



REVIEW PAPER

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Post-fire forest recovery at high latitudes: tree regeneration dominated by fire-adapted, early-seral species increases with latitude

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Abstract

Key message Above 40° N/S, increasing latitude is linked to greater post-fire tree regeneration. However, species dominance shifts from conifers to short-lived deciduous trees, which may negatively impact flora, fauna, and ecosystem services dependent on coniferous forests. These results were primarily driven by studies from North America, highlighting the need for more research that directly measures post-fire forest recovery in other high-latitude regions.

Context As the size and frequency of wildfires increase across many regions, high-latitude forests may be at particular risk for decreases in regeneration and state shifts post-fire.

Aims Through this systematic review, we sought to determine the general relationship between post-fire tree regeneration densities and latitude in forests above 40° N/S. We expected regeneration densities post-fire would decrease with increasing latitude, and that forest regeneration would be negatively impacted by high burn severities, forest management, harsh site conditions, and unprotected microsites. We also anticipated that light-demanding species with adaptations to fire would replace shade-tolerant species that lack such adaptations post-fire.

Methods We conducted a literature search that returned over 4500 articles. We selected those that directly measured post-fire regeneration at or above 40° N/S and retained 93 articles for analysis. Fire characteristics, pre- and post-fire tree species compositions and regeneration densities, and regeneration predictors were then extracted from the retained articles. We fit linear mixed models to post-fire regeneration density with latitude and species traits as explanatory variables and also explored the significance and magnitude of predictors that informed post-fire tree species response.

Results Contrary to our expectations, post-fire regeneration increased significantly with latitude. High burn severities and unprotected microsites had negative impacts on post-fire regeneration; higher elevations and more prolific pre- or post-fire reproduction were positively correlated with post-fire regeneration, while management of any type did not have an impact.

Conclusion Although forests are regenerating after wildfires at the most extreme latitudes included in this study (above 55° N), regeneration is often limited to only a handful of genera: aspen (*Populus*) and birch (*Betula*), for example. Regeneration was less abundant at the lower range of our study area. Certain lower latitude forests that occupy

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marginal habitats are under increasing stress from drier, warmer conditions that are exacerbated by wildfires. Results were largely driven by studies from Canada and the USA and may not be applicable to all high-latitude forests.

Keywords Boreal, Fire tolerance, Shade tolerance, Tree regeneration, Wildfire, Forest fire

1 Introduction

Climate change has increased the occurrence of conditions that produce and sustain forest fires globally (Pausas and Keeley 2021). Consequently, wildfire behavior has changed across many different regions and forest types in recent decades (Abatzoglou et al. 2018; Pausas and Keeley 2021). Increases in aridity have been shown to be connected to the size of wildfires in high-latitude, boreal forests (Abatzoglou et al. 2018), where millions of hectares of forest can burn yearly (e.g., Abatzoglou and Kolden 2011; Bahlai et al. 2021). Whether high-latitude forests have generally been resilient to increases in fire activity over the last two decades is largely understudied (Boucher et al. 2020). Certain high-latitude forest types, like boreal forests, are known to be adapted to fire and may even be benefiting from increased fire activity (e.g., Mekonnen et al. 2019). Still, given the harsh growing conditions at extreme latitudes, the potentially limited adaptability of low-diversity, high-latitude forests, and the increasing size and frequency of wildfires in general, post-fire recovery would ostensibly be more tenuous as latitude increases, which has been shown to be true for certain temperate forest types in the southern hemisphere (e.g., Mallik 2003, Paritsis et al. 2015, Urretavizcaya et al. 2022, Ruggirello et al. 2023a, 2023b). Across high latitudes ($\geq 40^\circ$), some forest types have more inherent resilience to fire than others. For example, ecosystems in which species from genera such as larch (*Larix*) and birch (*Betula*) are present may recover rapidly post-fire (Otoda et al. 2013), whereas other high-latitude forest types where only non-fire-adapted tree species are present, such as *Nothofagus* sp. in southern South America, may not recover contiguous forest cover at all post-fire (Paritsis et al. 2015; Ruggirello et al. 2023b).

Underlying a forest's post-fire response is its species' fire tolerances, or the adaptations given species have that either allow them to survive a wildfire (resistance) or reestablish successfully post-fire (resilience) (DeRose and Long 2014). One of the most significant resilience adaptations is the ability to resprout (Lloret et al. 1999). Post-fire colonization of burned landscapes can be driven by species that vegetatively resprout from top-killed individuals (e.g., Torres et al. 2014). Such a dynamic commonly plays out throughout the northern hemisphere at high latitudes where resprouter species from the genera aspen (*Populus*) and birch dominate post-fire landscapes (Otoda et al. 2013; Paudel et al. 2015). There are

seemingly fewer species capable of resprouting after wildfire in the southern hemisphere, although certain deciduous trees have shown this ability at extreme latitudes south of the equator (e.g., *Nothofagus antarctica*, Ruggirello et al. 2023c, 2023d). Serotinous cones can also be associated with fire-resilient conifer species and can play a significant role in post-fire tree regeneration dynamics (McCune 1988). Lodgepole pine (*Pinus contorta*) in the northern hemisphere is one of the species that regenerates most prolifically after wildfire through the fire-induced release of seeds. It has even been shown to outcompete native, non-serotinous South American tree species after fires (Cóbar-Carranza et al. 2015). The shade tolerance of a given tree species often, but not always, goes hand in hand with its fire tolerance. Early-seral, light-demanding genera, such as aspen, birch, larch, and many pine species, tend to be the first to colonize burned areas and often have adaptations that favor rapid post-fire recovery (e.g., Halpern and Antos 2022). Conversely, genera that thrive in the shade, such as most maple (*Acer*), fir (*Abies*), and hemlock (*Tsuga*) species, tend to dominate later in a community's seral development, often lack traits that allow them to recover rapidly post-fire (Shorohova et al. 2011).

Forests' responses to fire are not only driven by the fire and shade tolerances of the tree species present pre- and post-fire, but also by several key environmental and fire-impacted variables. Environmental variables, sometimes also thought of as site-specific variables, largely independent of and unchanged by fire, include elevation, slope, climate, and pre-fire forest structure, among others (Johnstone et al. 2020). Determining whether these environmental conditions favor or impede forest recovery will depend on the species present in a given ecosystem, but steep and exposed slopes and xeric conditions, for example, often deter the post-fire recovery of many tree species (e.g., conifer regeneration post-fire in the northwestern USA, Boag et al. 2020). Fire-impacted variables, as opposed to environmental variables, are forest conditions directly altered by fire. These include post-fire forest structure, distance to seed source, soil properties, herbaceous competition, and microsite conditions, for example (Dawe et al. 2020). Significant changes in these variables often mean that a fire has burned largely at high severity and that the post-fire landscape will favor the regeneration of aspen, birch, or certain oak and pine species, for example, that thrive in open, exposed

conditions (e.g., Shenoy et al. 2011; Halpern and Antos 2022). Collectively, many of these variables from both broader categories combine to determine the quality and quantity of regeneration sites available for seedling germination or asexual resprouting (López et al. 2021). For example, in harsh post-fire environments, seeds and suckers often require protected regeneration sites to successfully germinate and/or survive (e.g., Marzano et al. 2013; Klutsch et al. 2015). The need for protected microsites for many pine, spruce, and fir seedlings, for example, can be amplified in alpine forests in North America (Stine and Butler 2015).

Modulating all fire-impacted variables is fire severity, which describes the damage or change a fire induces, and often considers plant mortality and forest floor changes (Keeley 2009). Fire severity is of universal importance in understanding post-fire forest dynamics (e.g., Haire and McGarigal 2010; Shenoy et al. 2011; Croteau et al. 2013). High-severity fires are associated with extreme post-fire changes in ecological conditions, including total or near total overstory mortality and deep ground-layer consumption. Such conditions can impede the regeneration of many non-fire-adapted species (e.g., Holz et al. 2015; Donato et al. 2016), while creating favorable conditions for other species that are better adapted to the post-fire environment (e.g., Barker et al. 2022). One would expect the impacts of high-severity fire to reverse as time since fire increases, though this is not always the case, as wild-fire in non-fire-adapted ecosystems can lead to long-term ecological shifts (e.g., Ruggirello et al. 2023a, 2023b). Ultimately, environmental and fire-impacted variables, in combination with species' fire and shade tolerances, determine post-fire forest recovery or lack thereof.

Forest management, defined here as extraction or production activities such as logging or grazing (i.e., not tree planting), is neither an environmental nor fire-impacted variable, but it can also strongly impact forest recovery post-fire. Pre-fire management, for example, can have either a negative (e.g., illegal logging that removes the healthiest individuals from a forest) or positive (e.g., grazing to reduce fuel loads) impact on post-fire recovery (Kukavskaya et al. 2013; Lovreglio et al. 2014). Conversely, post-fire extractive management is more generally considered to be detrimental to forest recovery. For example, post-fire salvage logging is one of the most common post-fire management activities, yet it tramples seedlings and damages regeneration sites (e.g., Castro et al. 2012; Leverkus et al. 2014; Marcolin et al. 2019).

Through this systematic review of peer-reviewed articles published between January 1, 2000 and December 1, 2021, we sought to assess the correlations between post-fire forest regeneration at high latitudes and (i) latitude; (ii) environmental conditions; (iii) fire-impacted variables

and fire severity; (iv) unburned forest conditions within or adjacent to burned areas; (v) post-fire microsite conditions; (vi) pre- and post-fire forest management activities; and (vii) species fire and shade tolerances. Given that forests at high latitudes globally are subject to similarly challenging growing conditions (i.e., short-growing seasons, extreme cold temperatures, low tree-species diversity), we hypothesized that:

H1 As latitude increases from 40°, regeneration densities decrease.

H2 Unfavorable environmental and microsite conditions and extreme fire impacts reduce post-fire regeneration and these effects are worsened by forest management.

H3 Fire-tolerant and shade-intolerant species dominate post-fire landscapes.

2 Materials and methods

2.1 Defining “high-latitude”

The US National Oceanic and Atmospheric Administration's (NOAA) Space Weather Prediction Center (SWPC) classifies high latitude as 60° magnetic latitude or higher. If one defines high-latitude forests as those found at or over 60° magnetic latitude, northern hemisphere boreal forests are the only forest type present (Olson et al. 2001). However, there is not a consensus definition of “high latitude” that restricts it to being at or over 60° when referring to forests (e.g., Trahan and Schubert 2016; Robinne et al. 2020). For the purposes of this study, a high-latitude threshold was determined referencing the major world biomes accepted by the World Wildlife Fund (Olson et al. 2001). Within our definition, we sought to include temperate coniferous, temperate mixed broadleaf and coniferous, and boreal forests growing at or above 40° north or south. We chose this wider latitudinal range so as to be able to analyze regeneration responses to fire across a broader gradient of latitudes, environmental conditions, fire regimes, and biomes that are representative of both hemispheres.

2.2 Initial search and preliminary review

Using Elsevier's abstract and citation database Scopus, we searched for peer-reviewed publications, which studied the impacts of wildfire on tree regeneration. Our search string limited articles to those published in English and Spanish from the year 2000 onwards. Countries were limited to those containing land at high latitudes. Using a search string (Fig. 1), we returned the title, abstract, and keywords for 4537 articles. We then conducted a review of the title, abstract, and, when needed, the main text of each of the 4537 articles returned in our initial search (December 1, 2021).

Enter query string

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( TITLE-ABS-KEY ( "FOREST" ) AND TITLE-ABS-KEY ( wildfire ) OR TITLE-ABS-KEY ( fire ) OR TITLE-ABS-KEY (
burn ) AND TITLE-ABS-KEY ( "tree regen" ) OR TITLE-ABS-KEY ( response ) OR TITLE-ABS-KEY ( "sprout" ) OR
TITLE-ABS-KEY ( "seed" ) OR TITLE-ABS-KEY ( "survive" ) OR TITLE-ABS-KEY ( recuperation ) OR TITLE-ABS-KEY (
"recover" ) OR TITLE-ABS-KEY ( "wood" ) ) AND ( LIMIT-TO ( PUBYEAR,2022 ) OR LIMIT-TO ( PUBYEAR,2021 ) OR
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AND ( LIMIT-TO ( SUBJAREA,"AGRI" ) OR LIMIT-TO ( SUBJAREA,"ENVI" ) OR LIMIT-TO ( SUBJAREA,"EART" ) )
AND ( LIMIT-TO ( DOCTYPE,"ar" ) ) AND ( LIMIT-TO ( LANGUAGE,"English" ) OR LIMIT-TO (
LANGUAGE,"Spanish" ) ) AND ( LIMIT-TO ( AFFILCOUNTRY,"United States" ) OR LIMIT-TO (
AFFILCOUNTRY,"Canada" ) OR LIMIT-TO ( AFFILCOUNTRY,"United Kingdom" ) OR LIMIT-TO (
AFFILCOUNTRY,"Germany" ) OR LIMIT-TO ( AFFILCOUNTRY,"China" ) OR LIMIT-TO ( AFFILCOUNTRY,"Sweden" )
) OR LIMIT-TO ( AFFILCOUNTRY,"France" ) OR LIMIT-TO ( AFFILCOUNTRY,"Netherlands" ) OR LIMIT-TO (
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AFFILCOUNTRY,"Russian Federation" ) OR LIMIT-TO ( AFFILCOUNTRY,"Chile" ) OR LIMIT-TO (
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) OR LIMIT-TO ( AFFILCOUNTRY,"Czech Republic" ) OR LIMIT-TO ( AFFILCOUNTRY,"Estonia" ) OR LIMIT-TO (
AFFILCOUNTRY,"Denmark" ) OR LIMIT-TO ( AFFILCOUNTRY,"Ireland" ) OR LIMIT-TO (
AFFILCOUNTRY,"Lithuania" ) OR LIMIT-TO ( AFFILCOUNTRY,"Mongolia" ) OR LIMIT-TO (
AFFILCOUNTRY,"Ukraine" ) OR LIMIT-TO ( AFFILCOUNTRY,"Belarus" ) OR LIMIT-TO (
AFFILCOUNTRY,"Kazakhstan" ) OR LIMIT-TO ( AFFILCOUNTRY,"Latvia" ) )
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Fig. 1 Text string for our initial search

The search was rerun on August 24th, 2023, for articles published through December 1st, 2021, to check for articles that may have been missed in the initial search. Three additional articles were returned, but they did not meet the criteria for inclusion in the review. The search was rerun again on October 13th, 2023, and no additional papers appeared; six fewer articles were, in fact, returned.

We are aware that a small number of potentially appropriate articles were not returned through our search, although they are currently available through Scopus (namely, Larson et al. 2013, Stevens-Rumann and Morgan 2016, Whitman et al. 2019). These three studies not returned in our Scopus searches were conducted in regions (the western USA and northwest Canada) and forest types (pine-dominated, boreal, and mixed coniferous) that are very well represented in this review (n of articles > 30). It is well-documented that the main bibliometric databases principally used in systematic reviews (Scopus, Google Scholar, and Web of Science) all have limitations in journal coverage due to causes that include journal and database policies limiting the availability of certain articles at certain points in time, excluded publication types, underrepresented academic disciplines, and more (Harzing and Alakan-gas 2016; Mongeon and Paul-Hus 2016; Aksnes and Sivertsen 2019). Systematic review coverage is also sensitive to the specific keywords chosen for use in search engine queries and even when comprehensive keywords are chosen for a search, not all appropriate literature housed in a bibliometric database is returned (Linder et al. 2015).

We are also aware that journal language of publication and country of origin, namely, China and Russia in this review, can also result in potentially appropriate articles not being returned in a database search (Aksnes and Sivertsen 2019). However, both countries were represented in our Scopus search, which returned over 70 papers from China and over 25 from Russia, although only one study from each region was retained for further analysis. Among the most common reasons for elimination of articles from these regions was the extensive use of remote sensing to detect post-fire tree regeneration in these countries; this may be due to the vast and remote nature of their forests. Upon extensive validation of our search results, we believe the vast majority of relevant articles published through December 1st, 2021, that meet our search criteria were captured within our results, representing a critical mass of literature from high-latitude regions.

From our initial review, 226 articles were retained for further analysis. An additional 133 articles were excluded after further review, leaving us with a total of 93 articles (Table 4 in Appendix). The most common reasons for eliminating an article were as follows: that it addressed the relationship between fauna and wildfire ($n = 508$), or that the average study latitude did not fall within the desired latitudinal range ($n = 398$). Articles dealing with intentionally ignited fires (e.g., prescribed fires, pile burning, slash-and-burn agriculture), the interaction of fire effects with other variables such as insect activity or climate, plantation settings, manipulative experiments, indirect measurement of tree regeneration through remote sensing, fire history, or dendrochronology were also common and were eliminated. We retained only

those articles that directly measured post-wildfire tree regeneration within our geographical study area.

2.3 Data extraction

We extracted data from the 93 retained articles and used these data to create five distinct datasets (Fig. 2). All datasets include the same basic preliminary information: article name and number, country of study, latitude, biome, average elevation, and year of publication. Each dataset then include the following dataset-specific information:

- 1) Fire characteristics: as many studies included more than one fire, this dataset includes information on every fire studied across all articles. In total, it contains 268 distinct fires. Fire size, severity, date, and the time between the fire and field survey were extracted directly from information provided in the articles as defined by the articles' authors. Each row in this dataset corresponds to one fire.
- 2) Experimental design: number of plots, plot type (fixed-area or variable-area), and plot shape (belt,

quadrat, circle, point). Each row in this dataset corresponds to an individual article.

- 3) Relative species composition: approximately half of the articles reviewed provided information on the percent of plots where a given species or group of species were present after fire and pre-fire/without fire. There are a total of 80 rows in this dataset. Each article used in this dataset has two rows associated with it: one for shade intolerant and fire tolerant composition pre-fire/unburned and post-fire and another for shade tolerant and fire intolerant composition pre-fire/unburned and post-fire. For this dataset, we categorized each species shade and fire tolerance (described in the next section). Here, and throughout our different datasets, we retained species that were presented in groups only when all species in a given group had the same shade and fire tolerances.
- 4) Pre-fire/unburned and post-fire regeneration: there are 595 total rows in this dataset. Each row represents a "case" with values for post-fire regeneration and pre-fire/unburned regeneration, when available. A given

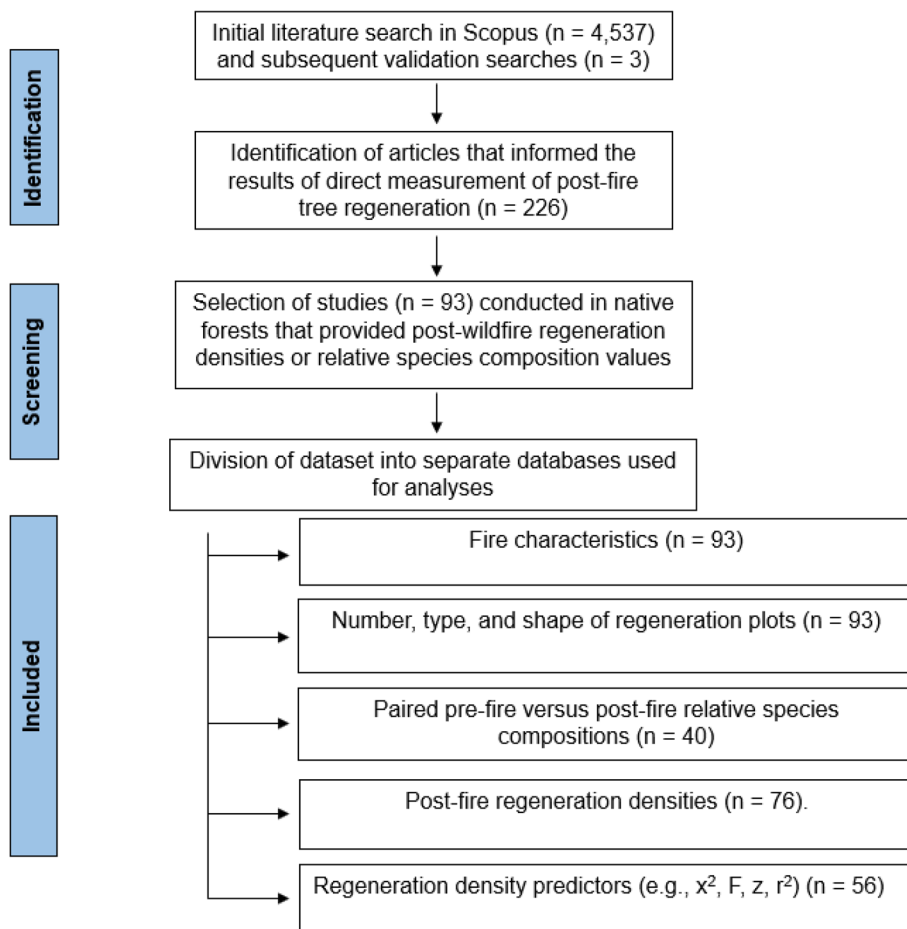


Fig. 2 PRISMA flow diagram detailing the filtering process from the initial literature search to the final number of studies retained for analysis

article could have multiple cases: for example, (i) regeneration density of *Pinus ponderosa* after a single, high-severity fire; (ii) regeneration density of *Pinus ponderosa* after multiple fires; or (iii) regeneration density of *Pinus contorta* 3 years after fire; (iv) regeneration density of *Pinus contorta* 15 years after fire. The particularities of different cases were determined by how data were presented in a given article, but each case represents a unique situation under which a species or group of species was regenerating as defined by an article's authors. Regeneration was considered as seedlings or saplings shorter than breast height (1.4 m) and with a diameter under 5 cm and was standardized to stems ha⁻¹.

- 5) Post-fire regeneration predictors: each row represents a correlation, the relationship between regeneration post-fire and a given predictor. We grouped these explanatory predictors into the following categories: (1) environmental variables, (2) fire-impacted variables, (3) pre-fire/unburned conditions, (4) microsites, and (5) management. More details on the specific predictors that make up each category are contained in Table 5 in [Appendix](#). In addition to predictor categories, this dataset contains model coefficients (e.g., F , z , β), p values, whether coefficients are positive or negative and significant ($p \leq 0.05$) or nonsignificant, and the number of observations used to calculate each model coefficient. In total, there are 547 correlations listed in this dataset. Interacting predictors (e.g., aspect*slope) were then eliminated from the dataset, leaving 520 correlations.

For datasets three and four, we gave pre-fire/unburned and post-fire/burned management designations for each row entry (0 = no management, 1 = management, blank = not informed). Studies that provided unburned controls did so in the form of either pre-fire data collected from an area that later burned, or data collected from an unburned area adjacent to a burn scar. These two control conditions were considered together as pre-fire/unburned controls. These datasets are available online through the Dryad digital depository (Ruggirello et al. [2023d](#)).

2.4 Species classifications

Datasets three (relative species abundance) and four (regeneration) required us to classify species by their

shaded conditions. Species were also divided into those having high fire tolerance, possessing significant adaptations known to aid in surviving fire and/or establishing successfully post-fire (e.g., widespread resprouting from top-killed individuals, prolific production of windblown seed, thick bark), or low fire tolerance species lacking such adaptations. Shade and fire tolerance classifications are available through the United States Forest Service Fire Effects Information System (FEIS) [2023](#) (available at <https://www.feis-crs.org/feis/>) for all major North American and some European tree species. Species silvics and fire responses described through the FEIS are supported by extensive peer-reviewed literature. For tree species not listed in the FEIS, we searched for substantiating peer-reviewed literature to classify their shade and fire tolerances. Whereas most literature on species not listed in the FEIS often directly references a species shade tolerance (e.g., Lusk [1996](#); Gutiérrez et al. [2009](#)), fire tolerance or fire-specific adaptations are often not referenced explicitly, particularly for South American and Asian species from areas where wildfires were historically infrequent. We used species fire-adapted reproduction or resistance strategies, e.g., the ability to resprout prolifically after disturbance, bark thickness, seed size, and dispersion method, to infer fire tolerance when appropriate. If sufficient evidence was not available to classify a species shade or fire tolerance, we classified its tolerance as unknown.

2.5 Data analysis

To explore our database, we averaged pre-fire/unburned- and burned-area regeneration across all cases in dataset 4. We then categorized mean case-by-case regeneration (stems ha⁻¹) and standard errors by latitude band (40–49.99°, 50–59.99°, >59.99°), biome (temperate coniferous, temperate mixed broadleaf and coniferous, and boreal), fire severity (low/moderate, high, mixed), and management status (with and without, pre- or post-fire). Mixed-severity fires were those containing a relatively balanced portion of low-, moderate-, and high-severity burn patches as defined by an article's authors. Low- and moderate-severity fires were combined into one category because of the limited number of wildfires described as having burned at moderate severity ($n = 4$). After calculating mean regeneration across all cases, the difference between pre-fire/unburned-area and burned-area regeneration was calculated as:

$$\left(\frac{\text{prefire or unburned area regeneration} - \text{burned area regeneration}}{\text{prefire or unburned area regeneration}} \right) * -100$$

shade and fire tolerances (Table 6 in [Appendix](#)). A given species was categorized as either shade tolerant or intolerant based on its ability to regenerate and persist in

To respond to the first and third hypotheses (i.e., the effect of latitude on post-fire regeneration and the

dominance of fire-tolerant, early-seral species), we fit linear mixed models (LMMs), to the natural log (ln) of post-fire regeneration at the case scale. By doing an ln transformation, we excluded 12 observations (2.2%) where regeneration was zero, but we substantially improved model fitting. We reran the models with ln (post-fire regeneration + 1) and the direction and magnitude of the effects remained similar (results not shown). For the first hypothesis, we used latitude, year, and average time since fire as fixed variables and the identity of the study as a random factor to account for the variability in sampling methods. We added species shade tolerance and fire tolerance as fixed factors to the previous model to answer the third hypothesis. Numerical predictor variables were standardized (Schiezeth 2010). We weighted each observation in the models by the precision of each study (i.e., the number of plots where regeneration was measured, Mengersen et al. 2013). Between-study heterogeneity accounted for most of the variation in post-fire recruitment, as the heterogeneity statistic I^2 index was 94.4% (Higgins and Thompson 2002). Furthermore, the random-effects meta-analytic model fitted the data better than the fixed-effect meta-analytic model in terms of the Akaike information criterion (AIC, Burnham and Anderson 2002). Thus, we adopted random-effects meta-analytic models, accounting for both between- and within-study heterogeneity with weighting. LMMs were fit using the lme4 package (Bates et al. 2015) in R (R Core Team 2022).

With dataset three and to further analyze the third hypothesis (fire and shade tolerances), we calculated relative species abundance means and standard error by shade and fire tolerance categories for pre-fire/unburned and burned areas at the article level. For each article that provided the appropriate information for this analysis, pre-fire/unburned and burned species compositions were relativized to 100% and summarized as (i) the percent of plots with shade tolerant versus intolerant species present with and without fire, and (ii) the percent of plots with fire-tolerant versus fire-intolerant species present with and without fire. With relative species abundances already expressed in percentages and relativized to 100, we calculated difference simply as mean burned-area relative species abundance minus mean pre-fire/unburned-area relative species abundance.

In response to the second hypothesis related to the drivers of post-fire regeneration, we transformed the predictor coefficients observed in each study (dataset five) into Z effect size for all statistic types except for β ($n = 162$) and H ($n = 2$) because the sample size for different treatments was not available (β), or the number

of groups was not available (H). We used the R package `esc` (Lüdtke 2019) for all statistic types except for Kendall's τ that was transformed following criteria established by Steyn (2020). For each predictor category (Table 5 in Appendix), to determine their impacts on post-fire regeneration, we studied the proportion of significant observations, and to explore the magnitude and direction of the effect we analyzed the distribution of Z effect sizes when possible.

3 Results

3.1 General overview

The 93 articles retained for analysis covered 268 distinct wildfires. The countries most represented in this study were the USA ($n = 52$ articles) and Canada ($n = 23$ articles). All other countries (Argentina, Chile, China, Estonia, Italy, Switzerland, Mongolia, Poland, and Russia) had fewer than five articles per country. In terms of individual fires, the countries most represented were the USA ($n = 147$ fires), Canada ($n = 55$ fires), Italy ($n = 39$ fires), and Switzerland ($n = 39$ fires). All other countries had fewer than five fires per country. The largest fires (>400,000 ha) were located in the USA and Canada. Over 50% of fires ($n = 143$) were 21,000 ha or smaller (Fig. 3). The majority of fires were described as mixed severity ($n = 128$), while 61 fires were defined as high severity, and 31 as low/moderate severity. In relation to time since fire, 75% of fires occurred within 16 years of field measurements. Of the 93 studies, 81 used fixed-area plots and 12 used variable-area plots (data not shown). Quadrats were the most common plot shape ($n = 43$), followed by belt transects ($n = 23$) and circular plots ($n = 22$). The point-intersection method was also used in two studies and three studies did not define their plot shape.

Post-fire regeneration densities increased relative to pre-fire regeneration densities (Table 1). The coniferous biome, which had less pre-fire regeneration than the other forest types, experienced the smallest post-fire increase in regeneration densities. Boreal forests had notably more post-fire regeneration than either of the two other forest biomes. Forests that experienced low/moderate fire had a similar post-fire regeneration response to those that experienced high-severity fire. Areas that experienced mixed-severity fires had the strongest tree regeneration response post-fire. Both pre-fire and post-fire management resulted in increases in regeneration relative to unmanaged forests with this response being notably larger with post-fire management, although that category also had

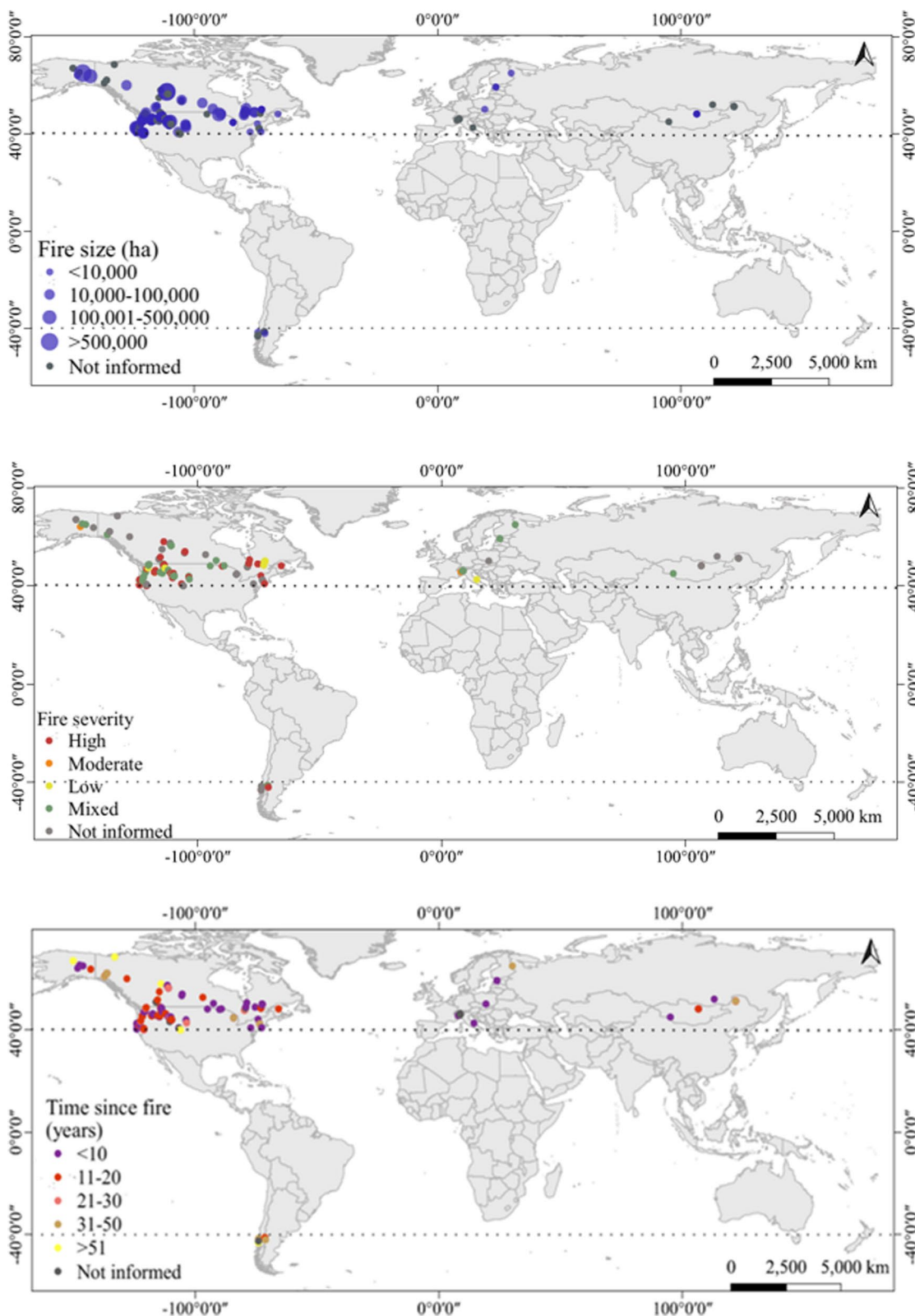


Fig. 3 An overview of fire size (top), severity (middle), and time since fire (bottom) of all fires described in the literature review for which this information was provided (northern and southern hemispheres); not all studies provided information for all three categories

Table 1 Mean regeneration density (\pm standard error) expressed as average stems per hectare pre-fire or in unburned areas and in burned areas. "Difference" was calculated by subtracting pre-fire/unburned average recruitment from burned average recruitment and then dividing by pre-fire/unburned recruitment and multiplying by -100

	Pre-fire/ unburned (stems ha ⁻¹)	Burned (stems ha ⁻¹)	Difference (%)
Total	3985 \pm 665	10,140 \pm 1553	+154
<i>Latitude</i>			
40–49.9°	2694 \pm 548	4457 \pm 907	+65
50–59.9°	5788 \pm 1281	15,335 \pm 2363	+165
>59.9°	12,364 \pm 4429	32,149 \pm 8276	+160
<i>Biome</i>			
Coniferous	1488 \pm 285	1994 \pm 290	+34
Broadleaf/mix	5028 \pm 1478	9291 \pm 2838	+85
Boreal	6634 \pm 1671	21,124 \pm 4028	+218
<i>Fire severity</i>			
Low/moderate	2577 \pm 729	7825 \pm 3387	+204
High	1713 \pm 343	5840 \pm 1549	+241
Mixed	7243 \pm 2068	21,750 \pm 5378	+200
<i>Management</i>			
No pre-fire	8398 \pm 1803	14,426 \pm 2782	+72
Yes pre-fire	4945 \pm 1593	19,232 \pm 6278	+289
No post-fire	2768 \pm 588	4460 \pm 1285	+61
Yes post-fire	10,043 \pm 2787	31,979 \pm 8217	+218

more regeneration pre-fire than any other management category.

3.2 Impact of latitude on post-fire regeneration

Regeneration densities increase with increasing latitude (estimate = 1.369, df = 64, $p < 0.001$) (Fig. 4, for more details see Figure 7 in [Appendix](#) and Table 7 in [Appendix](#)). This increase was greatest in forests with post-fire management and at latitudes $> 59.9^\circ$ and lowest in the coniferous biome and in forests without post-fire management (Table 1). In terms of latitude, forests in the 40–49.9° range experienced the smallest positive regeneration impact from fire, and, although forests $> 59.9^\circ$ experienced the greatest net increase in stems per hectare, the band from 50 to 59.9° had a nearly threefold increase in regeneration relative to pre-fire/unburned forests.

Post-fire regeneration density (stems ha⁻¹) was approximately one-hundred times higher as latitude approaches its maximum value compared to the lowest latitudes studied in this systematic review (Fig. 4, Table 7 in [Appendix](#)). There was a gap in regeneration

around 55°, resulting in a group of studies above and a group below this latitude. According to our model, time since fire was negatively associated with regeneration density (estimate = -0.728 , df = 77, $p = 0.043$), while year of study had no effect (estimate = -0.486 , df = 69, $p = 0.284$).

3.3 Effects of fire-impacted variables of post-fire regeneration

Environmental variables, fire-impacted variables, and microsites had the highest proportion of significant cases of the five predictor categories (Fig. 5). All subcategories of predictors had a proportion of significant cases greater than 0.50 with the exception of management and time since fire. The predictor subcategories with the highest proportion of significant cases were soil organic matter, high-severity fire, and wet/cool conditions. All predictor subcategories had at least 12 cases. Effect size was largest for the predictor subcategories elevation and reproductive variables (positive), and unprotected microsites (negative). Soil organic matter (negative), high-severity fire (negative), and unburned stand conditions (positive) also had effect sizes whose means did not intersect with zero.

3.4 Effects of shade and fire tolerances on post-fire regeneration

According to our model, a species shade tolerance did not significantly impact (estimate = -0.495 , df = 337, $p = 0.840$) its post-fire regeneration density (Table 8 in [Appendix](#), Figure 8 in [Appendix](#)). The dominance of shade-intolerant species did increase on average post-fire, but this increase was not significant considering covariates such as latitude, year, and time since fire. Still, shade-intolerants relative abundance increased post-fire overall (Fig. 6, Table 8 in [Appendix](#)) and across all classification categories with the exception of forests with pre-fire management (Table 2). This increase was strongest in broadleaf forests and with post-fire management. The 40–49.9° latitude band had a larger post-fire increase of shade-intolerant relative abundance than did forests in the 50–59.9°. Pre-fire relative abundance of shade-intolerants was highest in the coniferous biome, followed by the boreal, and then the broadleaf/mixed-coniferous biomes. The relative abundance of shade-intolerants was minimally impacted by high- and low/moderate-severity fire, but increased somewhat more after mixed-severity fire. In general, shade-intolerants were most present pre- and post-fire in forests that burned at high severity. The presence or absence of pre-fire management impacted

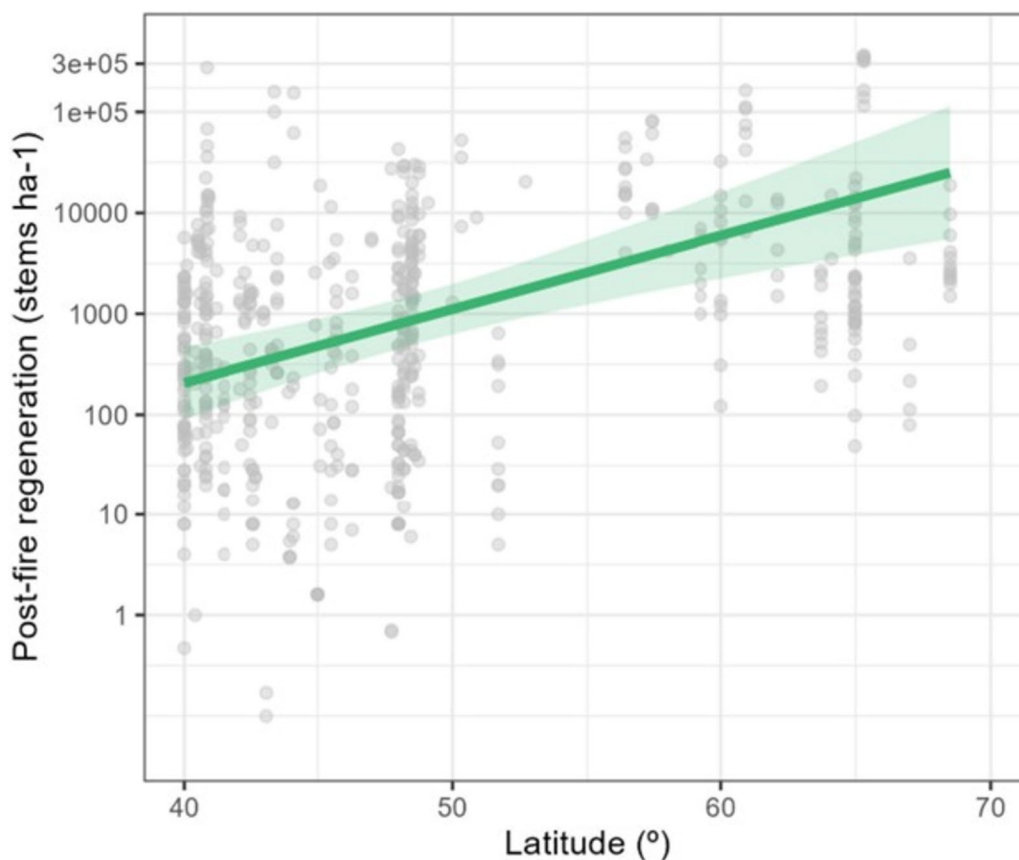


Fig. 4 The relationship between post-fire regeneration (stems ha^{-1}) and absolute latitude ($^{\circ}$) informed in reviewed articles. The line represents the prediction by linear mixed models; the shaded area is the confidence interval along the prediction, and the dots are observed values. Note that the Y axis is In-transformed

the relative species abundance of shade-intolerants with the only post-fire decrease in shade-intolerants having occurred in forests with pre-fire management.

According to our model, species' fire tolerances had a significant effect (estimate = -0.498 , $df = 365$, $p = 0.023$) on their post-fire regeneration densities (Table 9 in Appendix, Figure 9 in Appendix), indicating that the post-fire densities of fire-tolerant species were higher than densities of fire-intolerant species, after controlling for covariates such as latitude, year, and time since fire. Those species described as being fire-tolerant increased in dominance post-fire overall and across all classification categories with the exception of forests with pre-fire management and forests that experienced low/moderate-severity fire (Table 3, Figure 9 in Appendix). This increase was strongest in broadleaf forests and forests without pre-fire management. Pre-fire relative species abundance of fire-tolerants was

highest in the boreal biome, followed by the coniferous, and then the broadleaf/mixed-coniferous biomes. The differences between biomes persisted after fire, as fire-tolerant species in all three biomes increased. The prevalence of fire-tolerants was not impacted by fire severity, although fire-tolerant species did increase notably after high-severity fire. The presence or absence of pre-fire or post-fire management did not significantly impact the relative species abundance of fire-tolerants; however, fire-tolerant species experienced a greater than 20% increase post-fire in forests without pre-fire management and a 3.8% decrease after fire in forests with pre-fire management. Forests without post-fire management also experienced a greater increase in fire-tolerants post-fire than forests with post-fire management. Conversely, fire-intolerant species represented 62.2 ± 6.3 (%) of species present in pre-fire regeneration plots and 42.0 ± 5.2 (%) of those

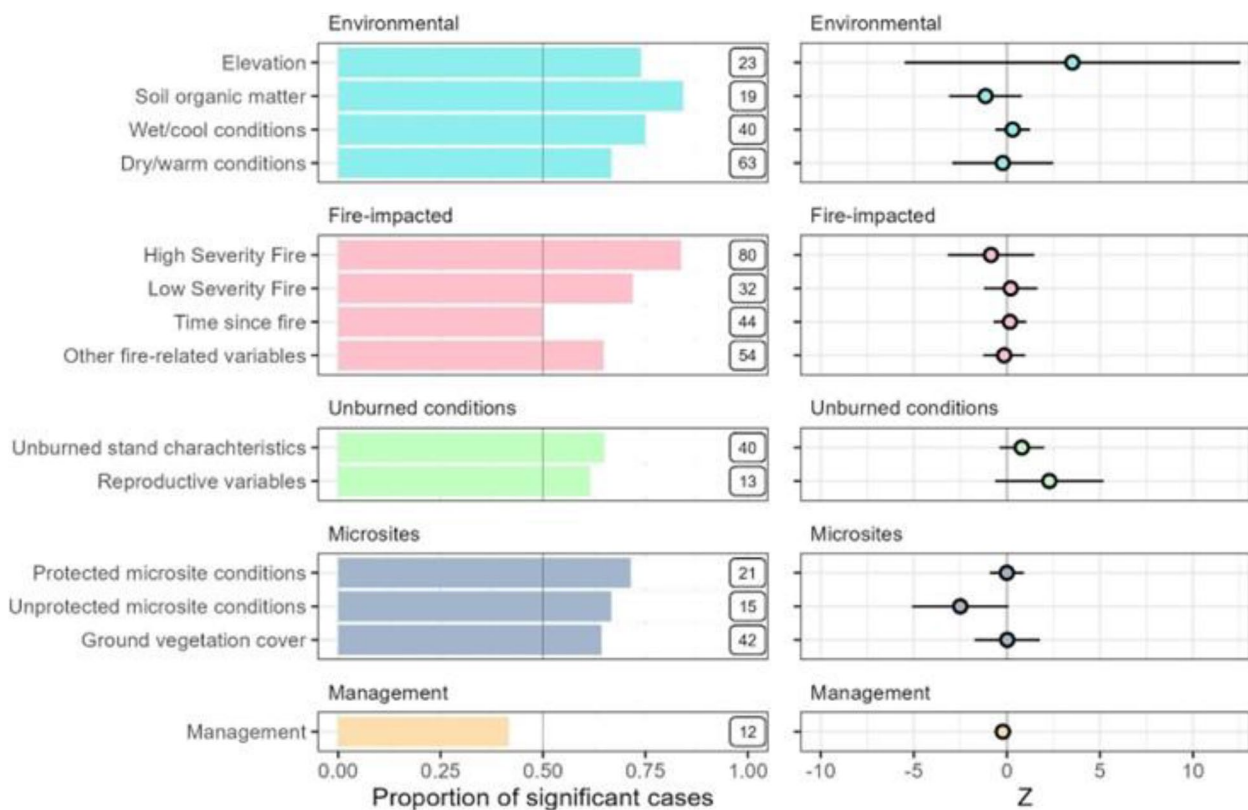


Fig. 5 Effect of predictor categories on post-fire regeneration in high-latitude forests. The colored bars show the proportion of significant cases per predictor category with the total number of cases within a square (left), and the circles and whiskers show the mean \pm standard deviation of effect size (right)

present in post-fire plots, resulting in a 20.2% decrease in fire-intolerant species post-fire.

Broken down by genus, aspen (*Populus*), pine (*Pinus*), and birch are found ubiquitously at high latitudes (present in 22, 28, and 14 studies, respectively) and generally responded very favorably to fire (Fig. 6). The post-fire regeneration responses of larch and willow (*Salix*) species were weaker than aspen, fire-adapted pines, and birch despite the fact that larch and willow are fire tolerant and shade intolerant. Although alder (*Alnus*) and oak (*Quercus*) responded very positively to fire, their presence at high latitudes and in this study (present in only two articles each) was limited. Hemlock was also only present in two studies as well. Spruce (*Picea*) was present in 23 different studies and was also one of the genera with the strongest positive regeneration responses to fire, despite being classified as fire intolerant and shade tolerant. With the exception of hemlock and spruce, the genera that responded most positively to fire were classified as being fire tolerant.

All fire-tolerant genera with the exception of fire-tolerant maple species rebounded strongly after fire (>5000 stems ha⁻¹). In general, maple and fir species experienced the weakest post-fire regeneration response of any major genera. Unfortunately, forests at high southern latitudes and their tree species' responses to fire were under-represented in the scientific literature. In the southern hemisphere, only Chile and Argentina produced usable studies ($n = 7$) that reported data for *Austrocedrus*, *Nothofagus*, and *Pilgerodendron* species. A complete list of all genera and species present in this systematic review is provided in the Appendix section (Figure 10 in Appendix).

4 Discussion

4.1 Increasing latitude does not deter post-fire regeneration

We refute the hypothesis that post-fire regeneration decreases as latitude increases from 40°, as our results suggest that the opposite is true. A myriad of linked

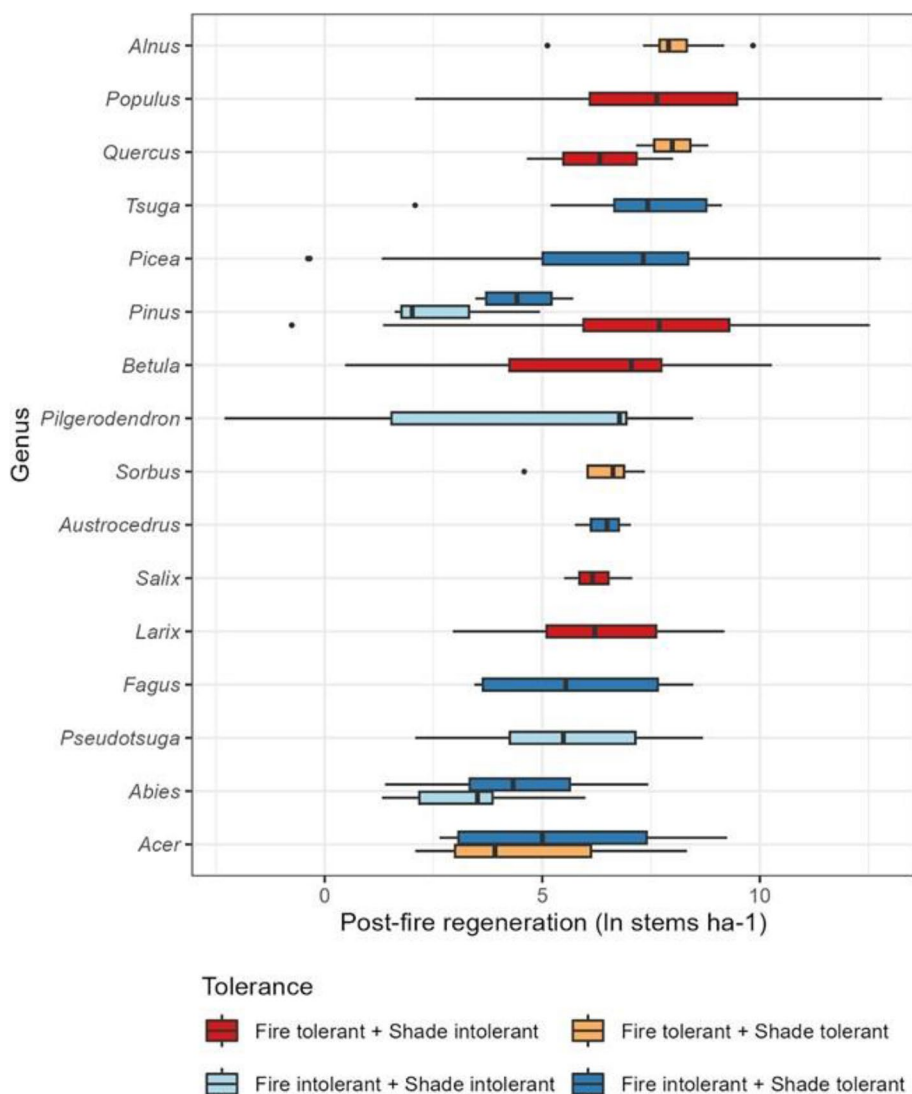


Fig. 6 Post-fire regeneration density of the most frequently studied genera grouped by fire and shade tolerance

factors can explain the positive relationship between latitude and post-fire regeneration, the impacts of increasingly drier and warmer conditions at lower latitudes may be principal among them, as the negative impacts of xeric conditions on forests are exacerbated as latitude decreases (e.g., Silva and Anand 2013). Our results could also be related to climate change in that species are increasingly regenerating more prolifically in the northern hemisphere at higher latitudes within their ranges of distribution as temperatures increase (Lenoir and Svenning 2015). Broad increases in temperature allow forests at higher latitudes where extreme cold was historically common to recover from

disturbance and even expand their cover more fully and rapidly than in the past (Alfaro-Sánchez et al. 2019; Noce et al. 2020; Palmero-Iniesta et al. 2020; Soler et al. 2022).

Changes in fire regimes are also linked to increases in temperatures and aridity associated with climate change (Seidl et al. 2017). Nearly all, if not all, studies included in our review were conducted in regions where wildfires were present historically. The degree to which fire was present on a given landscape, i.e., fire-return-intervals, the average size of fires, and typical fire severity, varied historically by geographical region and forest type. In the rainforests of central Chile, for example, wildfires

Table 2 Relative species abundance (%) of shade-intolerant species pre-fire or in unburned areas and in burned areas. "Difference" was calculated as the mean relative species abundance in burned areas minus mean relative abundance pre-fire or in unburned areas

	Pre-fire/ unburned (%)	Burned (%)	Difference (%)
Total	59.0 ± 5.2	69.0 ± 4.3	+10.0
<i>Latitude</i>			
40–49.9°	59.9 ± 5.8	71.1 ± 4.6	+11.2
50–59.9°	55.4 ± 12.8	62.8 ± 16.0	+7.4
>59.9°	No data	61.0 ^a	
<i>Biome</i>			
Coniferous	68.9 ± 4.7	73.5 ± 4.5	+4.6
Broadleaf/mix	36.4 ± 10.8	61.9 ± 9.8	+25.5
Boreal	56.3 ± 13.4	69.2 ± 9.7	+12.9
<i>Fire severity</i>			
Low/moderate	52.0 ^a	55.0 ± 25.5 ^a	+3.0
High	76.3 ± 6.5	77.3 ± 6.1	+1.0
Mixed	58.0 ± 7.7	65.4 ± 6.8	+7.4
<i>Management</i>			
No pre-fire	60.5 ± 6.0	65.0 ± 6.9	+4.5
Yes pre-fire	60.6 ± 18.8	58.4 ± 10.3	–2.2
No post-fire	72.8 ± 7.3	77.7 ± 4.6	+4.9
Yes post-fire	39.3 ± 8.5	53.6 ± 10.0	+14.3

^a n of studies < 5. Shade-tolerant species were not included in this table as they generally had the exact opposite numeric values as shade-intolerants in each category

Table 3 Relative species abundance (%) of fire-tolerant species pre-fire or in unburned areas and in burned areas. "Difference" was calculated as the mean relative species abundance in burned areas minus mean relative abundance pre-fire or in unburned areas

	Pre-fire/ unburned (%)	Burned (%)	Difference (%)
Total	39.5 ± 6.4	56.9 ± 5.2	+17.4
<i>Latitude</i>			
40–49.9°	39.1 ± 7.0	55.8 ± 5.7	+16.7
50–59.9°	40.8 ± 16.5	57.2 ± 18.3	+16.4
>59.9°	No data	63.5 ^a	
<i>Biome</i>			
Coniferous	39.3 ± 7.5	58.2 ± 5.4	+18.9
Broadleaf/mix	18.0 ^a	41.2 ± 12.1	+23.2
Boreal	54.2 ± 14.5	67.7 ± 10.7	+13.5
<i>Fire severity</i>			
Low/moderate	26.0 ^a	23.3 ^a	–2.7
High	40.6 ± 12.9	59.0 ± 8.1	+18.4
Mixed	42.4 ± 11.3	50.1 ± 7.2	+7.7
<i>Management</i>			
No pre-fire	24.9 ± 5.7	47.9 ± 6.9	+23.0
Yes pre-fire	66.5 ^a	62.7 ± 13.1	–3.8
No post-fire	42.3 ± 9.5	56.6 ± 6.4	+14.3
Yes post-fire	39.5 ± 13.6	43.8 ± 11.4	+4.3

^a n of studies < 5. Fire-intolerant species were not included in this table as they generally had the exact opposite numeric values as fire-tolerants in each category

were somewhat frequent before widespread Euro-Chilean settlement, but the frequency and severity of fires increased greatly after colonization and particularly over the last several decades (Holz and Veblen 2011).

In regions where tree diversity is low and those species that are present lack strong adaptations to fire, in the temperate mixed broadleaf and coniferous forests of the extreme south of South America (Ruggirello et al. 2023b) and southern Oceania (Holz et al. 2015), for example, colonization of burned landscapes by trees is tenuous and can result in the long-term loss of forest (e.g., Perry et al. 2014). However, no studies from these particular forests met the search criteria for this review article, as results from the extreme south of South America have only been published within the last year (Ruggirello et al. 2023a, 2023b, 2023c) and much of the native forest of southern Oceania has been converted to tree plantations (Robertson 2006; Downham and Gavran 2018), which were excluded from this review.

In the extreme northern hemisphere, study areas were dominated by boreal forests (Olson et al. 2001). Boreal forests have evolved over thousands of years

with intermittent wildfire (Walker et al. 2019). Although fire regimes are changing throughout much of the boreal biome (Kelly et al. 2013), the results of this systematic review and other studies (e.g., Paudel et al. 2015; Johnstone et al. 2020) suggest these forests generally recover ample tree cover after wildfire (Boulanger et al. 2018). However, increases in the number and size of fires produce large-scale shifts to forests dominated by early-seral species (Johnstone et al. 2020), and repeat wildfires in rapid succession can reduce regeneration densities altogether in boreal forests (e.g., Whiteman et al. 2019).

Much like boreal forests, temperate coniferous and temperate mixed broadleaf and coniferous forests closer to 40° north evolved in the presence of wildfire and contain many species that are dependent on fire to regenerate and thrive (Wright and Heinselman 2014). This is especially true in western North America, a region well represented in our review, where historically low- to moderate-severity, frequent fires ignited by lightning and native peoples maintained relatively open forest conditions favoring many pine, larch, and aspen species

(Vale 2002). However, our results indicate that although these forests had more regeneration post-fire than pre-fire, their post-fire regeneration densities were substantially lower than in boreal forests generally located further north.

With the widespread colonization of western North America by non-native peoples, frequent, low-severity fires were suppressed throughout much of the twentieth century, resulting in forests that were denser and more homogenous than was historically normal (Hessburg et al. 2019). These conditions, coupled with a warming, drying climate and a growing human population in wildland-urban interfaces, have increased the frequency, size, and severity of fires in recent decades (Abatzoglou and Williams 2016; Davis et al. 2019). After these “megafires,” seeds and suckers of tree species must establish in conditions that are typically drier and warmer than post-fire conditions in boreal forests further north (Kemp et al. 2019; Coop et al. 2020). Tree regeneration, in general, is sensitive to departures from historically normal regeneration conditions; these departures from normal have become more frequent and extreme as a result of the interplay between climate change and fire (e.g., Dobrowski et al. 2015). Consequently, areas that were marginal forest habitat before a fire, such as lower-latitude pine, larch, and aspen forests in western North America, become even more inhospitable after fire (Bell et al. 2014). The large number of studies of the forested ecosystems described above from western North America highly informed the positive relationship between post-fire regeneration and increasing latitude.

4.2 High-severity fire can create and compound unfavorable conditions for regeneration

Density of post-fire regeneration is not explained by a single variable (i.e., predictor), but rather by a complex web of interacting factors. These factors either compound the negative impacts of fire or lessen them. High-severity fire, the most significant predictor across studies, had a negative average effect size according to our results, as it produces well-documented adverse impacts on distance to seed source, favorable regeneration site abundance, and nutrient availability (e.g., Savage et al. 2013; Barker et al. 2022). High-severity fires cause complete or near complete overstory mortality, increasing the distance seeds need to disperse to cover burned areas (e.g., Abella and Fornwalt 2015; Shive et al. 2018), while also reducing forest structural complexity by burning leaf litter, logs, and bushes that could have served as favorable tree

regeneration sites (e.g., Busby et al. 2020; López et al. 2021). Whereas such conditions favor certain tree species that are able to germinate in bare-mineral soil and thrive in full sunlight, when such species are not present, forest regeneration may fail to establish (e.g., Urretavizcaya et al. 2022). This is consistent with the negative average effect that unprotected microsites had on post-fire regeneration.

High-severity fires have also been linked to decreases in soil organic matter, as they completely consume the duff and litter-layers of forest floors (e.g., Page-Dumroese et al. 2019). Reductions in organic matter can decrease nutrients (e.g., carbon) available for uptake by seedlings (Mack et al. 2021). However, we found a negative average effect of increased soil organic matter on post-fire regeneration. In this context, by reducing soil organic matter, high-severity fire may be favoring species that regenerate in bare-mineral soils. Still, the factors listed above often compound each other's negative effects to create post-fire landscapes that are inhospitable to seeds, suckers, and seedlings of many tree species. Conversely, elevation was positively correlated to post-fire regeneration in our results; this was likely driven by the wetter, cooler conditions associated with increasing elevation (Buttafuoco and Conforti 2021) that help to mitigate the dry, warm conditions that often dominate post-fire landscapes.

Pre-fire and post-fire management, in theory, can compound challenges to post-fire regeneration by exacerbating stress on seeds, suckers, and seedlings (e.g., Leverkus et al. 2014). However, management (most often in the form of logging and grazing) did not significantly affect post-fire regeneration across reviewed studies, although it did coincide with changes in species compositions in the post-fire landscape. Mechanized equipment used in post-fire salvage logging, for example, can further expose mineral soils after wildfires (Wagenbrenner et al. 2016), favoring species that require disturbed, bare-mineral-soil seedbeds to regenerate (Collins et al. 2012; Kleinman et al. 2020). Salvage logging can also trigger the resprouting response of genera such as aspen (Collins et al. 2012). These factors may have driven the general increase in post-fire regeneration in managed forests included in this review.

4.3 A handful of genera proliferate post-fire

While abundant tree regeneration at extreme high latitudes ensures that forest cover will return post-fire, this does not mean that the forests that return will be similar to those present before fire. Our results indicate that fire-tolerant species dominate post-fire landscapes, with fire

selecting for species with traits such as thick bark, small, wind-blown seeds, and those species with the ability to resprout from top-killed individuals. Changes in forest composition may trigger broader impacts on biodiversity, habitat type and quality, and nutrient cycling, for example.

Aspen and birch species generally performed well after fire, as they are early-seral, full-light tolerants that produce mass-quantities of lightweight seed and resprout prolifically after fire (e.g., Alexander and Mack 2016; Cooley et al. 2016). These genera are more ubiquitous above 50° north (Global Tree Search online database 2023). Hence, increases in forest regeneration at higher latitudes could be correlated with the geographic distribution of these highly fire-adapted species. These species may replace shade-tolerant, coniferous forests at sites where high-severity fire favors deciduous species recruitment (e.g., Alaska, USA—Johnstone et al. 2020).

In contrast to aspen and birch, pines had a more variable response to fire. Take whitebark and limber (*Pinus flexilis*) pine, for example, which both have a more nuanced response to fire. Both are found at high elevations where regeneration establishes sporadically and over long time periods because of the harsh mountain climate and environment that they inhabit (Klutsch et al. 2015; Dawe et al. 2020). Although both species ostensibly depend on fire to regenerate, normal challenges to whitebark and limber pine's post-fire recovery can be exacerbated by wildfires that greatly increase the distance from a seed source to the interior of burned areas or by compounding factors that exacerbate the negative impacts of fire and damage neighboring seed trees (Leirfallom et al. 2015). In situations where high elevation tree regeneration in species such as whitebark and limber pine fail, lower-latitude species may be capable of moving in to take their place after fire as alpine environments become suitable for a greater number of species (e.g., Elsen and Tingley 2015; Steinbauer et al. 2018). Still, in our review, high-elevation pine species, in particular, even at higher latitudes generally have a positive regeneration response to fire, which reinforces trends for these species that have been established over decades.

Still, changing fire behavior and shortening fire-return-intervals across different forested ecosystem worldwide (e.g., Abatzoglou and Williams 2016) threatens to alter historic post-fire species composition dynamics, often favoring fire-adapted deciduous and, to a lesser degree, fire-adapted coniferous species. Forests develop adaptations to survive in particular climatic

conditions and under specific disturbance regimes. With climate and disturbance regimes changing rapidly, post-fire ecosystems will increasingly follow alternate successional trajectories, which may, in turn, affect dependent ecosystem attributes (e.g., winter cover for fauna, cone production) and functions (e.g., nutrient cycling, water retention).

5 Conclusion

Wildfire characteristics continue to change globally, impacting a diverse array of ecosystems across the world. High-latitude forests are ostensibly sensitive to these changes due to their particularly harsh environmental conditions, low tree diversity, and extreme climates. To our knowledge, this study is the first conducted to date that reviews empirical evidence of post-fire tree regeneration in high-latitude forests in the northern, southern, western, and eastern hemispheres. Regeneration after wildfires consistently increased with greater latitude. Forests found toward the lower latitudes of our study area were far more likely to contain less post-fire regeneration than those found at higher latitudes. Although higher-latitude forests (above 55°) generally have abundant post-fire regeneration, this does not mean that large-scale conversions of late-seral, long-lived coniferous forests to early-seral, short-lived deciduous forests will not have adverse impacts on dependent flora, fauna, and ecosystem services.

Extrapolating the conclusions of this work broadly to the southern hemisphere and certain Asian regions (e.g., non-boreal China) is inadvisable, as the post-fire regeneration trends described in this study were largely driven by very well-studied species present across the northern hemisphere. Post-fire regeneration trends in the southern hemisphere, in particular, may be opposite of those seen in the northern hemisphere due to the general absence of historical fire. Our work calls to attention that the majority of post-fire studies that directly measure tree regeneration and that are published in either English or Spanish come from only a handful of geographic regions, namely, the western USA and boreal Alaska and Canada. There is a need for more literature to be produced from research that directly measures the post-fire response of high-latitude forests in the southern hemisphere, Russia, and China, in particular. Nonetheless, our review expands the knowledge of post-fire regeneration dynamics in high-latitude forests, while highlighting the need for more quality studies to be performed outside of the USA and Canada.

Appendix

Table 4 A full list of articles retained for data extraction in this systematic review

Article	Authors	Title	Year	Journal
1	Hoecker, T.J., Turner, M.G.	A short-interval reburn catalyzes departures from historical structure and composition in a mesic mixed-conifer forest	2022	<i>Forest Ecology and Management</i>
2	Errington, R.C., Pinno, B.D.	Relationships between overstory and understory components of young natural and reconstructed boreal aspen stands	2021	<i>Ecological Restoration</i>
3	Harris, L.B., Drury, S.A., Taylor, A.H.	Strong legacy effects of prior burn severity on forest resilience to a high-severity fire	2021	<i>Ecosystems</i>
4	Landesmann, J.B., Tiribelli, F., Paritsis, J., Veblen, T.T., Kitzberger, T.	Increased fire severity triggers positive feedbacks of greater vegetation flammability and favors plant community-type conversions	2021	<i>Journal of Vegetation Science</i>
5	Sakamoto, K., Tomonari, M., Ariya, U., Nakagiri, E., Matsumoto, T.K., Akaji, Y., Otoda, T., Hirobe, M., Nachin, B.	Effects of large-scale forest fire followed by illegal logging on the regeneration of boreal forests in Mongolia	2021	<i>Landscape and Ecological Engineering</i>
6	Johnstone, J.F., Celis, G., Chapin, F.S., Hollingsworth, T.N., Jean, M., Mack, M.C.	Factors shaping alternate successional trajectories in burned black spruce forests of Alaska	2020	<i>Ecosphere</i>
7	Dawe, D.A., Peters, V.S., Flannigan, M.D.	Post-fire regeneration of endangered limber pine (<i>Pinus flexilis</i>) at the northern extent of its range	2020	<i>Forest Ecology and Management</i>
8	Filicetti, A.T., Nielsen, S.E.	Tree regeneration on industrial linear disturbances in treed peatlands is hastened by wildfire and delayed by loss of microtopography	2020	<i>Canadian Journal of Forest Research</i>
9	Boag, A.E., Ducey, M.J., Palace, M.W., Hartter, J.	Topography and fire legacies drive variable post-fire juvenile conifer regeneration in eastern Oregon, USA	2020	<i>Forest Ecology and Management</i>
10	Busby, S.U., Moffett, K.B., Holz, A.	High-severity and short-interval wildfires limit forest recovery in the Central Cascade Range	2020	<i>Ecosphere</i>
11	Peeler, J.L., Smithwick, E.A.H.	Seed source pattern and terrain have scale-dependent effects on post-fire tree recovery	2020	<i>Landscape Ecology</i>
12	Rossmann, A.K., Bakker, J.D., Peterson, D.W., Halpern, C.B.	Long-term effects of fuels treatments, overstory structure, and wildfire on tree regeneration in dry forests of Central Washington	2020	<i>Forests</i>
13	Povak, N.A., Churchill, D.J., Cansler, C.A., Hessburg, P.F., Kane, V.R., Kane, J.T., Lutz, J.A., Larson, A.J.	Wildfire severity and postfire salvage harvest effects on long-term forest regeneration	2020	<i>Ecosphere</i>
14	Woodward, B.D., Romme, W.H., Evangelista, P.H.	Early postfire response of a northern range margin coast redwood forest community	2020	<i>Forest Ecology and Management</i>
15	Maringer, J., Wohlgemuth, T., Hackett-Pain, A., Ascoli, D., Berretti, R., Conedera, M.	Drivers of persistent post-fire recruitment in European beech forests	2020	<i>Science of the Total Environment</i>
16	Dunn, C.J., Johnston, J.D., Reilly, M.J., Bailey, J.D., Miller, R.A.	How does tree regeneration respond to mixed-severity fire in the western Oregon Cascades, USA?	2020	<i>Ecosphere</i>
17	McCord, M., Reilly, M.J., Butz, R.J., Jules, E.S.	Early seral pathways of vegetation change following repeated short-interval, high-severity wildfire in a low-elevation, mixed conifer – hardwood forest landscape of the Klamath mountains, California	2020	<i>Canadian Journal of Forest Research</i>
18	McIlroy, S.K., Shinneman, D.J.	Post-fire aspen (<i>Populus tremuloides</i>) regeneration varies in response to winter precipitation across a regional climate gradient	2020	<i>Forest Ecology and Management</i>
19	Downing, W.M., Krawchuk, M.A., Coop, J.D., Meigs, G.W., Haire, S.L., Walker, R.B., Whitman, E., Chong, G., Miller, C., Tortorelli, C.	How do plant communities differ between fire refugia and fire-generated early-seral vegetation?	2020	<i>Journal of Vegetation Science</i>
20	Hammond, D.H., Strand, E.K., Hudak, A.T., Newingham, B.A.	Boreal forest vegetation and fuel conditions 12 years after the 2004 Taylor Complex fires in Alaska, USA	2019	<i>Fire Ecology</i>

Article	Authors	Title	Year	Journal
21	Shi, L., Dech, J.P., Liu, H., Zhao, P., Bayin, D., Zhou, M.	Post-fire vegetation recovery at forest sites is affected by permafrost degradation in the Da Xing'an Mountains of northern China	2019	<i>Journal of Vegetation Science</i>
22	Littlefield, C.E.	Topography and post-fire climatic conditions shape spatio-temporal patterns of conifer establishment and growth	2019	<i>Fire Ecology</i>
23	Strand, E.K., Satterberg, K.L., Hudak, A.T., Byrne, J., Khalyani, A.H., Smith, A.M.S.	Does burn severity affect plant community diversity and composition in mixed conifer forests of the United States Intermountain West one decade post fire?	2019	<i>Fire Ecology</i>
24	Lee, C.-S., Robinson, G.R., Robinson, I.P., Lee, H.	Regeneration of pitch pine (<i>Pinus rigida</i>) stands inhibited by fire suppression in Albany Pine Bush Preserve, New York	2019	<i>Journal of Forestry Research</i>
25	Roberts, C.P., Donovan, V.M., Wonkka, C.L., Powell, L.A., Allen, C.R., Angeler, D.G., Wedin, D.A., Twidwell, D.	Fire legacies in eastern ponderosa pine forests	2019	<i>Ecology and Evolution</i>
26	Downing, W.M., Krawchuk, M.A., Meigs, G.W., Haire, S.L., Coop, J.D., Walker, R.B., Whitman, E., Chong, G., Miller, C.	Influence of fire refugia spatial pattern on post-fire forest recovery in Oregon's Blue Mountains	2019	<i>Landscape Ecology</i>
27	Kemp, K.B., Higuera, P.E., Morgan, P., Abatzoglou, J.T.	Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA	2019	<i>Ecosphere</i>
28	Filicetti, A.T., Nielsen, S.E.	Fire and forest recovery on seismic lines in sandy upland jack pine (<i>Pinus banksiana</i>) forests	2018	<i>Forest Ecology and Management</i>
29	Dzwonko, Z., Loster, S., Gawroński, S.	Effects of fire severity on understory community	2018	<i>Tuexenia</i>
30	Nemens, D.G., Varner, J.M., Kidd, K.R., Wing, B.	Do repeated wildfires promote restoration of oak woodlands in mixed-conifer landscapes?	2018	<i>Forest Ecology and Management</i>
31	Landesmann, J.B., Morales, J.M.	The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia	2018	<i>Plant Ecology</i>
32	Tucker, M.M., Kashian, D.M.	Pre-fire forest remnants affect post-fire plant community structure and composition	2018	<i>Forest Ecology and Management</i>
33	Rowe, E.R., D'Amato, A.W., Palik, B.J., Almendinger, J.C.	Early response of ground layer plant communities to wildfire and harvesting disturbance in forested peatland ecosystems in northern Minnesota, USA	2017	<i>Forest Ecology and Management</i>
34	Acker, S.A., Kertis, J.A., Pabst, R.J.	Tree regeneration, understory development, and biomass dynamics following wildfire in a mountain hemlock (<i>Tsuga mertensiana</i>) forest	2017	<i>Forest Ecology and Management</i>
35	Urza, A.K., Sibold, J.S.	Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest	2017	<i>Journal of Vegetation Science</i>
36	Donato, D.C., Harvey, B.J., Turner, M.G.	Regeneration of montane forests 24 years after the 1988 Yellowstone fires: a fire-catalyzed shift in lower treelines?	2016	<i>Ecosphere</i>
37	Harvey, B.J., Donato, D.C., Turner, M.G.	High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches	2016	<i>Global Ecology and Biogeography</i>
38	Kemp, K.B., Higuera, P.E., Morgan, P.	Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies	2016	<i>Landscape Ecology</i>
39	Paudel, S.K., Nitschke, C.R., Simard, S.W., Innes, J.L.	Regeneration dynamics of white spruce, trembling aspen, and balsam poplar in response to disturbance, climatic, and edaphic factors in the cold, dry boreal forests of the southwest Yukon, Canada	2015	<i>Journal of Forestry</i>
40	Parro, K., Metslaid, M., Renel, G., Sims, A., Stanturf, J.A., Jõgiste, K., Köster, K.	Impact of postfire management on forest regeneration in a managed hemiboreal forest, Estonia	2015	<i>Canadian Journal of Forest Research</i>
41	Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G., Conedera, M.	The synchronicity of masting and intermediate severity fire effects favors beech recruitment	2015	<i>Forest Ecology and Management</i>

Article	Authors	Title	Year	Journal
42	Klutsch, J.G., Goodrich, B.A., Jacobi, W.R.	Post-fire regeneration dynamics in whitebark pine (<i>Pinus albicaulis</i>) forests in Wind River and Absaroka Mountains, Wyoming, USA	2015	<i>Journal of Forestry Research</i>
43	Stine, M.B., Butler, D.R.	Effects of fire on geomorphic factors and seedling site conditions within the alpine treeline ecotone, Glacier National Park, MT	2015	<i>Catena</i>
44	Leirfallom, S.B., Keane, R.E., Tomback, D.F., Dobrowski, S.Z.	The effects of seed source health on whitebark pine (<i>Pinus albicaulis</i>) regeneration density after wildfire	2015	<i>Canadian Journal of Forest Research</i>
45	Cavallero, L., López, D.R., Raffaele, E., Aizen, M.A.	Structural-functional approach to identify post-disturbance recovery indicators in forests from northwestern Patagonia: a tool to prevent state transitions	2015	<i>Ecological Indicators</i>
46	Pounden, E., Greene, D.F., Michalletz, S.T.	Non-serotinous woody plants behave as aerial seed bank species when a late-summer wildfire coincides with a mast year	2014	<i>Ecology and Evolution</i>
47	Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., Sidders, D.	Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada	2014	<i>Canadian Journal of Forest Research</i>
48	Boucher, D., Gauthier, S., Noël, J., Greene, D.F., Bergeron, Y.	Salvage logging affects early post-fire tree composition in Canadian boreal forest	2014	<i>Forest Ecology and Management</i>
49	Harper, K.A., Drapeau, P., Lesieur, D., Bergeron, Y.	Forest structure and composition at fire edges of different ages: evidence of persistent structural features on the landscape	2014	<i>Forest Ecology and Management</i>
50	Bannister, J.R., Wagner, S., Donoso, P.J., Bauhus, J.	The importance of seed trees in the dioecious conifer <i>Pilgerodendron uviferum</i> for passive restoration of fire disturbed southern bog forests	2014	<i>Austral Ecology</i>
51	Cocking, M.I., Varner, J.M., Knapp, E.E.	Long-term effects of fire severity on oak-conifer dynamics in the southern Cascades	2014	<i>Ecological Applications</i>
52	Kukavskaya, E.A., Buryak, L.V., Ivanova, G.A., Conard, S.G., Kalenskaya, O.P., Zhila, S.V., McRae, D.J.	Influence of logging on the effects of wildfire in Siberia	2013	<i>Environmental Research Letters</i>
53	Abrams, M.D., Steiner, K.C.	Long-term seedling height growth and compositional changes following logging and wildfire in a Central Pennsylvania Oak Forest	2013	<i>Castanea</i>
54	Otoda, T., Doi, T., Sakamoto, K., Hirobe, M., Nachin, B., Yoshikawa, K.	Frequent fires may alter the future composition of the boreal forest in northern Mongolia	2013	<i>Journal of Forest Research</i>
55	Albornoz, F.E., Gaxiola, A., Seaman, B.J., Pugnaire, F.I., Armesto, J.J.	Nucleation-driven regeneration promotes post-fire recovery in a Chilean temperate forest	2013	<i>Plant Ecology</i>
56	Kulakowski, D., Matthews, C., Jarvis, D., Veblen, T.T.	Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (<i>Populus tremuloides</i>)	2012	<i>Journal of Vegetation Science</i>
57	Boiffin, J., Munson, A.D.	Three large fire years threaten resilience of closed crown black spruce forests in eastern Canada	2013	<i>Ecosphere</i>
58	Bannister, J.R., Donoso, P.J., Bauhus, J.	Persistence of the slow growing conifer <i>Pilgerodendron uviferum</i> in old-growth and fire-disturbed southern bog forests	2012	<i>Ecosystems</i>
59	Buma, B., Wessman, C.A.	Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience	2012	<i>Forest Ecology and Management</i>
60	McKenzie, D.A., Tinker, D.B.	Fire-induced shifts in overstory tree species composition and associated understory plant composition in Glacier National Park, Montana	2012	<i>Plant Ecology</i>
61	Veilleux-Nolin, M., Payette, S.	Influence of recent fire season and severity on black spruce regeneration in spruce-moss forests of Quebec, Canada	2012	<i>Canadian Journal of Forest Research</i>
62	D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L.	Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems	2011	<i>Forest Ecology and Management</i>

Article	Authors	Title	Year	Journal
63	Buma, B., Wessman, C.A.	Disturbance interactions can impact resilience mechanisms of forests	2011	<i>Ecosphere</i>
64	Pierce, A.D., Taylor, A.H.	Fire severity and seed source influence lodgepole pine (<i>Pinus contorta</i> var. <i>murrayana</i>) regeneration in the southern cascades, Lassen volcanic National Park, California	2011	<i>Landscape Ecology</i>
65	Lantz, T.C., Gergel, S.E., Henry, G.H.R.	Response of green alder (<i>Alnus viridis</i> subsp. <i>fruticosa</i>) patch dynamics and plant community composition to fire and regional temperature in north-western Canada	2010	<i>Journal of Biogeography</i>
66	Sannikova, N.S., Sannikov, S.N., Gritsenyuk, A.P., Egorov, E.V., Petrova, I.V.	Ecogeographical characteristics of the seed-bearing capacity and natural regeneration of pine on the fire-sites in pine forests of Transbaikalia	2010	<i>Contemporary Problems of Ecology</i>
67	Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S., Mack, M.C.	Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest	2010	<i>Global Change Biology</i>
68	Dodson, E.K., Peterson, D.W.	Mulching effects on vegetation recovery following high severity wildfire in north-central Washington State, USA	2010	<i>Forest Ecology and Management</i>
69	Reyes, G.P., Kneeshaw, D., De Grandpré, L., Leduc, A.	Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality	2010	<i>Journal of Vegetation Science</i>
70	van Gils, H., Odoi, J.O., Andrisano, T.	From monospecific to mixed forest after fire? An early forecast for the montane belt of Majella, Italy	2010	<i>Forest Ecology and Management</i>
71	Strong, W.L.	<i>Populus tremuloides</i> Michx. postfire stand dynamics in the northern boreal-cordilleran ecoclimatic region of central Yukon Territory, Canada	2009	<i>Forest Ecology and Management</i>
72	Ilisson, T., Chen, H.Y.H.	Response of six boreal tree species to stand replacing fire and clearcutting	2009	<i>Ecosystems</i>
73	Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E.	Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou mountains	2009	<i>Canadian Journal of Forest Research</i>
74	Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B., Law, B.E.	Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest	2009	<i>Journal of Ecology</i>
75	Redburn, M.J., Strong, W.L.	Successional development of silviculturally treated and untreated high-latitude <i>Populus tremuloides</i> clearcuts in northern Alberta, Canada	2008	<i>Forest Ecology and Management</i>
76	Bannister, J.R., Le Quesne, C.E., Lara, A.	Structure and dynamics of <i>Pilgerodendron uviferum</i> forests affected by fires in the coastal range of Chiloe Island Estructura y dinámica de bosques de <i>Pilgerodendron uviferum</i> afectados por incendios en la Cordillera de la Costa de la Isla Grande de Chiloé	2008	<i>Bosque</i>
77	Keyser, T.L., Lentile, L.B., Smith, F.W., Shepperd, W.D.	Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the black hills, South Dakota, USA	2008	<i>Forest Science</i>
78	Lloyd, A.H., Fastie, C.L., Eisen, H.	Fire and substrate interact to control the northern range limit of black spruce (<i>Picea mariana</i>) in Alaska	2007	<i>Canadian Journal of Forest Research</i>
79	Shatford, J.P.A., Hibbs, D.E., Puettmann, K.J.	Conifer regeneration after forest fire in the Klamath-Siskiyou: how much, how soon?	2007	<i>Journal of Forestry</i>
80	Ziegler, S.S.	Postfire succession in an Adirondack forest	2007	<i>Geographical Review</i>
81	Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noël, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., Swift, L.	The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed	2007	<i>Canadian Journal of Forest Research</i>
82	Johnstone, J.F., Chapin III, F.S.	Fire interval effects on successional trajectory in boreal forests of northwest Canada	2006	<i>Ecosystems</i>

Article	Authors	Title	Year	Journal
83	Jayen, K., Leduc, A., Bergeron, Y.	Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada	2006	<i>Ecoscience</i>
84	Kemball, K.J., Wang, G.G., Dang, Q.-L.	Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak	2005	<i>Canadian Journal of Botany</i>
85	Larson, A.J., Franklin, J.F.	Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA	2005	<i>Forest Ecology and Management</i>
86	Landis, R.M., Gurevitch, J., Fox, G.A., Fang, W., Taub, D.R.	Variation in recruitment and early demography in <i>Pinus rigida</i> following crown fire in the pine barrens of Long Island, New York	2005	<i>Journal of Ecology</i>
87	Bonnet, V.H., Schoettle, A.W., Shepperd, W.D.	Postfire environmental conditions influence the spatial pattern of regeneration for <i>Pinus ponderosa</i>	2005	<i>Canadian Journal of Forest Research</i>
88	Lampainen, J., Kuuluvainen, T., Wallenius, T.H., Karjalainen, L., Vanha-Majamaa, I.	Long-term forest structure and regeneration after wildfire in Russian Karelia	2004	<i>Journal of Vegetation Science</i>
89	Wang, G.G.	Early regeneration and growth dynamics of <i>Populus tremuloides</i> suckers in relation to fire severity	2003	<i>Canadian Journal of Forest Research</i>
90	Asselin, H., Fortin, M.-J., Bergeron, Y.	Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest	2001	<i>Forest Ecology and Management</i>
91	Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., Mellmann-Brown, S.	Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires	2001	<i>Ecology</i>
92	Peltzer, D.A., Bast, M.L., Wilson, S.D., Gerry, A.K.	Plant diversity and tree responses following contrasting disturbances in boreal forest	2000	<i>Forest Ecology and Management</i>
93	Cater, T.C., Chapin III, F.S.	Differential effects of competition or microenvironment on boreal tree seedling establishment after fire	2000	<i>Ecology</i>

Table 5 Regeneration predictor categories and their component variables used for effect size analyses

Predictor category	Predictor	Number of cases
Dry/warm conditions	Aspect—S	5
	Aspect—SE	2
	Aspect—SW	2
	Drought severity	3
	Evapotranspiration	2
	Growing degree-days	7
	Heat load	17
	Mean annual temperature	2
	Mean summer maximum temperature	2
	Mean summer minimum temperature	1
	Mean summer temperature	3
	Mean winter maximum temperature	1
	Minimum winter temperature difference with 30-year winter mean	1
	Moisture deficit (CMD)	4
	Number of frost-free days	1
	Number of growing days >5 °C	2
	Soil temperature	1
	Southness	2
	Vapor pressure deficit	5
	Total	63

Predictor category	Predictor	Number of cases
Elevation	Elevation	23
Ground vegetation cover	Ground vegetation cover	42
High-severity fire	Burned area dead basal area	2
	Canopy loss	1
	Distance from seed source	45
	Distance from unburned edge	6
	Fire severity	20
	Fire severity H vs. L severity	1
	Fire severity H vs. M severity	1
	Fire severity H vs. U severity	1
	Fire severity L vs. U severity	1
	Fire severity M vs. U severity	1
	Mean crown kill	1
	Total	80
Low severity fire	Burned area live basal area	5
	Burned area total basal area	5
	Burned area tree density and total basal area	2
	Canopy cover	8
	Diameter at breast height (DBH)	3
	Fire severity L vs. M severity	1
	Log density	2
	Post-fire tree density	2
	Relativized differenced normalized burn ratio	2
	Structural recovery index	1
	Understory biomass	1
	Total	32
Management	Fire and management	12
Other fire-related variables	0 years post-fire	6
	Bark beetle outbreak	2
	Early winter precipitation ratio	1
	Fire presence	16
	Fire severity—moderate fire severity	2
	Perch height	1
	Pre-fire community	1
	Reburn and single burn	3
	Rock	2
	Sand	1
	Seismic disturbance	4
	Soil clay	6
	Soil penetrability	1
	Topography	4
	Unburned stand age	4
	Total	54
Protected microsite conditions	Depression depth	1
	Downed woody debris	16
	Leaf litter	4
	Total	21

Predictor category	Predictor	Number of cases
Pre- and post-fire seed production	Cone density	2
	Cone production previous fall	2
	Cone production two years prior	2
	Masting	2
	Masting—half event	2
	Masting—light event	1
	Masting—sporadic	1
	Presence of serotinous cones	1
	Total	13
	Soil organic matter	Organic layer depth
Soil organic matter		9
Total		19
Time since fire	19 years post-fire	6
	3 years post-fire	1
	31 years post-fire	6
	4 years post-fire	6
	Fire-originated stand age	4
	Time since fire	21
	Total	44
Unburned stand characteristics	Pre-fire total basal area	9
	Pre-fire tree density	11
	Pre-fire undifferentiated basal area	11
	Refugia live basal area	3
	Refugia tree density	6
	Total	40
Unprotected microsite conditions	Bare mineral soil	1
	Distance from log	1
	Organic soil loss	1
	Proportion of browsed leaders	1
	Slope	11
	Total	15
	Wet/cool conditions	Aspect—NE
Aspect—NW		2
Growing season precipitation		1
Mean annual precipitation		2
Mean summer precipitation		1
Mean winter precipitation		4
Moist burn vs. dry burn		1
Moist sites		1
Northness		2
Number of days <0 °C		1
Post-fire spring snow water equivalent (SWE)		3
Precipitation of the first, second, and third summer after fire event		1
Soil moisture		5
Spring precipitation		1
Standardized precipitation evapotranspiration index (SPEI)		1
Topographic moisture index (north-east)		4
Topographic wetness index (TWI)		3
Total	40	

Table 6 Fire and shade tolerance classifications for each species encountered in the literature review

Species	Common name	Shade tolerance	Fire tolerance
<i>Abies amabilis</i>	Pacific silver fir	Tolerant	Intolerant
<i>Abies balsamea</i>	Balsam fir	Tolerant	Intolerant
<i>Abies concolor</i>	White fir	Tolerant	Intolerant
<i>Abies grandis</i>	Grand fir	Tolerant	Intolerant
<i>Abies lasiocarpa</i>	Subalpine fir	Intolerant	Intolerant
<i>Abies magnifica</i>	California red fir	Tolerant	Intolerant
<i>Acer glabrum</i>	Mountain maple	Tolerant	Tolerant
<i>Acer negundo</i>	Boxelder	Tolerant	Intolerant
<i>Acer obtusatum</i>	Bosnian maple	Tolerant	Unknown
<i>Acer pensylvanicum</i>	Striped maple	Tolerant	Intolerant
<i>Acer platanoides</i>	Norway maple	Tolerant	Intolerant
<i>Acer pseudoplatanus</i>	Sycamore maple	Tolerant	Unknown
<i>Acer rubrum</i>	Red maple	Tolerant	Intolerant
<i>Ailanthus altissima</i>	Tree-of-heaven	Tolerant	Intolerant
<i>Alnus viridis</i>	Green alder	Tolerant	Tolerant
<i>Amelanchier</i> spp.	Serviceberry	Tolerant	Tolerant
<i>Amomyrtus</i> sp.	Myrtle	Tolerant	Unknown
<i>Aralia</i> sp.	Spikenard	Intolerant	Tolerant
<i>Arbutus menziesii</i>	Pacific madrone	Intolerant	Intolerant
<i>Austrocedrus chilensis</i>	Patagonian cypress/ciprés de la cordillera	Tolerant	Intolerant
<i>Betula lenta</i>	Sweet birch	Intolerant	Tolerant
<i>Betula papyrifera</i>	Paper birch	Intolerant	Tolerant
<i>Betula pendula</i>	Silver birch	Intolerant	Tolerant
<i>Betula platyphylla</i>	Japanese white birch	Intolerant	Tolerant
<i>Betula pubescens</i>	Downy birch	Intolerant	Tolerant
<i>Caldcluvia paniculata</i>	Tiaca	Tolerant	Unknown
<i>Calocedrus decurrens</i>	Incense cedar	Tolerant	Intolerant
<i>Carya cordiformis</i>	Bitternut hickory	Intolerant	Intolerant
<i>Carya glabra</i>	Pignut hickory	Intolerant	Intolerant
<i>Carya ovata</i>	Shagbark hickory	Tolerant	Intolerant
<i>Carya tomentosa</i>	Mockernut hickory	Intolerant	Intolerant
<i>Cornus florida</i>	Flowering dogwood	Tolerant	Tolerant
<i>Crataegus</i>	Hawthorn	Tolerant	Tolerant
<i>Drimys winteri</i>	Winter's bark/canelo	Tolerant	Unknown
<i>Embothrium coccineum</i>	Notro	Intolerant	Unknown
<i>Eucryphia cordifolia</i>	Ulmo	Intolerant	Tolerant
<i>Fagus sylvatica</i>	European beech	Tolerant	Intolerant
<i>Fraxinus americana</i>	White ash	Intolerant	Tolerant
<i>Fraxinus ornus</i>	Flowering ash	Intolerant	Tolerant
<i>Gevuina avellana</i>	Avellano	Tolerant	Tolerant
<i>Juniperus communis</i>	Common juniper	Intolerant	Intolerant
<i>Juniperus occidentalis</i>	Western juniper	Intolerant	Intolerant
<i>Juniperus scopulorum</i>	Rocky mountain juniper	Intolerant	Intolerant
<i>Larix gmelinii</i>	Dahurian larch	Intolerant	Tolerant
<i>Larix laricina</i>	Tamarack	Intolerant	Intolerant
<i>Larix occidentalis</i>	Western larch	Intolerant	Tolerant
<i>Larix sibirica</i>	Siberian larch	Intolerant	Unknown
<i>Liriodendron tulipifera</i>	Tuliptree	Intolerant	Tolerant
<i>Notholithocarpus densiflorus</i>	Tanoak	Tolerant	Intolerant

Species	Common name	Shade tolerance	Fire tolerance
<i>Lomatia ferruginea</i>	Fuinque	Tolerant	Unknown
<i>Nothofagus dombeyi</i>	Coihue	Tolerant	Intolerant
<i>Nothofagus nitida</i>	Roble	Tolerant	Unknown
<i>Nothofagus pumilio</i>	Lenga	Tolerant	Intolerant
<i>Nyssa sylvatica</i>	Blackgum	Tolerant	Tolerant
<i>Ostrya carpinifolia</i>	European hop-hornbeam	Intolerant	Unknown
<i>Picea abies</i>	Norway spruce	Tolerant	Intolerant
<i>Picea engelmannii</i>	Engelmann spruce	Tolerant	Intolerant
<i>Picea glauca</i>	White spruce	Tolerant	Intolerant
<i>Picea mariana</i>	Black spruce	Tolerant	Intolerant
<i>Picea obovata</i>	Siberian spruce	Tolerant	Intolerant
<i>Pilgerodendron uviferum</i>	Ciprés de las Guaitecas	Intolerant	Intolerant
<i>Pinus albicaulis</i>	Whitebark pine	Intolerant	Intolerant
<i>Pinus attenuata</i>	Knobcone pine	Intolerant	Tolerant
<i>Pinus Banksiana</i>	Jack pine	Intolerant	Tolerant
<i>Pinus contorta</i>	Lodgepole pine	Intolerant	Tolerant
<i>Pinus flexilis</i>	Limber pine	Intolerant	Intolerant
<i>Pinus jeffreyi</i>	Jeffrey pine	Intolerant	Tolerant
<i>Pinus lambertiana</i>	Sugar pine	Tolerant	Intolerant
<i>Pinus monticola</i>	Western white pine	Intolerant	Intolerant
<i>Pinus ponderosa</i>	Ponderosa pine	Intolerant	Tolerant
<i>Pinus rigida</i>	Pitch pine	Intolerant	Tolerant
<i>Pinus sibirica</i>	Siberian pine	Tolerant	Intolerant
<i>Pinus strobus</i>	Eastern white pine	Tolerant	Intolerant
<i>Pinus sylvestris</i>	Scots pine	Intolerant	Tolerant
<i>Podocarpus nubigena</i>	Maniu macho	Tolerant	Unknown
<i>Populus balsamifera</i>	Balsam poplar	Intolerant	Tolerant
<i>Populus gradidentata</i>	Bigtooth aspen	Intolerant	Tolerant
<i>Populus tremula</i>	Eurasian aspen	Intolerant	Tolerant
<i>Populus tremuloides</i>	Quaking aspen	Intolerant	Tolerant
<i>Prunus americana</i>	American plum	Intolerant	Tolerant
<i>Prunus pensylvanica</i>	Pin cherry	Intolerant	Tolerant
<i>Prunus serotina</i>	Black cherry	Intolerant	Tolerant
<i>Prunus virginiana</i>	Chokecherry	Tolerant	Tolerant
<i>Pseudotsuga menziesii</i>	Douglas-fir	Intolerant	Intolerant
<i>Quercus alba</i>	White oak	Intolerant	Tolerant
<i>Quercus chrysolepis</i>	Canyon live oak	Tolerant	Tolerant
<i>Quercus coccinea</i>	Scarlet oak	Intolerant	Tolerant
<i>Quercus ilicifolia</i>	Scrub oak	Intolerant	Tolerant
<i>Quercus kelloggii</i>	California black oak	Intolerant	Tolerant
<i>Quercus montana</i>	Chestnut oak	Tolerant	Tolerant
<i>Quercus prinoides</i>	Chinkapin oak	Tolerant	Tolerant
<i>Quercus rubra</i>	Northern red oak	Tolerant	Tolerant
<i>Quercus sadleriana</i>	Oregon white oak	Intolerant	Tolerant
<i>Quercus velutina</i>	Black oak	Tolerant	Tolerant
<i>Raukaua laetevirens</i>	Traumen	Unknown	Unknown
<i>Salix bebbiana</i>	Bebb willow	Intolerant	Tolerant
<i>Salix caprea</i>	Goat willow	Intolerant	Tolerant
<i>Salix glauca</i>	Narrowleaf willow	Intolerant	Tolerant
<i>Salix planifolia</i>	Diamondleaf willow	Intolerant	Tolerant
<i>Sambucus nigra</i>	Blue elderberry	Intolerant	Tolerant

Species	Common name	Shade tolerance	Fire tolerance
<i>Sassafras albidum</i>	Sassafras	Intolerant	Tolerant
<i>Saxegothaea conspicua</i>	Mañío de hojas cortas	Tolerant	Unknown
<i>Sequoia sempervirens</i>	Redwood	Tolerant	Tolerant
<i>Sorbus aucuparia</i>	Rowan	Tolerant	Tolerant
<i>Taxus baccata</i>	English yew	Tolerant	Intolerant
<i>Tepualia stipularis</i>	Tepu	Intolerant	Tolerant
<i>Thuja occidentalis</i>	White cedar	Tolerant	Intolerant
<i>Thuja plicata</i>	Western red cedar	Tolerant	Intolerant
<i>Tsuga canadensis</i>	Eastern hemlock	Tolerant	Intolerant
<i>Tsuga heterophylla</i>	Western hemlock	Tolerant	Intolerant
<i>Tsuga mertensiana</i>	Mountain hemlock	Tolerant	Intolerant
<i>Ulmus americana</i>	American elm	Tolerant	Intolerant
<i>Weinmannia trichosperma</i>	Tineo	Intolerant	Intolerant

Table 7 Results of the linear mixed model to test the effect of latitude on post-fire recruitment

Effect	Group	Term	Estimate	Standard error	Statistic	df	p value
Fixed	NA	(Intercept)	6.8143638	0.291	23.379	59.42	<0.001
Fixed	NA	latitude_sc	1.369	0.292	4.686	64.32	<0.001
Fixed	NA	time_sc	-0.728	0.355	-2.052	77.57	0.043
Fixed	NA	year_sc	-0.486	0.451	-1.078	60.83	0.284
ran_pars	Article number	sd__(Intercept)	2.085	NA	NA	NA	NA
ran_pars	Residual	sd__Observation	4.209	NA	NA	NA	NA

Table 8 Results of the linear mixed models to test the effect of latitude, time since fire, and year of study on the shade tolerance of post-fire regeneration density

Effect	Group	Term	Estimate	Standard error	Statistic	df	p value
Fixed	NA	(Intercept)	6.445	0.336	19.142	47.41	<0.001
Fixed	NA	latitude_sc	1.588	0.314	5.052	49.51	<0.001
Fixed	NA	time_sc	-0.809	0.374	-2.163	61.78	0.034
Fixed	NA	year_sc	-0.147	0.482	-0.305	44.19	0.761
Fixed	NA	`Shade tolerance category`Tolerant	-0.045	0.223	-0.201	337.82	0.840
ran_pars	Article number	sd__(Intercept)	2.067	NA	NA	NA	NA
ran_pars	Residual	sd__Observation	4.046	NA	NA	NA	NA

Table 9 Results of the linear mixed models to test the effect of latitude, time since fire, and year of study on the fire tolerance of post-fire regeneration density

Effect	Group	Term	Estimate	Standard error	Statistic	df	p value
Fixed	NA	(Intercept)	6.690	0.342	19.557	50.62	<0.001
Fixed	NA	latitude_sc	1.539	0.315	4.880	49.26	<0.001
Fixed	NA	time_sc	-0.768	0.383	-2.003	59.49	0.049
Fixed	NA	year_sc	-0.089	0.481	-0.186	43.90	0.856
Fixed	NA	`Fire tolerance category`low/moderate	-0.498	0.219	-2.270	325.73	0.0238
ran_pars	Article number	sd__(Intercept)	2.060	NA	NA	NA	NA
ran_pars	Residual	sd__Observation	4.013	NA	NA	NA	NA

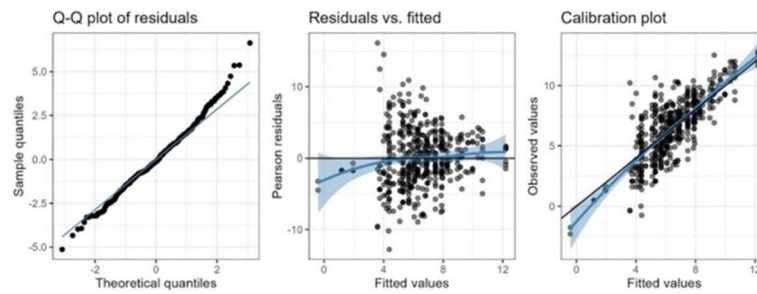


Fig. 7 Q-Q plot of residuals, residuals vs. fitted plot, and calibration plot for the linear mixed model to test the effect of latitude on post-fire recruitment

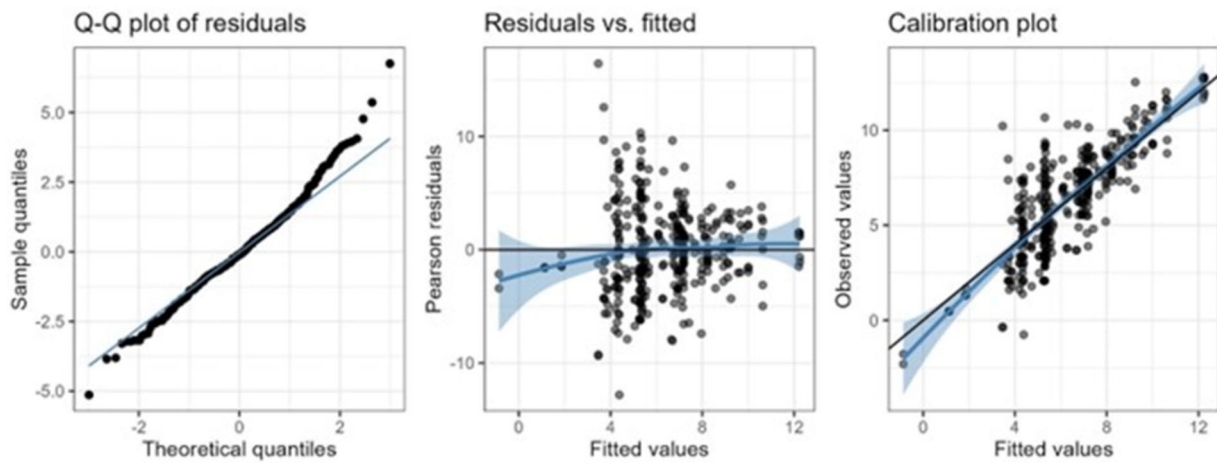


Fig. 8 Q-Q plot of residuals, residuals vs. fitted plot, and calibration plot for the linear mixed model to test the effect of shade tolerance of species on post-fire recruitment

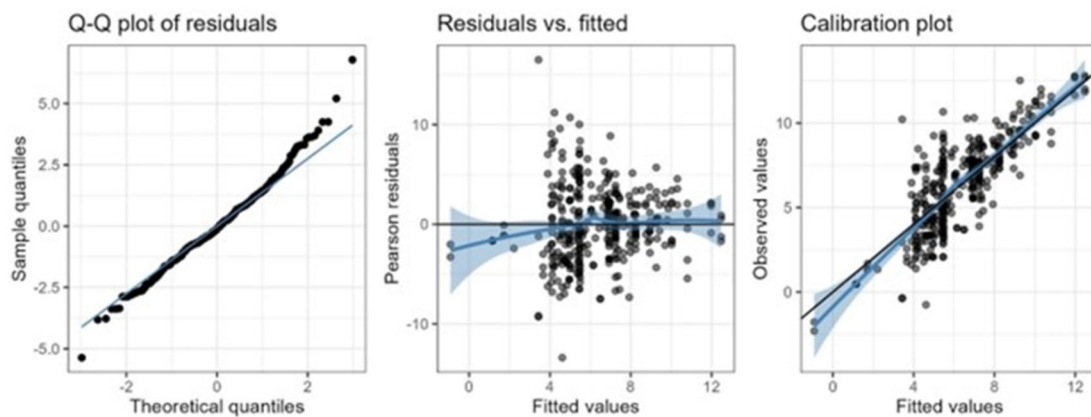


Fig. 9 Q-Q plot of residuals, residuals vs. fitted plot, and calibration plot for the linear mixed model to test the effect of fire tolerance of species on post-fire recruitment

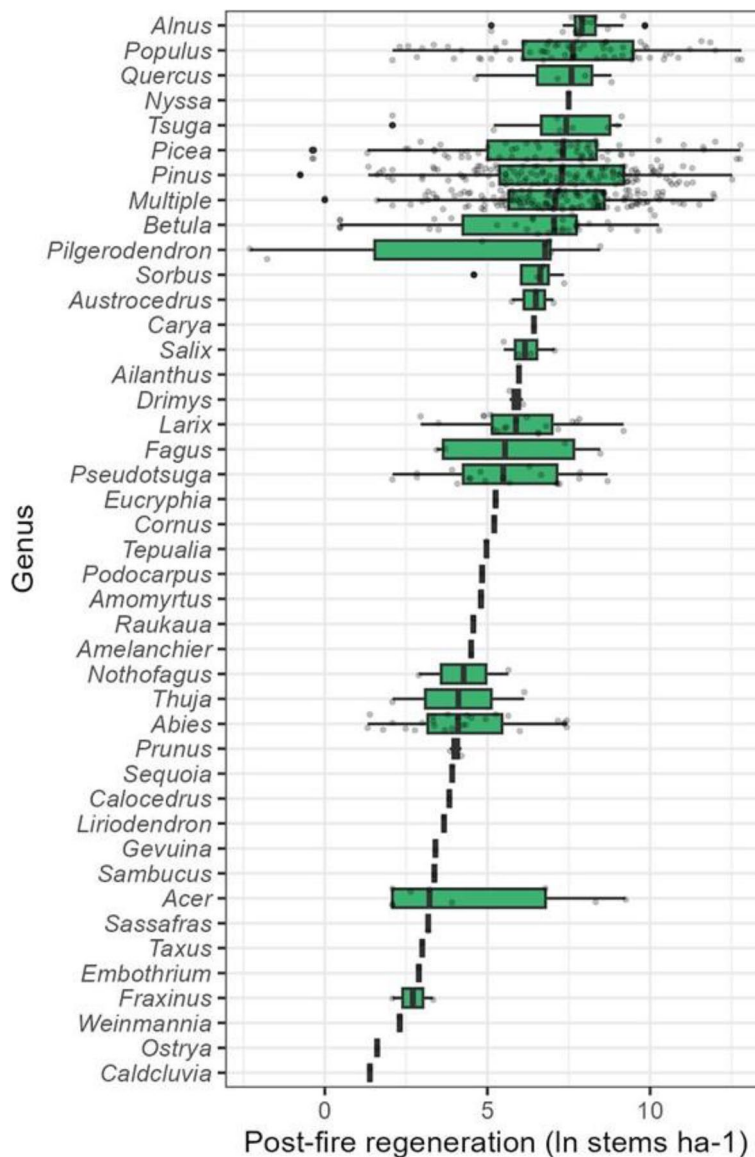


Fig. 10 Mean post-fire regeneration for each genus present in the reviewed articles

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Authors' contributions

M.R. and R.S. conceived of the premise behind this project and decided on the appropriate methodology for the review. M.R. did the initial data search and review of over 4000 articles and M.R., R.S., G.B., and P.R. conducted the data extraction and review in full of the initially retained articles. M.R., R.S., G.B., P.R., and V.C. contributed to making tables and figures. V.C. conducted the majority of the statistical analyses and created the majority of the figures, but she takes no responsibility over the literature review and data extraction process. M.R. wrote the first draft of the manuscript, which was added to and modified by all authors. All authors have read and approved the final manuscript.

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Data Availability

The datasets supporting the conclusions of this article are available through Dryad, <https://doi.org/10.5061/dryad.8pk0p2ntm>.

Code availability

Not applicable.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent to participate

Not applicable.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

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