difference of the cover reaches that line, the cover has recovered to the control state. The entire time span displayed on the x-axis is roughly ~150 years. The vegetation trajectories of the first decades after fire follow the patterns that our meta-analysis indicated. (a2) Fires, as well as a warmer climate, promote shrub encroachment. After a fire, shrubs gain dominance because of their ability to regenerate quickly from surviving plant parts and keep it because of changed climatic conditions. (a3) Transition to a graminoid-dominated state because of an increased fire frequency (<40 years intervals). Fire symbols and dashed lines show the fire disturbances after the initial fire event. (b) Expected post-fire recovery with no climate change and trajectories under a warmer climate with climate-fire induced transitions towards two alternative ecosystem states: One with increased woody abundance under low fire frequency and another towards increased grass abundance, induced by short fire intervals. This figure shows dry lichen-dominated tundra as an example for the original vegetation.

Drawing from studies in other ecosystems, we understand that two fires occurring in rapid succession can significantly alter an ecosystem's composition, promoting, for example, shifts from resprouter (i.e. shrubs) to seeder (i.e. grasses) dominance (Batllori et al., 2015). Post-fire climatic shifts, such as increased aridity, can drive ecosystem shifts by synergistically interacting with fire effects, impacting vegetation resilience and colonisation abilities (Baudena et al., 2020). For example, growth and ramet sprouting of the shrub species *Betula nana* are inhibited by decreased summer precipitation (Li et al., 2016), and moisture stress may also hinder growth of Arctic and subarctic trees (Timoney et al., 2019). In addition, shrub cover was much reduced relative to grasses after multiple fires in rapid succession (Hollingsworth et al., 2021).

If continued climate change leads to increased Arctic moisture levels that in turn decrease fire frequency (Higuera et al., 2008), grass-dominated ecosystems may transition towards greater woody dominance. Furthermore, shrub growth under future warmer conditions is positively linked to increased moisture levels (Ackerman et al., 2017; Keuper et al., 2012).

3.4 | Hypothetical post-fire vegetation trajectories for different tundra ecosystem types

The Arctic region is composed of diverse landscapes that encompass various tundra ecosystem types. Tundra ecosystems burn when environmental conditions are suitable, with fire susceptibility varying among vegetation types; areas dominated by shrubs or graminoids, which have higher above-ground biomass, are generally more prone to fires than low-biomass areas like barren tundra, particularly if moisture levels are low (Rocha et al., 2012).

Thawing permafrost and microtopographic changes alter drainage characteristics and impact moisture availability, which in turn influence post-fire predominance of shrub or graminoid-dominated ecosystem types (Chen, Hu, et al., 2021). Consequently, these site-specific factors may be critical drivers of divergent successional trajectories in tundra ecosystems, especially where ice wedge degradation results in wetter troughs and drier high-centred polygons (Jones et al., 2015; Miller, Jones, et al., 2023). Existing data constraints limit our ability to provide conclusive evidence on how different tundra ecosystems will respond to the combined effects of fire and climate change. Nevertheless, we

propose that post-fire trajectories under a warmer climate may share common patterns across various tundra ecosystem types: (1) increased woody vegetation or (2) increased grass vegetation, both driven by interactions between climate, fire characteristics and vegetation feedbacks.

Most research on post-fire succession has concentrated on tussock tundra, prevalent in areas with frequent tundra fires (Raynolds et al., 2019; Walker et al., 2005). A known outcome of these fires is an increase in shrub cover compared with pre-fire levels after 24 years (Racine et al., 2004). Gaglioti et al. (2021) proposed that fire and wetting from permafrost thaw could lead tussock tundra towards a more productive, shrub-dominated state (Figure 3b). Other studies indicate that graminoid cover often rises in the years immediately following a fire (Jones et al., 2013; Racine et al., 2006) with long-term vegetation responses varying based on fire severity and frequency. For instance, Hollingsworth et al. (2021) found that high-severity fires and increased fire frequency boosted grass abundance, resulting in a stable graminoid-forb-rich tundra rather than a shift to shrub dominance.

Fire impacts differ between lowland and upland tundra, with shrub cover decreasing in lowlands and increasing in dry uplands due to fire and climate change. The extent of shrub cover increase in uplands positively correlates with fire severity, likely due to greater nutrient release and reduced competition in more severely burned areas (Chen, Hu, et al., 2021). In addition, upland tundra is often dominated by slow-growing lichen mats that need decades to recover, which means that fire opens space for shrub encroachment.

The interaction of fire with treeline expansion remains unclear. It is anticipated that this relationship will involve dynamic interactions among vegetation, climate, and disturbance factors (Lloyd et al., 2002). Fire promotes tree invasion into tundra (Landhäusser & Wein, 1993), but increased fire frequency could also halt treeline advance (Payette et al., 2008). The uncertainty stems from the interplay between fire frequency, vegetation recovery dynamics and climate feedbacks. A single fire event may thereby facilitate treeline expansion through permafrost thaw and the provision of seedbeds for tree establishment (Landhäusser & Wein, 1993). Conversely, fires can directly reduce forest cover through tree mortality, and when coupled with drought stress from a warming climate, they can impede forest expansion in some regions (Payette et al., 2008).

3.5 | Challenges and opportunities for the definition of post-fire trajectories

Uncertainty surrounding ecosystem transitions and shifts after tundra fires under climate change demands scientific attention. We advocate for remote sensing analyses that cover larger spatial scales than field studies alone, and modelling approaches to extend temporal scales (Beamish et al., 2020), while also emphasising the need for more field studies in understudied Arctic regions and tundra ecosystems.

Our meta-analysis reveals both strengths and limitations in available data on post-fire vegetation recovery. Reliance on satellite imagery for identifying old burn areas restricts the time scale, while alternative methods like charcoal sampling lack precise dating (Jones et al., 2013). Most studies focus on general vegetation categories or major plant groups over time, limiting the analysis of more detailed vegetation composition or fire frequency/severity impacts. Limited data on vegetation responses to climate change over decades adds uncertainty.

In our meta-analysis, we addressed missing variance by imputing it, a common practice that enhances the robustness of our results (Kambach et al., 2020). This approach allowed us to analyse a larger dataset over a longer timescale, providing a comprehensive view of vegetation changes. We included a subset analysis without imputed values in the **Supporting Information**, Materials to ensure transparency and verify that trends remain consistent with our main analysis (Figure S1). Without the data points that include imputed data, we observed modest differences in recovery patterns in three of the five PFTs over a shorter timescale (46 vs. 70 years post-fire). Lichen cover increased but did not reach unburnt levels, indicating slow recovery. Bryophyte cover increased, exceeding unburnt levels, which is the primary difference from the main analysis. The trend for shrubs is also equivalent, with the difference from the main analysis being a quadratic rather than a linear relationship, suggesting a plateau in shrub cover 30 years after fire. That the results between the two analyses differ is not unexpected due to the subset analysis having both a smaller sample size and shorter timeframe, which we interpret to obscure long-term trends. Nonetheless, the overall recovery patterns for both analyses support our hypotheses, aligning with known impacts of fire and climate change on these ecosystems.

Our current knowledge of fire effects on the Arctic tundra biome stems mostly from Alaskan tussock tundra, especially from the more accessible Seward Peninsula (Hollingsworth et al., 2021; Holt et al., 2008; Jandt et al., 2008; Racine et al., 2004). Less is known about other parts of the circumpolar region, particularly the vast remote areas of the Siberian tundra (Heim et al., 2021; Loranty et al., 2014). Thus, there is a strong geographical bias in studies that have investigated vegetation change after tundra fires (Figure 2f). A reduction of this bias becomes even more urgent with recent extreme fire seasons during 2019–2021 in central and eastern Siberia (Scholten et al., 2022).

The species composition of circumpolar Arctic vegetation is relatively similar compared with other biomes (Walker et al., 2005).

Herds of wild caribou are common in Alaska and Siberia, and several areas in Siberia have been influenced by reindeer pastoralism (Forbes & Kumpula, 2009). As herbivory strongly affects tundra vegetation dynamics (Osterrieth & Bosker, 2024; Steketee et al., 2022; Sundqvist et al., 2019), it is also likely that grazing influences post-fire vegetation trajectories (Jandt et al., 2008). Climate change (Bjorkman et al., 2020), fire, and herbivory (Frost et al., 2020; Jandt et al., 2008) affect Arctic tundra ecosystem types through reductions in lichens and increases in vascular plant species. However, it is unclear how herbivory impacts post-fire vegetation.

Many fire studies were conducted in relatively moist terrain with predominantly moist tussock graminoid-dominated tundra (Jones et al., 2013; Narita et al., 2015), and less is known about vegetation recovery in non-tussock tundra ecosystem types (Frost et al., 2020). Many Arctic tundra ecosystem types are currently underrepresented in research because they are difficult to access, generally rare, or because fire occurrence in the ecosystem type is generally lower.

3.6 | Moving forward

To better understand post-fire successional trajectories in the Arctic tundra biome, we must address five key questions that emerge from the challenges and knowledge gaps identified above. The associated sub-questions indicate how these key questions can be tackled in a tractable manner:

1. To what extent are post-fire successional trajectories related to climate and climate change? What are the specific climatic factors (e.g. temperature, precipitation, growing season length) that most strongly influence post-fire vegetation recovery?
2. How do fire regime changes (i.e. frequency and severity) interact with vegetation dynamics in tundra ecosystems, potentially contributing to AES? What are the key thresholds or tipping points in the fire – vegetation feedback mechanisms that lead to shifts between different tundra ecosystem states?
3. To what degree do other disturbances such as herbivory and permafrost thaw influence post-fire successional pathways in tundra ecosystems? What are the specific mechanisms by which herbivory and permafrost thaw influence post-fire vegetation recovery?
4. What are the impacts of changing Arctic fire regimes on tundra ecosystems and the services they provide? How do the impacts of changing fire regimes vary across different tundra ecosystem types and regions? How are plant functional traits linked to flammability and post-fire succession?
5. Beyond anthropogenic climate change, how are human activities interlinked with changing fire regimes and post-fire vegetation dynamics, and how do these ecological shifts, in turn, affect Indigenous communities and livelihoods? What are the specific human activities (e.g. resource extraction, infrastructure development, tourism) that most significantly influence fire regimes and post-fire vegetation dynamics in the Arctic tundra?

Because of the temporal limitations of field studies, process-based dynamic vegetation modelling is a useful tool to address many of these questions (e.g. Euskirchen et al., 2022; Kantzias et al., 2015). Similarly, remote sensing analyses that leverage high-resolution data will be necessary to extrapolate results to larger spatial scales and to better document historical unrecorded fires (Miller, Baughman, et al., 2023). However, there are still several constraints that limit the accuracy of modelling. Long-term monitoring and more field data from a wider range of Arctic regions will help to understand whether fire-induced AES shifts are already under way in recent tundra burns and to better constrain model analyses.

Studies that have performed experimental burning in the Arctic are rare (Alexander et al., 2018; Hermesdorf et al., 2022). Controlled fire experiments are beneficial as they allow direct measurement of the antecedent properties of the burnt area, rather than relying on space-for-time substitutions. Experimental burns can help address questions related to short-term recovery and/or severity impacts on recruitment. However, to fully characterise the recovery process, such experiments would need to span several decades, if not a century.

Tundra biome changes have not only ecological but also human and cultural dimensions. For instance, the Nenets in Eastern Europe and the Yamal-Nenets and Western Siberia rely on lichen as a crucial food source for their reindeer herding practices (Forbes, 2013). In these regions, a reduction in lichen abundance caused by tundra fires would threaten the livelihoods of Indigenous Peoples and rural communities, as well as reindeer or caribou habitat (Gustine et al., 2014).

Ecological understanding of tundra fires is thus crucial for making informed decisions on wildfire management. This includes determining how different PFTs alter flammability and fuel loads. Moreover, future studies must investigate the interactive effects of tundra fire and vegetation change, as well as subsequent impacts on biodiversity, plant functional traits, and ecosystem function. With this information, managers can then decide whether to suppress fires or allow them to burn. Equally important, however, is the urgent need to expand our knowledge of the global impacts of tundra fires and the potential AES, as vegetation changes profoundly influence surface energy fluxes, permafrost thaw, and greenhouse gas emissions. The Arctic tundra is experiencing significant ecological transformations due to climate change, particularly through increased temperatures and altered fire regimes. These changes not only impact ecosystem dynamics and biodiversity but also highlight the potential for persistent new ecosystem states.

AUTHOR CONTRIBUTIONS

Ramona Julia Heim: Conceptualisation; data curation; formal analysis; investigation; methodology; visualisation; writing—original draft; writing—review and editing. **Adrian V. Rocha:** Conceptualisation; writing—review and editing. **Vitalii Zemlianskii:** Investigation; writing—review and editing. **Kirsten Barrett:** Investigation; writing—review and editing. **Helga Bültmann:** Investigation; writing—review and editing. **Amy Breen:** Investigation; writing—review

and editing. **Gerald Verner Frost:** Investigation; writing—review and editing. **Teresa Nettleton Hollingsworth:** Investigation; writing—review and editing. **Randi Jandt:** Investigation; writing—review and editing. **Maria Kozlova:** Investigation; writing—review and editing. **Anastasiya Kurka:** Investigation; writing—review and editing. **Mark Torre Jorgenson:** Investigation; writing—review and editing. **Simon M. Landhäusser:** Investigation; writing—review and editing. **Michael Mark Loranty:** Investigation; writing—review and editing. **Eric A. Miller:** Investigation; writing—review and editing. **Kenji Narita:** Investigation; writing—review and editing. **Evgeniya Pravdolyubova:** Investigation; writing—review and editing. **Norbert Hözel:** Conceptualisation; writing—review and editing. **Gabriela Schaeppman-Strub:** Conceptualisation; methodology; resources; writing—review and editing.

AFFILIATIONS

¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland; ²Institute of Landscape Ecology, University of Münster, Münster, Germany; ³Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana, USA; ⁴School of Geography, Geology, and the Environment, University of Leicester, Leicester, UK; ⁵International Arctic Research Center, University of Alaska Fairbanks, Fairbanks, Alaska, USA; ⁶Alaska Biological Research, Inc., Fairbanks, Alaska, USA; ⁷PNW Research Station, USDA Forest Service, Washington, District of Columbia, USA; ⁸Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, USDA Forest Service, Fort Collins, Colorado, USA; ⁹Department of Mycology and Algology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia; ¹⁰Aurorin Polar-Alpine Botanical Garden-Institute of Kola Scientific Centre RAS, Apatity, Russia; ¹¹Alaska Ecosystems, Fairbanks, Alaska, USA; ¹²Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada; ¹³Department of Geography, Colgate University, Hamilton, New York, USA; ¹⁴Bureau of Land Management, Alaska Fire Service, Fort Wainwright, Alaska, USA; ¹⁵Department of Education and Human Studies, Akita University, Akita, Japan and ¹⁶Institute of Science and Technology Austria, Klosterneuburg, Austria

ACKNOWLEDGEMENTS

We would like to express our sincere gratitude to all the data providers who carried out fieldwork in different regions of the Arctic and published their data, which we used for our meta-analysis. We recognise the hard work and dedication of these individuals, without whom this paper would not have been possible. We are grateful to the editor and the anonymous reviewer for their time and valuable feedback on this manuscript. We particularly appreciate the detailed and constructive comments provided by reviewer Mara Baudena, which significantly strengthened our work. We also acknowledge the Indigenous peoples and rural communities of the Arctic, whose traditional knowledge, rights, and interests are integral to the stewardship and study of these ecosystems. This work was funded in part by the U.S. National Aeronautics and Space Administration (NASA) grant 80NSSC22K1256 (GVF). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70022>.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of our meta-analysis are openly available in Zenodo: <https://doi.org/10.5281/zenodo.10410798> (Heim, 2023).

ORCID

Ramona Julia Heim  <https://orcid.org/0000-0002-2503-7075>
 Adrian V. Rocha  <https://orcid.org/0000-0002-4618-2407>
 Vitalii Zemlianskii  <https://orcid.org/0000-0001-6597-2415>
 Gerald Verner Frost  <https://orcid.org/0000-0002-5134-0334>
 Michael Mark Loranty  <https://orcid.org/0000-0001-8851-7386>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Trends in the long-term development of vegetation cover of five functional types after tundra fires (A: lichens, B: bryophytes, C: herbs, D: graminoids, E: shrubs).

Table S1. Studies included in the meta-analysis with the description of the Arctic tundra ecosystem type that was used in the individual publications, the PFTs provided and details on the controls as.

Table S2. Bayesian pseudo R^2 for the models of different PFTs for the full dataset and the dataset without imputed values.

Appendix S1. Methods meta-analysis.

How to cite this article: Heim, R. J., Rocha, A. V., Zemlianskii, V., Barrett, K., Bültmann, H., Breen, A., Frost, G. V., Hollingsworth, T. N., Jandt, R., Kozlova, M., Kurka, A., Jorgenson, M. T., Landhäusser, S. M., Loranty, M. M., Miller, E. A., Narita, K., Pravdolyubova, E., Hözel, N., & Schaeppman-Strub, G. (2025). Arctic tundra ecosystems under fire—Alternative ecosystem states in a changing climate? *Journal of Ecology*, 113, 1042–1056. <https://doi.org/10.1111/1365-2745.70022>