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# Exploration of Large-Scale Vegetation Transition in Wet Ecosystems: a Comparison of Conifer Seedling Abundance Across Burned Vs. Unburned Forest-Peatland Ecotones in Western Patagonia

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# Exploration of large-scale vegetation transition in wet ecosystems: a comparison of conifer seedling abundance across burned vs. unburned forest-peatland ecotones in Western Patagonia

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Altered fire regimes, combined with a warmer and drier climate, have been eroding the resilience of temperate rainforests and peatlands worldwide and leading to alternative post-fire vegetation communities. Chronic anthropogenic burning of temperate rainforests at the forest-peatland ecotone in western Patagonia appears to have shifted vegetation communities in poorly-drained sites from forests dominated by the threatened conifer, *Pilgerodendron uviferum*, to peat-accumulating wetlands covered by *Sphagnum* mosses. We collected and modeled post-reburn field data using ordinations and hierarchical Bayesian regressions to examine mechanisms through which *P. uviferum* forests may recover following fire or become locked into alternative development pathways by comparing biophysical factors of a reburned ecotone to those of an unburned (control) ecotone. We found that, (1) the significantly higher densities of *P. uviferum* trees and seedlings in the forested patches at both the reburned and control sites were associated with significantly lower seasonal water tables, lower cover of *Sphagnum* mosses and higher cover of other mosses (i.e., not in the *Sphagnum* or *Dicranaloma* genera); (2) despite abrupt boundaries in vegetation at both sites, successive fires homogenized the environment at the reburned site; and (3) the distinct life forms and individual species that characterized the understory plant communities across the ecotones affected seedling abundance by shaping microtopography and the substrates available for establishment. Together, our results suggest that fire can push edaphically wet *P. uviferum*-dominated sites towards a non-forested state by reducing the diversity of microsite structure and composition, thereby placing *P. uviferum* seedlings in direct competition with *Sphagnum* mosses and potentially limiting the availability of microsites that are protected from both seasonal inundation and seasonal drought.

If wildfires continue under increasingly warmer and drier conditions, the forest-peatland ecotone of western Patagonia may be susceptible to large-scale transformation towards a non-forested state.

#### KEYWORDS

*Pilgerodendron uviferum*, ciprés de las Guaitecas, post-reburn establishment, *Sphagnum*, Western Patagonia, temperate rainforests, anthropogenic burning

## 1 Introduction

Ecosystems worldwide are experiencing heightened frequencies, spatial extents and severities of wildfire due to the interactive effects of climate change and land use practices (McDowell et al., 2020; Duane et al., 2021; Pausas and Keeley, 2021). Such is the case in landscapes dominated by temperate forests in both the Northern and Southern Hemisphere where the increasing intensity and length of drought conditions coupled with changes in the frequency of human-based ignitions of wildland fire have caused seemingly irreversible shifts from forested to non-forested patches (e.g., Odion et al., 2010; Wood and Bowman, 2012; Holz et al., 2015; Paritsis et al., 2015; Whitlock et al., 2015; Donato et al., 2016; Kitzberger et al., 2016; Tepley et al., 2016; Sommerfeld et al., 2018). Given repeated patterns in how ecosystems are shifting over time (Wilson and Agnew, 1992; Suding and Hobbs, 2009; Pausas and Bond, 2020), the potentially wide geographical scales of such transformations (e.g., Coop et al., 2020), and that they can happen rapidly and with little advance warning (Scheffer et al., 2001; Scheffer and Carpenter, 2003), understanding the drivers and mechanisms underlying shifts in ecosystem states, including post-fire vegetation trajectories, is a major theme of theoretical and applied research (Ratajczak et al., 2018; Falk et al., 2022; Seidl and Turner, 2022).

Repeated patterns in ecosystem transition are observed not just over time, but also across space. “Ecotones” (di Castri et al., 1988; Yarrow and Marín, 2007) may be the best places in which to pursue questions regarding ecological resilience or ecological change (Desjardins et al., 2015) given their sensitivity to altered climate (Allen and Breshears, 1998) and disturbance regimes (Myster, 2012). Franklin et al.’s (2021) recent synthesis on forest edges highlights the notion that ecotones can be ‘inherent’ or ‘induced’. That is, transitions between ecological systems across space can occur due to overlying climatic gradients or underlying biophysical gradients (e.g., those observed at latitudinal and altitudinal treelines, respectively; Risser, 1995), but ecotones can also be induced by the external forcing of natural or anthropogenic disturbances (Franklin et al., 2021). Thus, studying how boundaries are generated and maintained between the ecological systems that form long-standing, widely-occurring spatial ecotones may help us understand the causes and likelihood of persistence of newly-induced shifts in ecological system states (Walker et al., 2010; Scheffer et al., 2012).

Shifts in the location and abundance of forest-non-forest ecotones as the result of altered fire regimes have been investigated from patch (e.g., Kitzberger et al., 2016) to landscape (e.g., Lindenmayer et al., 2011) to biome (e.g., Oliveras and Malhi, 2016) scales across different parts of the globe. However, temperate forest-peatland ecotones (especially those of the Southern Hemisphere)

have generally received less attention than other forest-non-forest ecotones (Arroyo et al., 2005; Joosten, 2016; León et al., 2021), despite increasing concern about the impacts of persistent temperate forest loss on the one hand and persistent peatland loss on the other. Investigating ecological dynamics across forest-peatland ecotones may be particularly relevant to understanding feedbacks between climate, fire and vegetation given that changes in precipitation and temperature regimes can alter local environmental conditions such that peatlands or forests expand or contract (Crawford, 2003; Ratcliffe et al., 2017; Morris et al., 2018; van der Velde et al., 2021), with concurrent effects on carbon sequestration or release (Hartshorn et al., 2003; Simard et al., 2007; Running, 2008; Turetsky et al., 2014; Goodrich et al., 2017), flammability (Turetsky et al., 2014), and water storage (Waddington et al., 2014; Perez-Quezada et al., 2023).

Our research takes place in the temperate forest-peatland ecotone of western Patagonia in southern South America (ca. 47°S), where the impact of Euro-Chilean settlers and climate change on its fire regimes and vegetation dynamics has been pervasive (Huber and Markgraf, 2003; Szeicz et al., 2003; Holz and Veblen, 2011; Holz et al., 2012a,b, 2016). The current mosaic of mesic temperate rainforest patches and sparsely- to non-forested wetland sites (many of which are peatlands, or at least peat-accumulating ecosystems or “mires”; *sensu* Rydin and Jeglum, 2006) differs from what it had been historically as evidenced by charred snags and stumps that rise from carpets of orange peat moss (*Sphagnum magellanicum*). These observations, in combination with an apparent lack of regeneration of the keystone wetland conifer *Pilgerodendron uviferum* (Don) Florin, Cupressaceae (ciprés de las Guaitecas) since the 1970s (Holz, 2009), sometimes even in the presence of surviving seed sources, suggests that a transition away from tree dominance has occurred in at least some burned areas (Supplementary Figure 1). The question, then, is whether *P. uviferum* forests will ultimately recover following fire (and under the drought conditions projected for Patagonia; Boisier et al., 2018 and Garreaud, 2018), reassemble to altered states of forest structure and/or composition (Falk et al., 2022; Seidl and Turner, 2022), or be replaced by non-forest systems entirely (e.g., those dominated by *Sphagnum* mosses).

Research on *P. uviferum* forest dynamics conducted further north in warmer south-central Chile (e.g., Bannister et al., 2012, 2017; Galindo et al., 2021) and investigations of conifer regeneration in the presence of *Sphagnum* spp. in wet forests in other parts of the world (e.g., Hörnberg et al., 1997; Roy et al., 2000; Camill et al., 2010), indicate that the life history characteristics of these plants (especially their contrasting growth rates) and their different physiological responses to environmental conditions such as water table depth (Gengarely and Lee, 2005; Waddington et al., 2014; Holmgren et al., 2015), light levels and climatic conditions

(Fenton et al., 2007; Heijmans et al., 2013; Pacé et al., 2018; Bengtsson et al., 2021), may drive post-fire trajectories in the forest-peatland ecotone of western Patagonia. More specifically, dynamics across the ecotone may be controlled by feedbacks that are mediated by climatic conditions and disturbance severity (Figure 1): (1) A *water table depth-sun exposure-Sphagnum* feedback initiated by allogenic disturbances (e.g., fire), which kill trees thus promoting water-logging (Díaz et al., 2007) and high light levels. Such conditions favor rapid surface colonization by *Sphagnum* mosses (Díaz and Armesto, 2007), whose growth habit raises the surface relative to the water table so that the survival of young tree seedlings may be compromised during the summer growing season due to desiccation (Bannister et al., 2019). 2) An *evapotranspiration-shading-tree recruitment* feedback whereby as the density of trees encroaching upon forest-peatland boundaries increases, interception and evapotranspiration reduces saturation and reinforces tree establishment. The lower light levels generated through canopy closure hamper *Sphagnum* moss development, further promoting tree establishment.

Successful *P. uviferum* seedling establishment following fire, including multiple instances of burning across the same area (i.e., “reburns”), may thus be the most critical process for determining the structure and composition of the ecosystems that develop afterward, and this may depend on the abundance of microsites that are suitable for germination, growth and survival given the species’ physiological constraints under the prevailing climatic and edaphic conditions. Due to dynamic interactions between water tables and seasonal climatic patterns in wet temperate environments, microsites that promote tree regeneration must be “safe” from both long-term inundation and seasonal drought (Hörnberg et al., 1997; Albornoz et al., 2013). Biotic interactions (e.g., competition or facilitation) with understory plants including and in addition to *Sphagnum* mosses may also affect the likelihood that *P. uviferum* seedlings can grow and survive on microsites characterized by more extreme environmental conditions (Kroiss and HilleRisLambers, 2015).

Besides shedding light on forest resilience in climatically and edaphically wet places, understanding the mechanisms driving successful post-fire or post-reburn *P. uviferum* regeneration in wetland areas is key to determining the conservation and management needs (González et al., 2014) of this long-lived, slow-growing (i.e., < 1 mm/year), globally-threatened (Souto et al., 2013) and culturally significant (Zaret, 2011) conifer species. In particular, land managers need to know whether or which restoration activities are feasible and effective in *P. uviferum* habitats (e.g., Galindo et al., 2021) or if alternative ecosystem services should be encouraged following fire (e.g., the extraction of peat moss, or the protection of freshwater reservoirs and potential carbon pools encompassed by *Sphagnum*-dominated sites; León et al., 2016, 2021; Iturraspe and Urciuolo, 2021).

Given the above observations and concerns, the overarching aim of our study was to explore whether similar mechanisms maintain a transition from forested to non-forested conditions across a forest-peatland ecotone induced by reburns versus a long-standing forest-peatland ecotone in western Patagonia. We examined whether and why *P. uviferum* forests may recover following fire or may become locked into alternative development pathways by comparing abiotic and biotic factors of the reburned

ecotone to those of the unburned (i.e., proxy of, and hereafter, “control”) ecotone. Specifically, we asked:

- (a) How do the properties of air temperature, vapor pressure deficit, photosynthetically active radiation, water table depth, substrate and understory plant community differ between reburned patches that are characterized by varying densities of *P. uviferum* trees and seedlings (i.e., forested vs. non-forested)? Do the same properties differ similarly across patches at the control site?
- (b) Which of the above variables best predict *P. uviferum* seedling abundance at the microsite scale, and how do these compare between the reburned and control sites?

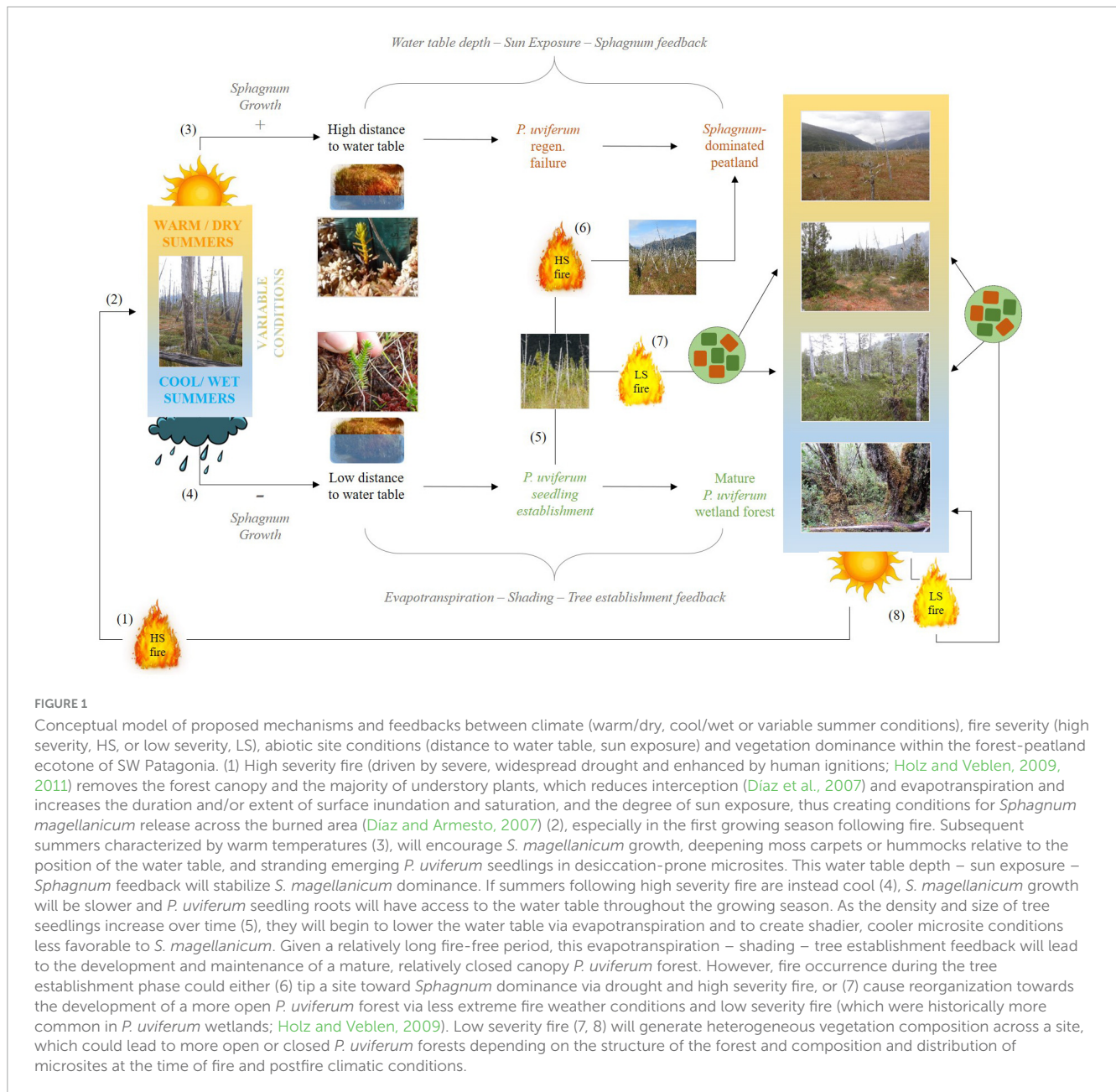
Overall, we expected that forested patches (i.e., patches dominated by live *P. uviferum* individuals greater than 5 cm in diameter at 1.3 m in height) would differ from non-forested patches in consistent ways (e.g., cooler, moister and darker conditions, water tables further below the surface, and substrates and understory plant communities characterized by non-*Sphagnum* mosses and other temperate rainforest taxa) regardless of fire history. Based on our conceptual model (Figure 1), we expected *P. uviferum* seedling abundance to be most strongly associated with light level, water table and substrate variables, and we expected to find patch-level effects within sites rather than major differences in predictors between the reburned and control sites. Most importantly, similarities in the above abiotic and biotic properties between the non-forested patches would indicate that the once-forested but now *Sphagnum*-dominated patch at the reburned site was on a trajectory towards a peatland rather than forest state, with associated implications for ecosystem functioning and potential for resource use/management.

To address our research questions, we collected data using automated sensors and field observations. The sensors yielded hourly readings of water level, air temperature, and relative humidity across multi-week to multi-month periods, thus offering a larger temporal context in which to interpret the snapshot observations of environmental conditions that were made manually. We used non-metric multidimensional scaling to explore differences in understory plant communities, analysis of variance to test for differences in select variables and seedling counts between patches within and across sites, and hierarchical Bayesian regression models to identify the factors most strongly associated with seedling abundance. Ultimately, our findings contribute much-needed information about the ecological dynamics of understudied high-latitude but *non-boreal* forest-peatland ecotones (Davies et al., 2013; Joosten, 2016) and offer land managers insight into which characteristics of *P. uviferum* habitats should be targeted for monitoring following fire(s) or to evaluate a site for its restoration potential.

## 2 Materials and methods

### 2.1 Field study sites

We investigated *P. uviferum* patches and seedling abundance across two temperate forest-peatland ecotones in coastal areas of



the Aysén Region of Chile in western Patagonia (Figure 2). Given the landscape-scale burning that was used to clear land during colonization of the Aysén District, very few sites encompassing the forest-peatland ecotone remain that are accessible and represent historic (i.e., prior to Euro-Chilean settlement) conditions where Indigenous burning existed but was comparatively minimal (Holz and Veblen, 2011; Holz et al., 2016). Thus, our control (unburned) and reburned (hereafter referred to simply as 'burned') sites were approximately 445 km apart on a north-south gradient. Both sites were located to the west of the Andes Mountains where the climate is temperate hyperhumid, strongly influenced by westerly winds off the Pacific Ocean and orographic uplift, and characterized by a seasonal cycle whereby the warmest temperatures and least precipitation occur during the austral summer (December through February) and the coldest temperatures and greatest precipitation occur during the winter

(June through August; Garreaud et al., 2013). The control and burned sites were subject to somewhat different temperature and precipitation regimes given their latitudinal positions and locations relative to the ocean and Patagonian icefields (details below), and consequently were characterized by slightly different ecoregions (Veblen et al., 1995) within the Temperate Broadleaf and Mixed Forest biome (Dinerstein et al., 2017). However, both sites experienced strong year-round maritime hyperhumidity, and the total local precipitation observations at our control site (2,617 mm/year) were only around 4% higher than those of the burned site (2,515 mm/year; Dirección General de Aguas [DGA], 2015, 2022). In addition, both sites were found in similar topographic conditions: they were located in valley bottoms shaped by glacial, fluvioglacial and fluvial processes and characterized by imperfectly to poorly drained soils (Pfeiffer et al., 2010; Casanova et al., 2013).

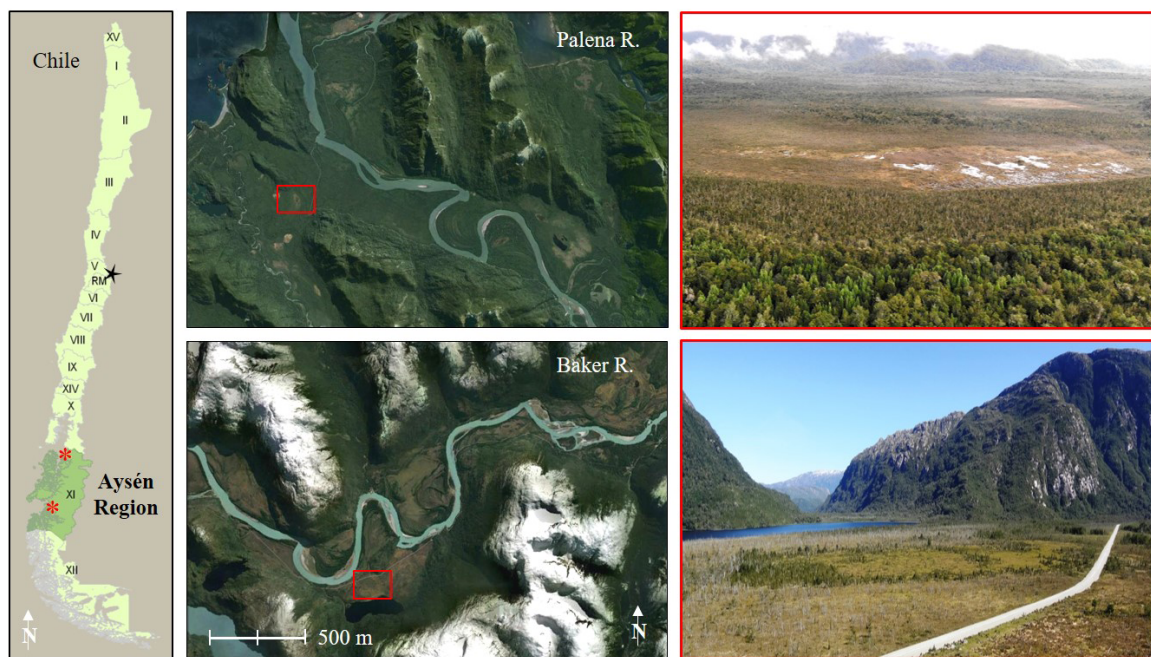


FIGURE 2

Location of the control site (Palena River;  $43^{\circ}52'34''\text{S}$ ,  $72^{\circ}57'36''\text{W}$ , top panels) and burned site (Baker River;  $47^{\circ}49'2''\text{S}$ ,  $73^{\circ}25'38''\text{W}$ , bottom panels) in the Aysén District, Chile. The top right photo was taken toward the west in April 2019; photo credit: Rodrigo Poliche. The bottom right photo was taken toward the southwest in July 2013.

The control site ( $43^{\circ}52'34''\text{S}$ ,  $72^{\circ}57'36''\text{W}$ ) was situated near the town of Puerto Raúl Marín Balmaceda (RMB) and about 5 km from the open ocean in a portion of the Palena River watershed that has experienced relatively little land use disturbance since settlement began in the 1910s (Holz and Veblen, 2011). The river valley has been traversable by road only since 2009, and local livelihoods were historically oriented around fishing and fine-scale timber harvest, though they have more recently (since the 1990s) turned to aquaculture and tourism. While long-term instrumental data are lacking, meteorological records from 2001 through 2018 show that average annual precipitation at the RMB station was 2617 mm, with an annual minimum of 1,759 mm and a maximum of 5,582 mm (Dirección General de Aguas [DGA], 2015, 2022). Modeled temperatures for Chaitén, 100 km to the north along the coast, indicate an average annual temperature of  $7.4^{\circ}\text{C}$  from 2001 through 2018, with an average summer temperature of  $14.5^{\circ}\text{C}$  and average winter temperature of  $2.8^{\circ}\text{C}$  (Alvarez-Garretón et al., 2018). The vegetation mosaic of the lower Palena River valley is characterized by North Patagonian rainforests (Veblen et al., 1995), with scattered marshes, mires and peatlands. *P. uviferum* occupies emergent positions in drier substrate with dominant and codominant *Nothofagus nitida*, *N. betuloides*, *Drymis winteri*, and several myrtles from the Myrtaceae family, and dominant and codominant positions with the tall, multi-stemmed shrub *Tepualia stipularis* in saturated bog-forests ecotones. Many of these latter sites are virtually inaccessible given the density of the surrounding forest; for example, it can take two hours to travel 600 meters by foot. Only one single fire-scarred tree was observed within the study site, and it is likely that no major fire events have affected the area in the last ~200–300 years based on ages of *P. uviferum* trees (Holz et al., in review). The historic fire regime was characterized

by mixed severity fires with mostly patchy, fine-scale events (Holz and Veblen, 2011).

The burned study site was adjacent to Lake Cute (pronounced, 'kú-teh';  $47^{\circ}49'2''\text{S}$ ,  $73^{\circ}25'38''\text{W}$ ) near the town of Caleta Tortel in the lower Baker River watershed. Like the control site, the burned site is influenced by maritime conditions; the site is 3 km from an inlet in the fjords and about 90 km from the open ocean. The meteorological station at Tortel recorded average annual precipitation of 2,515 mm from 2006 through 2018 (excluding 2013 due to a dearth of data), with an annual minimum of 1,611 mm and a maximum of 3122 mm (DGA 2022). Modeled temperatures for a location 50 km to the northeast (i.e., more continental conditions;  $47^{\circ}30'15.25''\text{S}$ ,  $72^{\circ}58'47.37''\text{W}$ ) indicate an annual average of  $5.2^{\circ}\text{C}$  from 2001 through 2018, with an average summer temperature of  $9.5^{\circ}\text{C}$  and average winter temperature of  $0.6^{\circ}\text{C}$  (Alvarez-Garretón et al., 2018). Euro-Chilean settlers began arriving and establishing in the area in the 1920s, and fire was the primary tool by which they cleared forested areas to create homesteads and grazing lands (Holz and Veblen, 2011). Thus, much of the lower Baker River valley bottom has been affected by fire since then. While there are remnant forest stands characteristic of the transition zone between North Patagonian and Magellanic temperate rainforests (Veblen et al., 1995), much of the low-lying, flat terrain is now characterized by extensive lawns of *S. magellanicum* with charred snags of *P. uviferum*. Aerial imagery reveals the extent to which the vegetation mosaic of the lower Baker River valley has been affected by fire (e.g., Figure 2, lower right image). Fire scar dates from the burned study site indicate that at least 23 fires (mostly human-initiated burns) occurred between the 1920s and early 2000s, with the most recent fire in 2004 and a mean fire return interval (MFI) of 3.5 years (Holz, 2009). Prior to European settlement this area

experienced a mixed-severity fire regime similar to that of the control site (Holz and Veblen, 2011). That the site once had a more extensive forest cover than presently is reflected in historical imagery (Supplementary Figure 2) and soil profiles: Rodriguez (2015) found shallower and more thoroughly decomposed organic soils under remnant patches of tree cover. In addition to multiple burns, the site—which is located on an old meander bend of the Baker River (Rodriguez, 2015)—has been affected by glacial lake outburst floods (GLOFs; Rodriguez, 2015). At least 23 GLOFs have occurred between 2008 and 2020 (Vandekerkhove et al., 2021), but neither the total number of historic events nor those that have affected the hydrology of the burned site is known.

## 2.2 Data collection

The sampling in the control (unburned) and burned sites were stratified by patch type based on vegetation structure and composition and hydrologic regime using information obtained via aerial and satellite imagery interpretation and analysis (e.g., ESRI World Imagery, Google Earth, and high-resolution multi-spectral imagery) and on-site reconnaissance in 2016 and earlier (see Zaret, 2011). At both sites, three patch types were identified that appeared to encompass the historic (in the case of the burned site) transition from forest to peatland. These included the Forest, Bog Forest and Bog patches at the control site, and the Burned Forest, Transition, and Cushion patches at the burned site (Supplementary Figures 3, 4). Field sampling was conducted in 2017 and 2018.

### 2.2.1 Seasonal water level and microclimate

To understand how abiotic environmental properties varied across the forest-peatland ecotone, we used sensors to continuously measure water level, air temperature and relative humidity over multi-week to multi-month periods. Sensors were only available for some combinations of patch, site and field season dates. Our goal was to capture high temporal resolution data across key periods of the growing season at each site and to use these data to aid our interpretations of one-time measurements made within microsites, as discussed in more detail in subsequent sections.

Two water level monitoring wells (Supplementary material) were established in the control and burned site in the patches with the greatest and least tree cover. In the burned site, wells were established in the Transition and Burned Forest patches, and in the control site, they were established in the Forest and Bog patches (Supplementary Table 1). Continuous one-hour interval readings were collected using In-Situ Rugged TROLL 100 water level sensors.

We used iButton Hygrochron Temperature/Humidity Loggers by Maxim Integrated to measure air temperature and relative humidity at hour intervals. These were suspended under plastic cones to protect them from precipitation, while allowing for air flow, and the cones were hung from wooden stakes at about 30 cm from the ground to better capture the conditions experienced by understory plant communities and juvenile trees. iButtons were deployed in all patches of the control and burned sites during both the 2017 and 2018 field seasons (Supplementary material). To examine differences in light levels between patches, measurements of photosynthetically active radiation (PAR) were made using a

hand-held LI-COR Light Sensor Logger at the same locations where iButtons were deployed; readings per site were obtained on the same day under uniform weather conditions.

### 2.2.2 Understory vegetation, *Pilgerodendron* tree and seedling abundance and microsite conditions

Plots of 10 x 10 m were placed along transects ca. 40 m from each other that crossed the relatively abrupt forest-peatland ecotone at each site. At the control site, the first transect was established haphazardly to center fieldwork on the eastern side of the site and along the presumed gradient in hydrology. All remaining transects crossed two vegetation types, as Bog plots were clumped to the north and Bog Forest plots to the south, while Forest plots were established roughly in the middle of that patch type, away from the edge of the narrow band of transitional forest to the west or the edge of the riparian gallery forest to the east (Supplementary Figure 3). At the burned site, the first transect was established haphazardly to center fieldwork along the transition from the open bog (i.e., the ‘Cushion’ patch) to the burned forest on the eastern side of the site, thus following gradients in hydrology and slope (i.e., from W to E) (Supplementary Figure 4). Due to time constraints and low evidence of fire effects, the Cushion patch was not sampled for seedling abundance or vegetation composition, but seasonal air temperature and humidity were investigated.

Within each 100 m<sup>2</sup> plot ( $n = 27$  at the control site,  $n = 18$  at the burned site), the height and diameter at breast height (DBH at 1.3 m) of all *P. uviferum* trees  $\geq 5$  cm were recorded. Along the centerline of each plot, four 80 cm diameter (2 m<sup>2</sup>) circular subplots were established ( $n = 108$  subplots at the control site,  $n = 72$  subplots at the burned site; Supplementary Figure 7) to collect the following data pertaining to *P. uviferum* regeneration and abiotic and biotic factors that may influence seedling establishment and performance: (1) counts and height measurements for *P. uviferum* seedlings (all individuals  $< 5$  cm DBH were tallied; heights were recorded for all individuals  $> 5$  cm height); (2) photosynthetically active radiation (PAR); (3) distance to the water table (DWT); (4) percent cover of individually identified vascular plant species; and (5) percent cover of select ‘substrate types’ (i.e., pool, bare ground, litter, wood, trunk, cushion-forming plants, *Sphagnum* spp., *Dicranaloma* spp., and other moss species (i.e., those not in the aforementioned moss genera). To assess differences in PAR at the short and tall seedling height, PAR was measured at two heights (0.3 m and 1.3 m) at each of three locations per subplot using a LI-COR LI-1500 Light Sensor Logger. DWT was measured at the same locations as PAR and represented the distance from the top of whichever substrate would have been first hit when dropping a pin from breast height down to the water table; distances were recorded as negative values if the substrate top was below the water table (i.e., if there was surface water), otherwise as positive values. If the water table was not evident at or above the surface within the subplot, a bore hole was created adjacent to the subplot using a 2.75 inch diameter Eijkelkamp Edelman soil auger and metal rulers with magnetic levels were used to measure DWT at the select within-subplot locations. Of the substrate types, “wood” referred to relatively flat, thin pieces of wood scattered on the ground surface, whereas “trunk” referred to live or dead, vertical, less-than-vertical or fallen tree trunks.

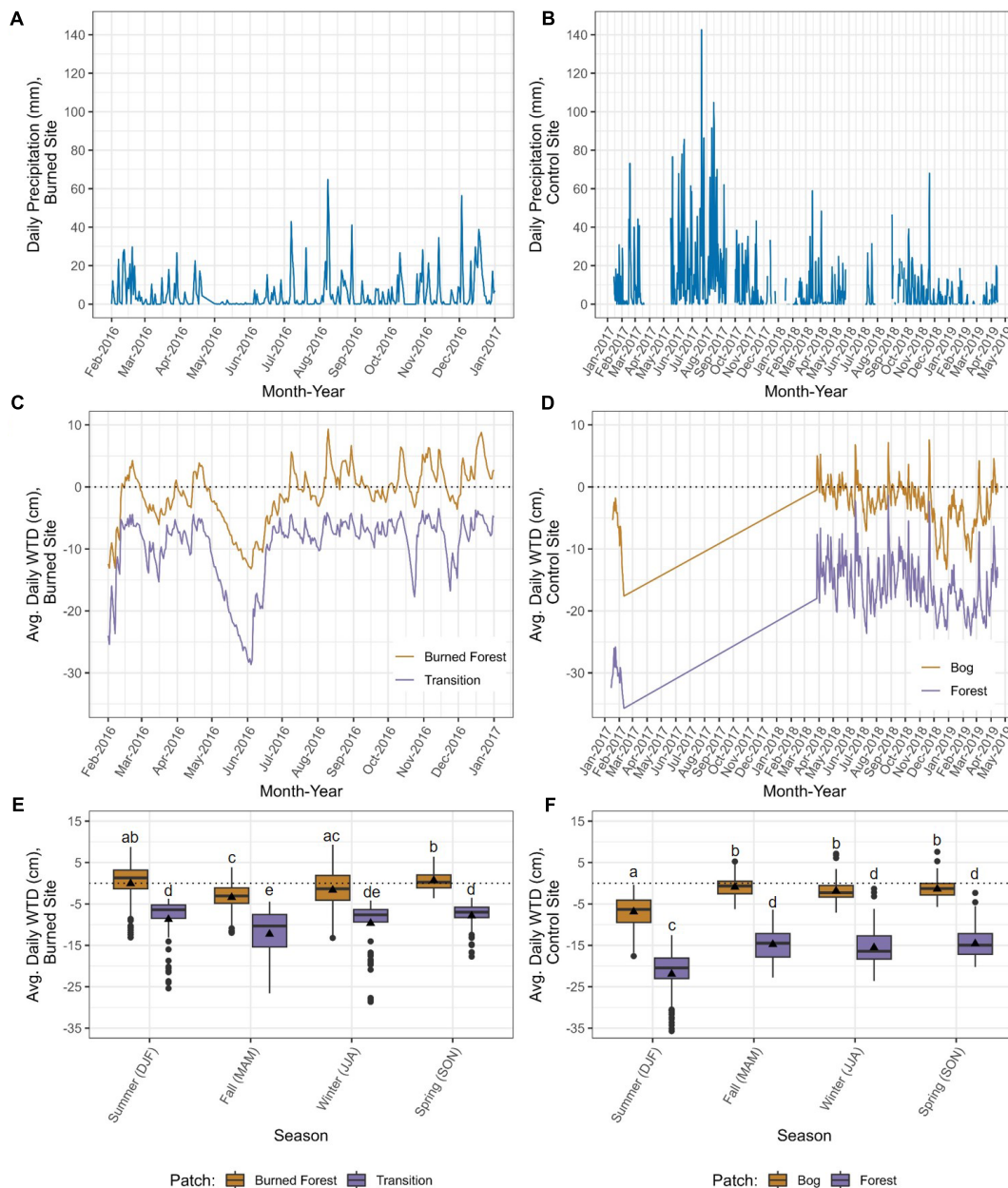


FIGURE 3

Daily precipitation (Dirección General de Aguas [DGA], 2022, Caleta Tortel and Raul Marin Balmaceda meteorological stations) (A,B), daily average water table depths (WTDs) (C,D), and daily average WTDs summarized across seasons (Summer = DJF, Fall = MAM, Winter = JJA, Spring = SON) (E,F) for the burned site (left) and control (unburned) site (right). Water table depths were recorded at hour intervals by data loggers suspended in PVC wells in the vegetation patches in each site with the highest (Transition, Forest) and lowest (Burned Forest, Bog) densities of live tree cover. Different letters indicate significant differences between means using Welch's one-way ANOVA and *post-hoc* Games-Howell tests ( $P < 0.05$ ).

## 2.3 Data analysis

### 2.3.1 Seasonal water level and microclimate

Water level, temperature and relative humidity data were downloaded and corrected (as needed) per the instruments' standard software procedures (Supplementary material). The "lubridate" (Grolemund and Wickham, 2011), "dplyr" (Wickham et al., 2021), "ggplot2" (Wickham, 2016), "FSA" (Ogle et al., 2022), and "stats" software packages in R 4.1.2 (R Core Team, 2021) were used to aggregate hourly water level depths, temperature,

and relative humidity readings to mean daily values, derive and test for differences between summary statistics, and plot results. Instrumental records of daily precipitation were downloaded (Dirección General de Aguas [DGA], 2022) for the Caleta Tortel and Raul Marín Balmaceda meteorological stations and plotted to facilitate interpretation of water level data. We statistically compared mean water table depths across patches and seasons using Welch's one-way analysis of variance (ANOVA) and Games-Howell post-hoc tests due to unequal variances across those groups (Ruxton and Beauchamp, 2008). Temperature and relative



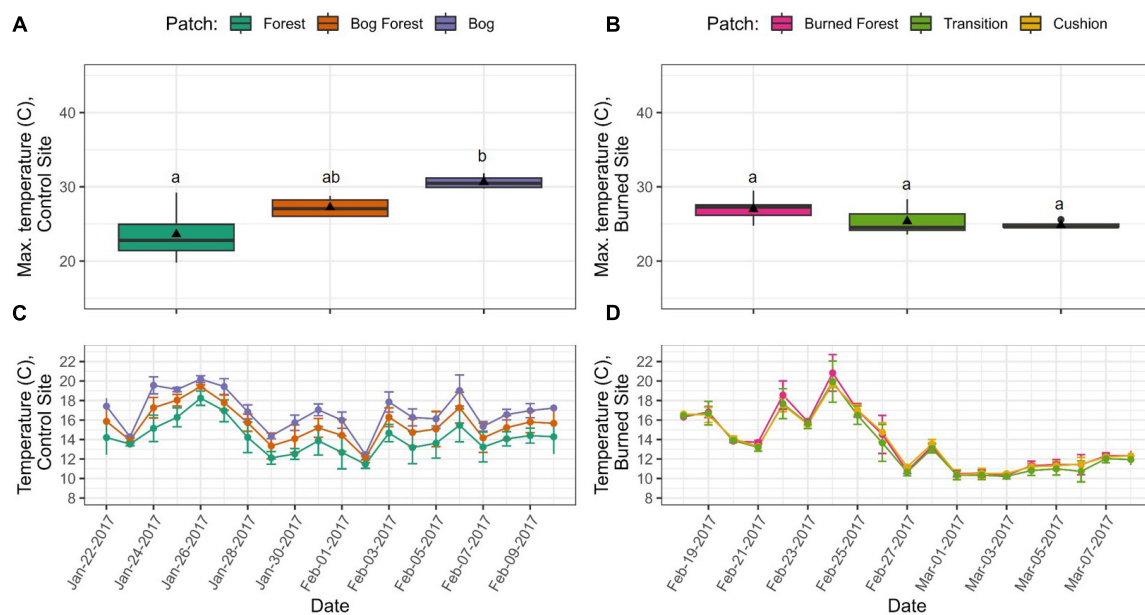


FIGURE 4

Comparison of summer temperatures within and across sites (control left, burned right). Boxplots in (A,B) represent the 10% hottest hours recorded per iButton per patch across the sampling period ( $n = 48$  hours control site,  $n = 46$  hours burned site). Different letters indicate significant differences between means within sites using Kruskal-Wallis one-way ANOVA and post-hoc Dunn's tests ( $P < 0.05$ ). Time series (C,D) are of average daily temperature  $\pm 2$  standard deviations for each treatment or patch. Temperature data were recorded at hour intervals by iButtons:  $n = 12$ , Forest;  $n = 4$ , Bog Forest and Bog;  $n = 7$ , Burned Forest and Transition;  $n = 6$ , Cushion.

humidity data were used to estimate vapor pressure deficit (VPD) following Jones (1992). To explore microclimatic conditions most representative of seasonal drought, we identified the 10% warmest and driest hours, respectively, per iButton per patch (i.e., the highest temperatures and VPD values) and then tested for statistical differences between their means using Kruskal-Wallis one-way ANOVA due to non-normal distributions but equal variances across groups. We conducted group-wise comparisons using Dunn's tests with "Benjamini-Hochberg" corrections to increase power and control the false detection rate given small sample sizes per patch (Benjamini and Hochberg, 1995). Since seasonal water level and microclimate data were collected during different time periods per site, we were most interested in comparing the relationships between parameters within sites and patch types.

### 2.3.2 Understory vegetation

Non-metric multidimensional scaling (NMDS) was conducted to examine differences in vegetation species assemblages among subplots in the patch types per site. For the vegetation ordinations, only species that occurred in two or more subplots per site were included in the analysis, resulting in a total of 42 species for the control (unburned) site and 30 species for the burned site (i.e., leaving 3 and 13 species out of further analyses from the control and burned sites, respectively).

NMDS ordinations were conducted using PC-ORD version 6.22 (McCune and Mefford, 2011) following Peck (2010). For both sites, ordinations were run using Bray-Curtis dissimilarity measures. Based on the results of autopilot stress tests, a final 3-dimensional solution was chosen for the ordination for the control site while a final 2-dimensional solution was chosen for the burned site. Multi-response permutation procedure (MRPP)

was used to test the null hypothesis of no significant difference in vegetation species assemblages among patches per site. To identify the understory plant types most characteristic of each patch, indicator species analysis (ISA) was run using the Donoso (1993), Peck (2010). Vector fitting based on Pearson's  $r$ -squared and Kendall's tau rank correlations between explanatory variables and ordination axes was conducted to identify abiotic and biotic factors associated with differences in species assemblages among subplots.

### 2.3.3 Seedling abundance and microsite conditions

We investigated the relationships between *P. uviferum* regeneration and abiotic and biotic components of the microsite environment at two different scales. At the patch scale, we summarized field data across subplots to the plot level (if applicable) and then tested for differences between patches within and across sites using one-way ANOVA (Supplementary material). We were particularly interested in whether select variables differed significantly between forested and non-forested patches, as defined by the presence of live *P. uviferum* trees of at least 5 cm DBH at the time of sampling (i.e., Forest vs. Bog patches at the control site, or Transition vs. Burned Forest patches at the burned site), indicating that patterns in microsite composition and distribution may help to maintain those patch boundaries (Peters et al., 2006).

To identify the microsite-scale variables that were most strongly associated with seedling counts, Bayesian hierarchical models were used to examine the response of *P. uviferum* seedling counts to alternative combinations of abiotic and biotic predictors. We chose to use a Bayesian rather than frequentist statistical approach to propagate uncertainty across the levels of our models, thus

increasing the accuracy of parameter estimates given our relatively small sample sizes per site (Muth et al., 2018). To investigate whether the relationships between *P. uviferum* seedling abundance and microsite characteristics differed given local site histories and legacies of natural disturbance and land use (e.g., fire, surface inundation, ditching, road construction), we fit separate series of candidate models to data from the control and burned site, respectively.

Following Gelman et al. (2020), we used a Bayesian workflow to construct, check the fit of, validate, and compare models within each series per site. Our approach to model-building was one of iterative model expansion: from the set of variables hypothesized to be associated with *P. uviferum* seedling abundance, we used Spearman rank correlations to determine which had stronger associations with seedling counts while minimizing multicollinearity within sites and allowing us to include the same suite of predictors in models for both sites (Supplementary Figures 8, 9). Prior to model fitting, PAR was log-transformed and all quantitative predictors were standardized. Patch was included as a nominal variable with three levels for the control site (Forest, Bog Forest, and Bog) and two levels for the burned site (Transition, Burned Forest).

While differing in their fixed effects, all of the models that we constructed contained a multilevel structure in which plots were included as random effects to account for the lack of independence and any resulting autocorrelation inherent in our study design (i.e., four subplots nested within each plot; Zuur et al., 2009). In addition, all models predicted the shape (i.e., overdispersion) parameter as a function of patch (given the high numbers of zeros in the Bog and Burned Forest patches), and all model parameters were specified with weakly informative prior distributions (Lemoine, 2019; Supplementary material). As discussed in more detail in the Supplementary material (see Models of Seedling Counts), we first fit a series of simple, single-predictor candidate models and then used those results to build more complex models. Ultimately, we selected one or two models from each site for interpretation and comparison to our expectations regarding the relationships between *P. uviferum* seedling abundance and individual predictors (Supplementary Table 2). All data exploration and analysis were conducted using R 4.1.2 (R Core Team, 2021); models were fit using the 'brms' package (Bürkner, 2021). The 'tidybayes' package (Kay, 2022) was used to summarize and plot parameter estimates for the final model(s) per site.

## 3 Results

### 3.1 Seasonal water level and microclimate

#### 3.1.1 Seasonal water level

In general, changes in water table depth (WTD) at each of the four monitoring wells followed peaks and troughs in daily precipitation and trends in monthly precipitation (Figures 3A–D). For example, at the burned site, WTD values were lowest in both patches in June 2016, which followed 2.5 months of consistently low to zero precipitation; and in the control (unburned) site, the abrupt

peak in precipitation in November 2018 was followed by low daily values and WTDs in both patches responded in kind.

Despite their similar responsiveness to the precipitation regime, WTDs differed between the two sites as follows: Water tables tended to be closer to the surface at the burned site, as reflected in daily (Figures 3C, D) and seasonal (Figures 3E, F) averages. There also tended to be a smaller difference in WTDs between the patches in the burned site than between those in the control site (average differences plus or minus the standard deviation, of  $8.5 \pm 1.7$  and  $14.64 \pm 3.35$  cm, respectively).

Water table dynamics at both sites were patch-dependent. Mean WTDs differed significantly between the two patches within each site across all seasons. In addition, patches within sites differed in their hydropatterns (i.e., depth and duration of surface inundation). Within the burned site, the water table was above the surface in the Burned Forest patch during 43% of the days sampled and in all months except May and June 2016; the average depth of surface water (i.e., WTDs > 0 cm) was  $2.34 \pm 1.1$  cm (Supplementary Table 12). In contrast, the water table was never above the surface in the Transition patch; rather, the WTD in that patch seemed to frequently return to about 5 cm below the ground surface, never rising far above that level and only dropping substantially lower during periods of low to no precipitation (Supplementary Table 13). At the control site, the average surface water depth in the Bog patch was  $1.69 \pm 1.03$  cm (Supplementary Table 14). The water table was only above the surface in the Bog patch during 19% of the days sampled; it never rose above the surface during January and February 2017 or December 2018 through February 2019, and it reached the lowest levels (i.e., greatest depths below the ground surface) during those months. The Forest patch was never inundated and the subsurface water table was variable, with monthly averages of  $-12.7$  to  $-29.3$  cm (Supplementary Table 15).

#### 3.1.2 Seasonal microclimate

Microsite climatic conditions during the 2017 austral summer tended to differ substantially across patches at the control site while they were relatively uniform at the burned site. Within the Forest patch at the control site, we found no statistical differences in temperature or VPD, respectively, between microsites with abundant *P. uviferum* regeneration and those with no regeneration; thus we lumped and plotted those data together. At the control site, temperatures were warmest in the Bog patch, intermediate in the Bog Forest patch and lowest in the Forest patch, and this trend held across the temporal resolutions at which we examined the data. Of the 10% hottest hours recorded during the summer sampling period, the average maximum temperature ( $\pm$  SD) was significantly higher in the Bog patch ( $30.6 \pm 1.6^\circ\text{C}$ ) than in the Forest patch ( $23.6 \pm 4.0^\circ\text{C}$ ;  $P < 0.05$ ), while the average maximum temperature in the Bog Forest ( $27.2 \pm 2.3^\circ\text{C}$ ) was not significantly different from the others (Figure 4A). The above trends were also observed over time for mean daily temperatures (Figure 4C). At the burned site, there were no significant differences between the average 10% hottest hours in the Burned Forest, Transition and Cushion patches, which was also reflected in daily temperatures (Figures 4B, D).

Within site trends in vapor pressure deficit (VPD) were similar to those observed for temperature during the austral summer at the control site (Supplementary Figure 15). However, in the

burned site, rather than uniform values across the three patches, the maximum average VPD in the Burned Forest patch ( $2.09 \pm 0.94$  kPa) was significantly higher than that of the Cushion patch ( $1.54 \pm 0.49$  kPa;  $P < 0.05$ ), while neither were significantly different from the Transition patch ( $1.74 \pm 0.92$  kPa). This pattern only applied to the warmest and driest hours of the day; there was substantial overlap in mean daily VPD values across the three patches.

During the 2018 austral autumn sampling period, trends in microsite temperatures and VPD were somewhat different from those observed in the austral summer. In the control site, there was substantial overlap between the temperatures recorded in the Bog and Bog Forest patches, whose average 10% hottest hours were significantly higher than those in the Forest patch (Supplementary Figure 16). In the burned site, there was substantial overlap in mean daily temperatures across the three patches, but of the 10% hottest hours, the maximum average temperatures in the Burned Forest and Transition patches were  $17.1 \pm 2.1^\circ\text{C}$  and  $16.8 \pm 3.1^\circ\text{C}$ , respectively, which were significantly higher than that of the Cushion patch ( $14.8 \pm 1.8^\circ\text{C}$ ;  $P < 0.05$ ). Regarding VPD in the control site, trends between patches mirrored those observed for temperature: of the 10% warmest/driest hours, the average VPD for the Forest patch was close to zero ( $0.06 \pm 0.06$  kPa) and significantly lower than the average VPDs for the Bog and Bog Forest patches ( $0.93 \pm 0.25$  kPa and  $0.75 \pm 0.33$  kPa, respectively,  $P < 0.05$ ; Supplementary Figure 17). In the burned site, there were significant differences between the average 10% maximum VPD values for the Burned Forest and Cushion patches ( $0.95 \pm 0.30$  kPa,  $0.74 \pm 0.24$ , respectively;  $P < 0.05$ ), but these trends did not hold across all days sampled.

### 3.2 Understory vegetation

For both the control and burned sites, vegetation species assemblages at the subplot level were clustered in ordination space by patch type (Figure 5). In the control site, subplots from the three patch types were most clearly grouped along the first of three orthogonal axes (see Supplementary Figures 18, 19 for additional biplots). Understory plant communities in subplots from the Forest patch were most tightly clustered and were located at the end of Axis 1 that was strongly correlated with higher abundances of live *P. uviferum* trees ( $r = 0.74$ ), and the percent cover of moss species not in the *Sphagnum* or *Dicranaloma* genera ( $r = 0.80$ ), ferns ( $r = 0.67$ ) and taller shrubs (i.e., those that did not form dense, low-lying mats;  $r = 0.63$ ; Supplementary Table 16). The understory plant communities in the Bog subplots were located at the other end Axis 1, which was correlated with PAR at 0.3 m above the ground ( $r = -0.69$ ) and the percent cover of low-lying, mat-forming shrubs ( $r = -0.62$ ). Vegetation community assemblages from the Bog Forest patch were generally situated between those of the other patches. They tended to be either, (1) clustered near the Forest patch assemblages along Axis 1 or at the end of Axis 2 that was correlated with the percent cover of understory trees (excluding *P. uviferum*;  $r = -0.60$ ), or (2) closer to the Bog vegetation assemblages along Axis 1 and clustered toward the end of Axis 3 that was most strongly correlated with *Sphagnum spp.* ( $r = 0.63$ ). Subplots within patches were

more similar to one another than expected by chance alone, as indicated by the statistic of multi-response permutation procedure (MRPP) within-group agreement, which was greater than zero at the  $P < 0.001$  significance level for each pairwise comparison between patches for the control site vegetation ordination (Forest vs. Bog Forest,  $A = 0.164$ ; Forest vs. Bog,  $A = 0.215$ ; Bog Forest vs. Bog,  $A = 0.100$ ). The top two indicator species (identified to at least genus) for each of the three patches, respectively, were as follows: *Philesia magellanica* (a climbing evergreen shrub) and *Gaultheria antarctica* (a short-statured evergreen shrub in the heath family) for the Forest patch; *Schoenoplectus californicus* (a widely-distributed bulrush in the sedge family) and *Dicranaloma spp.* (mat-forming mosses associated with forest floors and tree trunks) for the Bog Forest patch; and *Myrteola nummularia* (a short-statured, mat-forming evergreen shrub in the myrtle family) and *Tetroncium magellanicum* (a member of the arrowgrass family) for the Bog patch; (Supplementary Table 17).

For the burned site, subplot vegetation species assemblages were grouped by patch along the first of two orthogonal ordination axes (Figure 5). In the Transition patch, they were generally associated with the end of Axis 1 that was most strongly correlated with counts of live *P. uviferum* trees ( $r = 0.69$ ), and the percent cover of *Dicranaloma spp.* ( $r = 0.70$ ), cushion plants ( $r = 0.70$ ) and low, mat-forming shrubs ( $r = 0.66$ ; Supplementary Table 19). The majority of the vegetation assemblages in the Burned Forest subplots were tightly clustered at the opposite end of Axis 1, which was strongly correlated with the percent cover of *Sphagnum spp.* ( $r = -0.95$ ). The MRPP within-group agreement statistic was greater than zero for vegetation species assemblages in the Transition vs. Burned Forest patches ( $A = 0.325$ ,  $P < 0.001$ ), and the top two indicator species for each of the two patches, respectively, were *Dicranaloma spp.* and *Lepidothamnus fonckii* (a dwarf conifer in the Podocarpaceae family) for the Transition patch; and *Marsippospermum grandiflorum* (a species of rush) and *S. magellanicum* for the Burned Forest patch (Supplementary Table 20).

### 3.3 Seedling abundance and microsite conditions

#### 3.3.1 Patch scale

*P. uviferum* seedling abundances differed across forested and non-forested patches and tended to be highly variable within patches (Figure 6 and Table 1; see Supplementary Table 22 for count estimates per hectare). At the control site, median ( $\pm$  MAD) seedling counts in 2 m<sup>2</sup> microsites were highest in the Forest patch ( $18 \pm 14$  seedlings), followed by the Bog Forest ( $10 \pm 8$  seedlings) and Bog ( $0 \pm 0$  seedlings) patches. At the burned site, counts were higher in the Transition patch ( $11 \pm 9$  seedlings) than the Burned Forest patch ( $1 \pm 1$  seedling). Analysis of variance and post-hoc multiple comparison tests failed to reject the null hypotheses of no significant differences between median seedling counts amongst the Forest, Bog Forest and Transition patches, while seedling counts in those patches were significantly higher than those in the Bog and Burned Forest patches.

Counts of *P. uviferum* trees and the percent cover of *Sphagnum spp.* also differed significantly between patches at

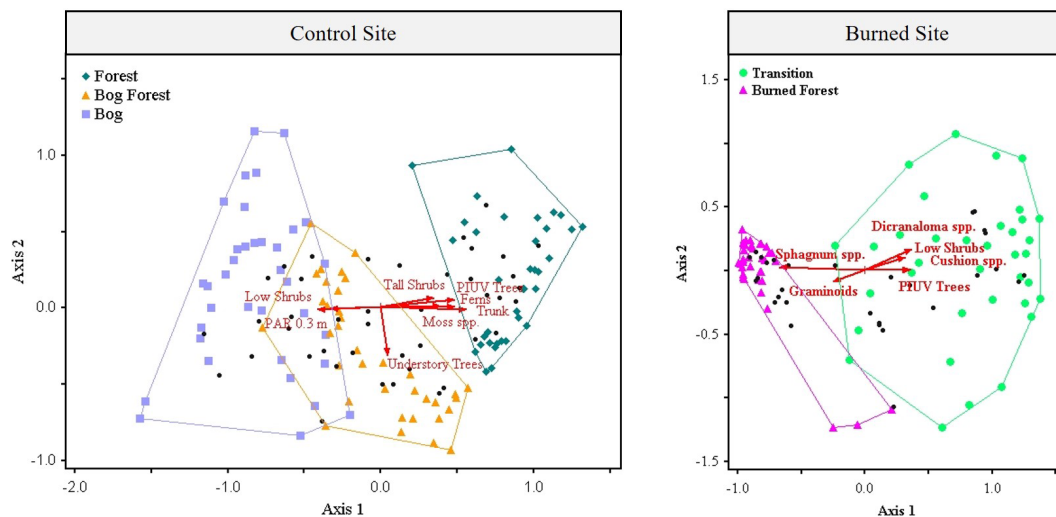


FIGURE 5

Biplots of first two (of three) orthogonal ordination axes produced through non-metric multidimensional scaling (NMDS) of the percent cover of 42 vegetation species in 108 2 m<sup>2</sup> subplots (36 subplots per Forest, Bog Forest or Bog patches) at the control site, and two orthogonal ordination axes produced through NMDS of the percent cover of 30 vegetation species in 72 2 m<sup>2</sup> subplots (36 subplots per Burned Forest or Transition habitat patches) at the burned site. Each ordination was conducted using a Bray-Curtis distance matrix; the mean stress of 250 runs with real data for the control site NMDS was 12.912, that for the burned site was 14.375. The vegetation analysis included the following 19 explanatory variables: DWT (distance to the water table from the top of substrates), PAR 0.3 (log-transformed photosynthetically active radiation at 0.3 m above the ground), PAR 1.3, PIUV Trees (count of live *P. uviferum* trees > 5 cm DBH), and the percent cover of *Sphagnum* spp., *Dicranaloma* spp., other moss species (i.e., those not in the *Sphagnum* or *Dicranaloma* genera), cushion plants, graminoids, forbs, ferns, low/mat-forming shrubs, other/taller shrubs, understory trees, pool, bare ground, litter, wood, and trunk (i.e., of standing live or dead trees). Vectors in red (scaled to 50%) represent those explanatory variables with Pearson coefficient of determination of at least 0.35.

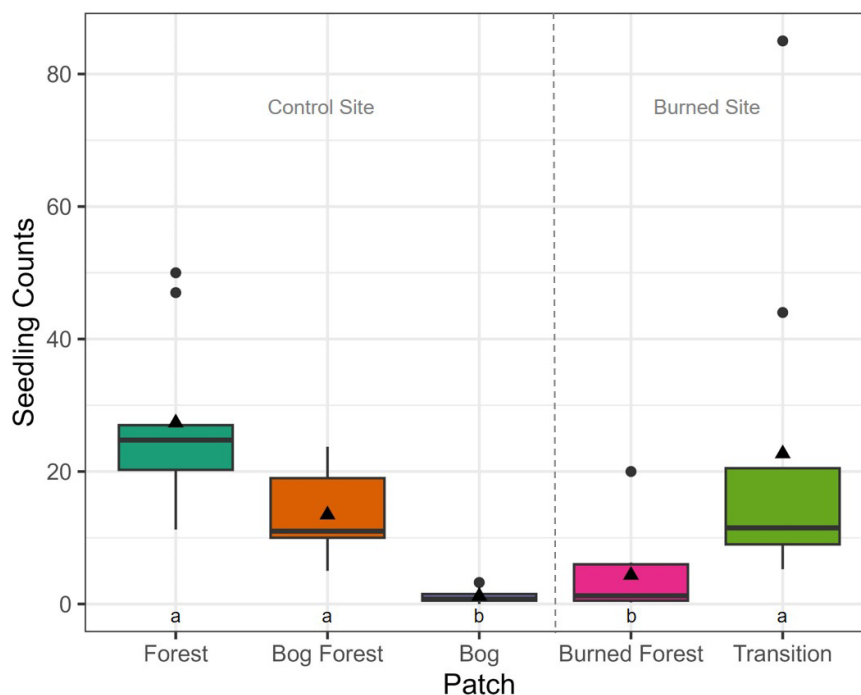


FIGURE 6

Boxplots of *P. uviferum* seedling (DBH < 5 cm; all heights) counts per patch: Forest, Bog Forest and Bog patches in the control site, Burned Forest and Transition patches in the burned site. Seedlings were tallied in four 2 m<sup>2</sup> subplots per plot, nine plots per patch. Boxes represent the interquartile range of the data summarized to plot and patch; thick horizontal lines and black triangles represent median and mean seedling counts, respectively; and vertical lines indicate variability in seedling counts outside of the interquartile range with black circles are outliers. Different letters indicate significant differences between median counts across sites using Kruskal-Wallis one-way ANOVA and post-hoc Dunn's tests ( $P < 0.05$ ).

TABLE 1 Summary statistics by patch for *P. uviferum* seedling counts and quantitative variables observed in subplot microsites.

Patch:	Control site			Burned site	
	Forest	Bog forest	Bog	Burned forest	Transition
<b>Count of <i>P. uviferum</i> seedlings</b>					
Mean	27 ± 46 <sup>a</sup>	14 ± 20 <sup>a</sup>	1 ± 4 <sup>b</sup>	4 ± 20 <sup>b</sup>	23 ± 80 <sup>a</sup>
Med. (± 2 MAD)	18 ± 28 <sup>a</sup>	10 ± 16 <sup>a</sup>	0 <sup>b</sup>	1 ± 4 <sup>b</sup>	11 ± 18 <sup>a</sup>
<b>Count of <i>P. uviferum</i> trees<sup>1</sup></b>					
Mean	16 ± 11 <sup>a</sup>	2 ± 7 <sup>b</sup>	0 <sup>b</sup>	1 ± 3 <sup>b</sup>	7 ± 9 <sup>a</sup>
Med. (± 2 MAD)	15 ± 3 <sup>a</sup>	0 <sup>b</sup>	0 <sup>b</sup>	0 <sup>b</sup>	5 ± 3 <sup>a</sup>
<b>Measurements of <i>P. uviferum</i> trees<sup>2</sup></b>					
DBH (cm)	16.83 ± 18.98 <sup>a</sup>	4.15 ± 5.32 <sup>b</sup>	NA	8.91 ± 5.93 <sup>c</sup>	7.17 ± 3.99 <sup>c</sup>
Height (m)	6.54 ± 0.52 <sup>a</sup>	1.86 ± 1.34 <sup>b</sup>	NA	4.31 ± 2.73 <sup>c</sup>	3.28 ± 1.20 <sup>c</sup>
No. trees measured	146	16	NA	8	59
PAR 0.3 <sup>3</sup> m	61.31 ± 240.45 <sup>a</sup>	376.82 ± 614.19 <sup>bc</sup>	688.12 ± 856.99 <sup>c</sup>	190.59 ± 149.12 <sup>b</sup>	307.93 ± 491.49 <sup>abc</sup>
PAR 1.3 <sup>3</sup> m	121.78 ± 283.86 <sup>a</sup>	748.45 ± 673.11 <sup>b</sup>	745.47 ± 858.86 <sup>bc</sup>	218.14 ± 144.48 <sup>ad</sup>	352.26 ± 399.23 <sup>cd</sup>
DWT <sup>4</sup> (cm)	40.22 ± 35.64 <sup>a</sup>	27.14 ± 39.62 <sup>ab</sup>	7.25 ± 20.90 <sup>c</sup>	16.31 ± 21.72 <sup>bc</sup>	13.58 ± 13.92 <sup>bc</sup>
<b>Seedbed / rooting substrates (% cover)</b>					
Pool	4.64 ± 14.07 <sup>ab</sup>	16.06 ± 39.47 <sup>ab</sup>	34.58 ± 61.41 <sup>b</sup>	5.00 ± 20.28 <sup>ab</sup>	1.64 ± 9.75 <sup>a</sup>
Bare ground	0.89 ± 4.19 <sup>a</sup>	0.53 ± 3.69 <sup>a</sup>	12.25 ± 47.81 <sup>a</sup>	0.56 ± 1.01 <sup>a</sup>	0.61 ± 0.99 <sup>a</sup>
Litter	12.53 ± 13.74 <sup>a</sup>	10.75 ± 12.95 <sup>ac</sup>	3.72 ± 10.00 <sup>b</sup>	9.83 ± 18.98 <sup>abc</sup>	5.64 ± 11.31 <sup>bc</sup>
Wood	0.67 ± 1.79 <sup>ab</sup>	0.06 ± 0.47 <sup>a</sup>	0.00 ± 0.00 <sup>a</sup>	1.47 ± 5.29 <sup>b</sup>	0.92 ± 3.26 <sup>b</sup>
Trunk	57.11 ± 47.88 <sup>a</sup>	16.56 ± 51.79 <sup>bc</sup>	0.00 ± 0.00 <sup>b</sup>	0.89 ± 0.64 <sup>c</sup>	1.97 ± 7.49 <sup>bc</sup>
<i>Sphagnum</i> spp.	1.50 ± 7.95 <sup>a</sup>	36.25 ± 85.89 <sup>ac</sup>	35.67 ± 71.08 <sup>c</sup>	90.28 ± 49.62 <sup>b</sup>	13.28 ± 32.50 <sup>ac</sup>
<i>Dicranaloma</i> spp.	2.53 ± 6.42 <sup>ac</sup>	10.81 ± 33.95 <sup>abc</sup>	0.11 ± 0.64 <sup>c</sup>	0.83 ± 1.69 <sup>a</sup>	24.22 ± 39.03 <sup>b</sup>
Cushion plants	0.00 ± 0.00 <sup>a</sup>	2.36 ± 23.72 <sup>a</sup>	26.17 ± 66.32 <sup>ab</sup>	0.56 ± 1.01 <sup>a</sup>	26.31 ± 50.31 <sup>b</sup>
Other mosses	95.42 ± 13.18 <sup>a</sup>	46.28 ± 76.80 <sup>b</sup>	15.39 ± 44.02 <sup>bc</sup>	3.25 ± 14.21 <sup>c</sup>	13.47 ± 29.28 <sup>b</sup>
<b>Understory plants (% cover)</b>					
Trees <sup>5</sup>	24.51 ± 50.20 <sup>ac</sup>	40.53 ± 36.52 <sup>a</sup>	13.93 ± 41.12 <sup>bc</sup>	3.56 ± 13.69 <sup>b</sup>	3.44 ± 12.93 <sup>b</sup>
Other shrubs	27.08 ± 36.04 <sup>a</sup>	5.33 ± 1982 <sup>b</sup>	0.94 ± 3.71 <sup>b</sup>	4.71 ± 13.95 <sup>b</sup>	3.19 ± 10.52 <sup>b</sup>
Low shrubs	0.01 ± 0.17 <sup>a</sup>	3.93 ± 15.31 <sup>ab</sup>	17.99 ± 32.21 <sup>bc</sup>	5.13 ± 13.87 <sup>ab</sup>	28.00 ± 34.82 <sup>bc</sup>
Ferns	14.92 ± 21.25 <sup>a</sup>	3.14 ± 8.57 <sup>b</sup>	0.08 ± 0.38 <sup>b</sup>	2.24 ± 7.93 <sup>b</sup>	0.31 ± 0.87 <sup>b</sup>
Forbs	0.43 ± 0.35 <sup>a</sup>	5.46 ± 10.12 <sup>b</sup>	7.74 ± 14.02 <sup>b</sup>	2.40 ± 8.64 <sup>ab</sup>	3.39 ± 20.01 <sup>ab</sup>
Graminoids	0.93 ± 3.79 <sup>a</sup>	6.97 ± 15.88 <sup>c</sup>	4.96 ± 14.53 <sup>ac</sup>	23.50 ± 28.14 <sup>b</sup>	5.88 ± 17.49 <sup>ac</sup>

<sup>1</sup>Counts of *P. uviferum* trees were made at the plot scale and included live trees ≥ 5 cm in diameter at 1.3 m in height for the Forest and Transition patches or 0.3 m for the Bog Forest patch.

<sup>2</sup>Measurements of live *P. uviferum* trees located inside and adjacent to plots and meeting the diameter and height requirements as above.

<sup>3</sup>Units are mmol/m<sup>2</sup>.

<sup>4</sup>Distance to the water table from substrate tops.

<sup>5</sup>Species other than *P. uviferum*. Values are means plus/minus the standard deviation unless otherwise noted. For each variable, values sharing the same letter in superscript were not significantly different at  $P \leq 0.05$ .

both the control and burned site (Figures 7, 8). There were greater numbers of trees and lower coverages by *Sphagnum* spp. within the forested Forest and Transition patches as compared to the non-forested Bog and Burned Forest patches; however, the percent cover of *Sphagnum* spp. ranged from low to high values across microsites in the Bog Forest patch. In contrast to the above variables, PAR and DWT measurements were significantly different between forested and non-forested patches at the control site, but relatively uniform across patches at the burned site (Figures 9, 10; see also Supplementary Figures 20, 21).

### 3.3.2 Microsite Scale

Within microsites, different sets of covariates better predicted *P. uviferum* seedling counts at the control versus burned site (Figure 11). For the control site, our final model included the following predictors: patch, interactions between patch and DWT and log (PAR 1.3), the number of nearby *P. uviferum* trees, the percent cover of *Sphagnum* spp. and cushion plants, and the interaction between patch and the percent cover of 'other' shrubs (i.e., those that were not mat-forming and generally taller in stature). Of these, the 'Bog' level of patch had the greatest effect on seedling counts relative to the reference condition of 'Forest'

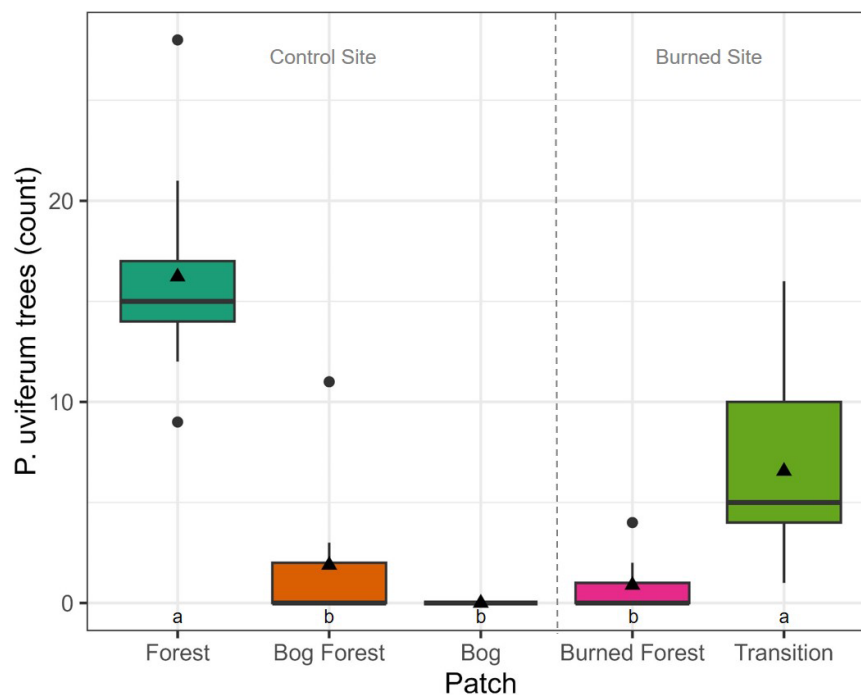


FIGURE 7

Boxplots of live *P. uviferum* tree (DBH  $\geq$  5 cm) counts per patch: Forest, Bog Forest and Bog patches in the control site, Burned Forest and Transition patches in the burned site. Trees were tallied in nine 100 m<sup>2</sup> plots per patch. Boxes represent the interquartile range of the data; thick horizontal lines and black triangles represent median and mean counts, respectively; and vertical lines indicate variability in counts outside of the interquartile range with black circles are outliers. Different letters indicate significant differences between median counts across sites using Kruskal-Wallis one-way ANOVA and post-hoc Dunn's tests ( $P < 0.05$ ).

(median point estimates of  $-4.43$  and  $4.51$ , 90% and 95% credible intervals, CI, respectively). Subplots in the Bog Forest patch were also predicted to have fewer seedlings than those in the Forest patch, though the marginal effect size was smaller than for the Bog patch ( $-1.79$ , 95% CI). Within the Bog and Bog Forest patches, seedling counts were predicted to be further reduced by increasing levels of PAR at 1.3 m, with the greatest effect in the Bog patch ( $-1.51$  and  $-0.74$ , respectively; 95% CI). In contrast, there was a positive effect of PAR at 1.3 m on seedling counts in the Forest patch ( $0.43$ , 95% CI). In the Forest patch, seedling counts were also associated, albeit negatively, with the percent cover of other shrubs ( $-0.33$ , 95% CI). The percent cover of cushion plants had a positive effect ( $0.40$ , 95% CI) on seedling counts across the pooled data. Parameter estimates for the count of *P. uviferum* trees and percent cover of *Sphagnum* spp. did not exclude zero with at least 80% probability and were thus considered “not significant” (Supplementary Table 23). Regarding the overdispersion and plot-level components of the model: seedling counts in the Bog patch ( $-1.68$ , 95% CI) were overdispersed compared to those in the Forest patch ( $0.97$ , 95% CI; the shape parameter is inversely related to the variance, so the larger the negative value, the greater the variance and overdispersion), and there was a slight positive random effect of plot on seedling counts across patches ( $0.20$ , 95% CI).

For the burned site, we chose to examine two final models *P. uviferum* seedling counts. These differed in whether the percent cover of *Sphagnum* spp. was included as a predictor. The first model was fit using the following covariates: patch, the interaction

between patch and DWT, count of *P. uviferum* trees, percent cover of *Dicranaloma* spp., and interactions between patch and the percent cover of cushion plants, other moss species, other shrubs and understory trees. We decided to fit and interpret a second model that included *Sphagnum* spp. given (1) our strong expectation of an association between the percent cover of the mosses and *P. uviferum* seedling counts, (2) inclusion of the predictor in the final control site model, (3) a trend toward significant marginal effects of *Sphagnum* spp. by patch in one of the simple candidate models for the burned site (Supplementary Table 11), and (4) the idea that microsites not dominated by *Sphagnum* may be characterized by a different suite of factors that affect *P. uviferum* seedling germination, growth and survival than those dominated by the peat moss. To avoid the potential for autocorrelation among covariates, *Sphagnum* spp. could only be included if the count of *P. uviferum* trees and percent cover of *Dicranaloma* spp. were removed (Supplementary material).

According to the model without *Sphagnum* spp., *P. uviferum* seedling abundance was most strongly affected by the percent cover of other/taller shrubs. This marginal effect was strongest and positive in the Burned Forest patch (median point estimate of  $0.51$ , 80% CI), while it was negative in the Transition patch ( $-0.33$ , 80% CI). Seedling counts in the Burned Forest patch also tended to be positively associated with the percent cover of understory trees, but the parameter estimates did not exclude zero with 80% probability (median point estimate of  $0.57$ ). Seedling counts in the Transition patch were positively affected by the percent cover of cushion plants

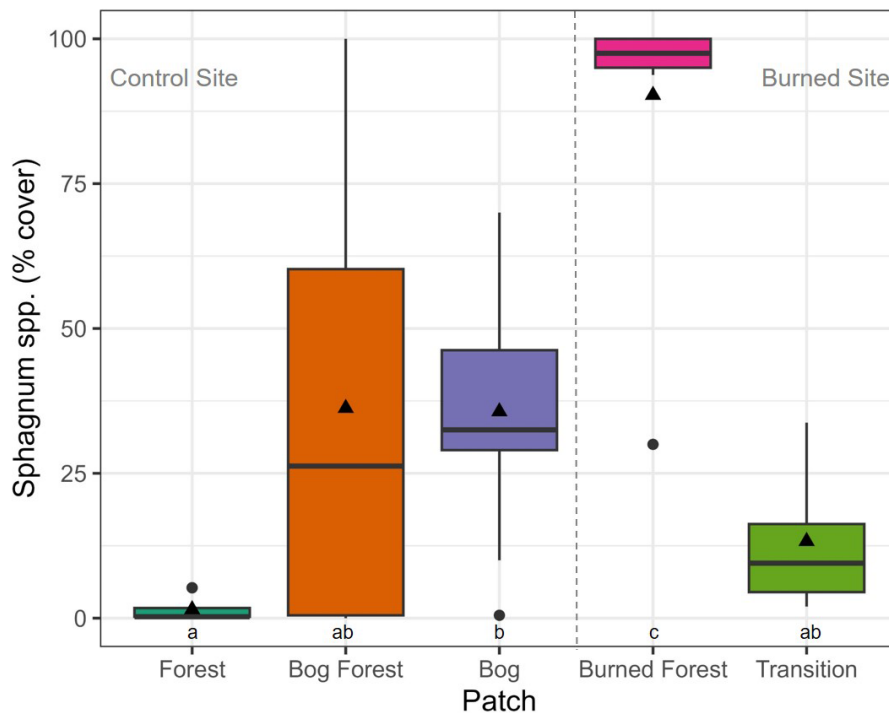


FIGURE 8

Boxplots of the percent cover of *Sphagnum spp.* per patch: Forest, Bog Forest and Bog patches in the control site, Burned Forest and Transition patches in the burned site. Percent cover was estimated across four 2 m<sup>2</sup> subplots per plot, nine plots per patch. Boxes represent the interquartile range of the data summarized to plot and patch; thick horizontal lines and black triangles represent median and mean percent cover, respectively; and vertical lines indicate variability in percent cover outside of the interquartile range with black circles are outliers. Different letters indicate significant differences between mean percent cover across sites using Welch's one-way ANOVA and post-hoc Games-Howell tests ( $P < 0.05$ ).

(0.33, 90% CI) and other mosses (0.31, 95%), but neither had a significant effect in the Burned Forest patch. The percent cover of *Dicranaloma spp.* was negatively associated with seedlings across patches ( $-0.24$ , 80% CI). There was no evidence for significant effects of the interaction between patch and DWT or the number of *P. uviferum* trees on seedling abundance (Supplementary Table 24).

The signs of the parameter estimates for the model with *Sphagnum spp.* were similar to the first model with regard to the predictors that they had in common, though the strengths and the confidence intervals of the parameter estimates differed. For example, the effect of cushion plants on seedling abundance in the Transition patch was stronger in the model with *Sphagnum spp.* (0.49, 95% CI), while the effect sizes for the interactions between other shrubs and either patch decreased and their variability increased such that their confidence intervals no longer excluded zero with at least 80% probability. In this model, the percent cover of *Sphagnum spp.* had a stronger effect than any other predictor in either of the models: there was a positive effect on *P. uviferum* seedling counts in the Transition patch (0.81, 95%), though no significant effect was observed in the Burned Forest patch (Supplementary Table 25). There was also a relatively strong effect of the percent cover of understory trees on seedling counts in the Burned Forest patch (0.64, 80% CI). In both of the models, seedling counts in the Burned Forest patch were overdispersed; however there was no overall "significant effect" of "Burned Forest" on seedling counts.

## 4 Discussion

This study shows that the significantly higher densities of *P. uviferum* trees and seedlings in the forested patches at both, burned and control, sites (as compared to the non-forested patches) were associated with significantly lower seasonal water tables, lower cover of *Sphagnum spp.* moss and higher cover of mosses that were not in the *Sphagnum* or *Dicranaloma* genera. *S. magellanicum* was in fact an indicator species of non-forested patches in the burned and control sites. We also found distinct understory plant communities across patches and sites in response to different factors: differences in vegetation structure and composition were associated with gradients in abiotic conditions at the control site, whereas the environment had become homogenized across the repeatedly-burned site even though patches were separated by abrupt boundaries in vegetation. A scale-dependent influence of microsite structures and environments (within patches) at both sites on tree seedling establishment was identified and was characterized by intricate and multifarious effects, sometimes via abiotic conditions and/or biotic elements that differed from those that were most prevalent at the larger patch scale (Figure 12). We discuss our findings in more detail below in the context of post-reburn *P. uviferum* forest reorganization under drought conditions and their implications for the maintenance of forest-peatland ecotone boundaries (i.e., reproduction, establishment, modification of abiotic conditions, and biotic interactions).

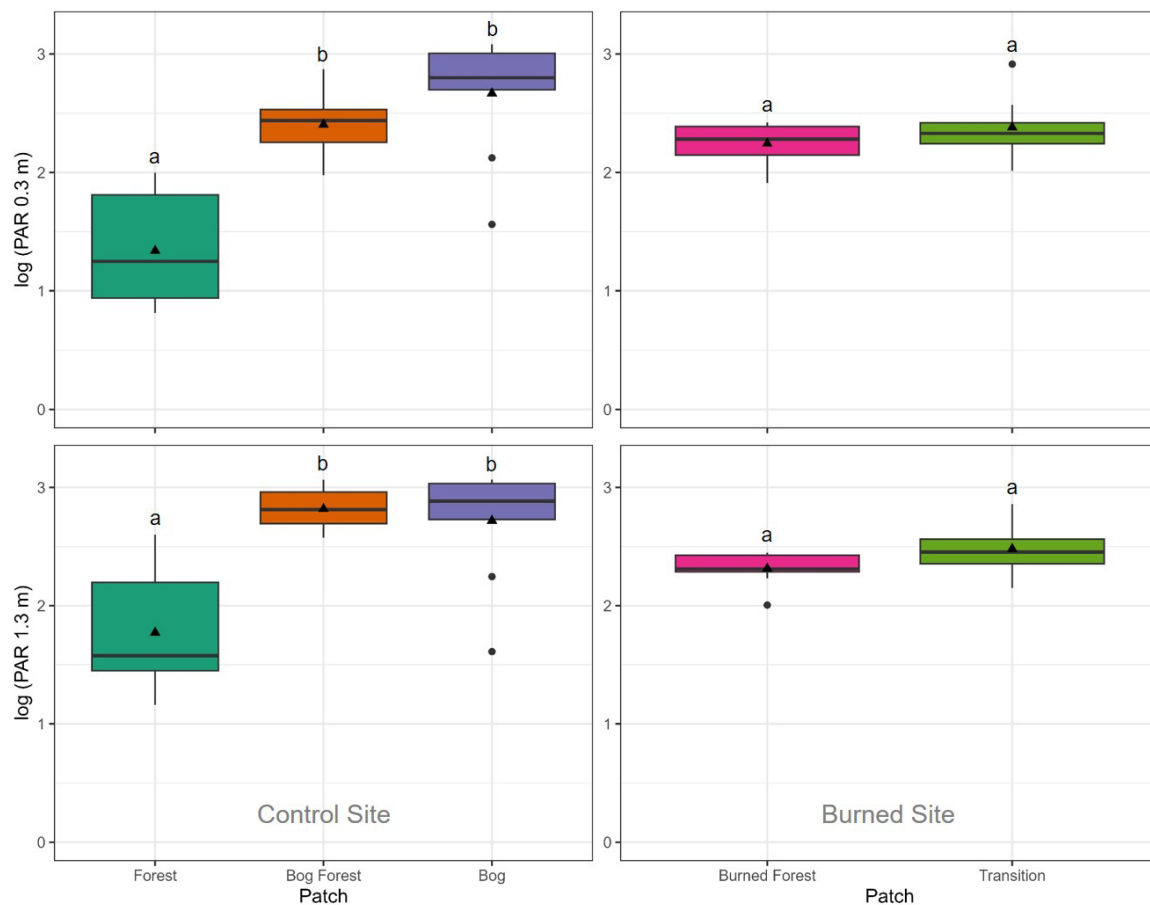


FIGURE 9

Boxplots of log-transformed photosynthetically active radiation (PAR; millimoles/m<sup>2</sup>) measured at 0.3 and 1.3 m above the ground surface in the Forest, Bog Forest and Bog patches of the control site and the Burned Forest, Transition and Cushion patches of the burned site. Photosynthetically active radiation was measured using a hand-held light sensor at three systematic locations per 2 m<sup>2</sup> subplot (four subplots per plot, nine plots per patch). Boxes represent the interquartile range of the data summarized to plot and patch; thick horizontal lines and black triangles represent median and mean PAR readings, respectively; and vertical lines indicate variability in PAR outside of the interquartile range with black circles are outliers. Different letters indicate significant differences between mean PAR readings within sites using Kruskal-Wallis one-way ANOVA and post-hoc Dunn's tests ( $P < 0.05$ ).

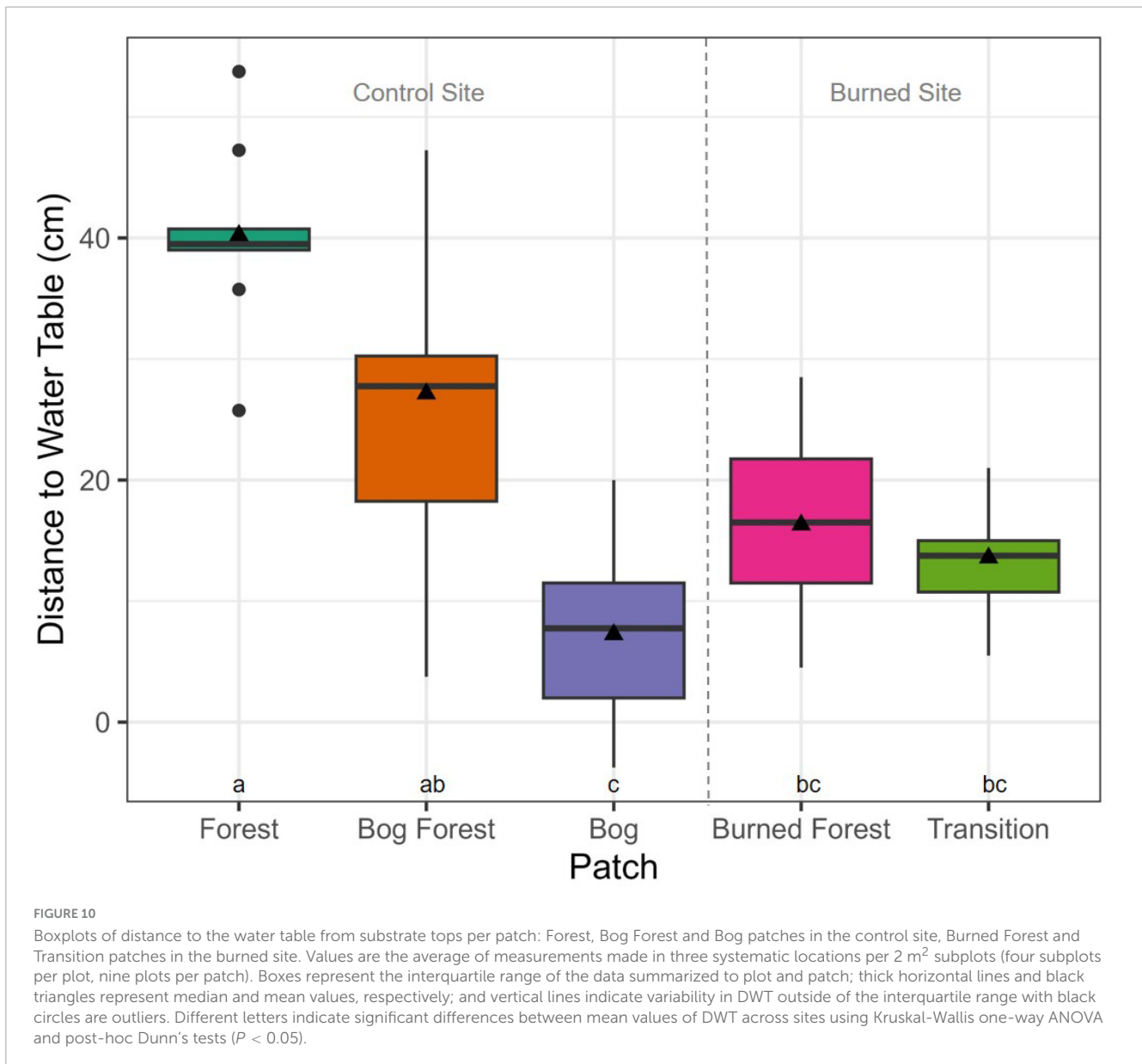
## 4.1 Post-reburn reorganization

### 4.1.1 Reproduction

At the repeatedly-burned site, the patch with the greatest abundance of *P. uviferum* seedlings also had the greatest abundance of seed trees, as was found at the unburned control site. Reproductively-mature trees that remain within or near disturbance perimeters can be important biological legacies (Bannister et al., 2012) that initiate forest regeneration via seed dispersal for tree species that lack re-sprouting capabilities, like *P. uviferum*. In a comparative study of *P. uviferum* regeneration on burned bog or upland sites on Chiloé Island (ca. 42° S), Bannister et al. (2012) only observed regeneration where seed trees survived fire or established shortly thereafter (and were sexually mature at the time of their study). Within the forested patch of the burned site (i.e., the Transition patch), mature *P. uviferum* individuals may have survived repeated burning given the wet conditions of the adjacent cushion bog to the west coupled with westerly winds, which could have reduced fire severity and contributed to patchy fire effects (Holz and

Veblen, 2009, 2011). Low-severity fires typically have spatially heterogeneous effects, which might also have allowed seedlings to establish and mature between successive fires (Holz, 2009; Holz et al., in review). This in turn seems likely given the relatively young ages of the trees in the forested patch in the burned site: the oldest minimum age observed was 118 years with 51 years as the average minimum age; in contrast, the oldest minimum age in the forested patch at the control site (i.e., the Forest patch) was 517 years, with an average minimum age of 235 years (Zaret, 2011). While the density of potential seed trees and seedlings tended to be lower within the forested patch at the burned site than the forested patch at control site, seed availability does not appear to be limiting the potential for at least a portion of the burned site to recover to a *P. uviferum* forest similar in structure to that of the control site. The time needed for that to happen likely depends on multiple factors, including masting cycles, dispersal capabilities, substrate, and hydroclimatic patterns. For instance, successful *P. uviferum* establishment was found to be strongly associated with wetter conditions (Holz et al., in review), but its growth has been





observed to be substantially slower on saturated as compared to well-drained soils on burned sites (e.g., requiring on average 70 vs. 40 years to reach a root collar diameter of 5 cm; [Bannister et al., 2012](#)). Under forecasted warmer and drier conditions (and in the absence of future burning), tree growth rates could increase and canopy closure may occur faster than historically ([Holz et al., 2018](#)).

*P. uviferum*'s ability to colonize new sites or to re-colonize disturbed sites via sexual reproduction may be hampered by limited dispersal distances even in instances where seed trees are nearby (and even numerous): though seeds have wings, seedling recruitment is most abundant within 20 m of seed trees, and the majority of seedlings and saplings are found clustered within 5 m of such trees ([Bannister et al., 2014](#); [Galindo et al., 2021](#)). Seedlings were less abundant in the non-forested patch of the control site (i.e., the Bog patch) than in that of the burned site (i.e., the Burned Forest patch), perhaps due to differences in the direction of the predominant westerly winds coupled with

distances to seed trees. At the burned site the non-forested patch was downwind of the seed trees located in the adjacent forested patch; in contrast, the non-forested patch at the control site was upwind of potential seed trees. Despite the favorable wind direction, seed rain into the non-forested patch of the burned site is likely irregular (following masting cycles of 7–9 years; [Donoso, 1993](#); [Galindo et al., 2021](#)) and may also be limited by the relatively short stature of the slow-growing mature, potentially cone-bearing trees in the adjacent forested patch (average of  $3.28 \pm 1.20$  m,  $n = 59$ ; [Table 1](#)). Thus, forest regeneration may proceed within the non-forested patch of the repeatedly-burned site, but at a slow rate as sets of successive seed trees establish, mature and produce seed along a shifting edge into the patch. Ultimately, a 'restructured' forest may develop (i.e., one still dominated by *P. uviferum*, but with lower density). Such a forest could differ in understory plant composition, abiotic conditions and biotic interactions as compared to the *P. uviferum* forest at the control site (see below).

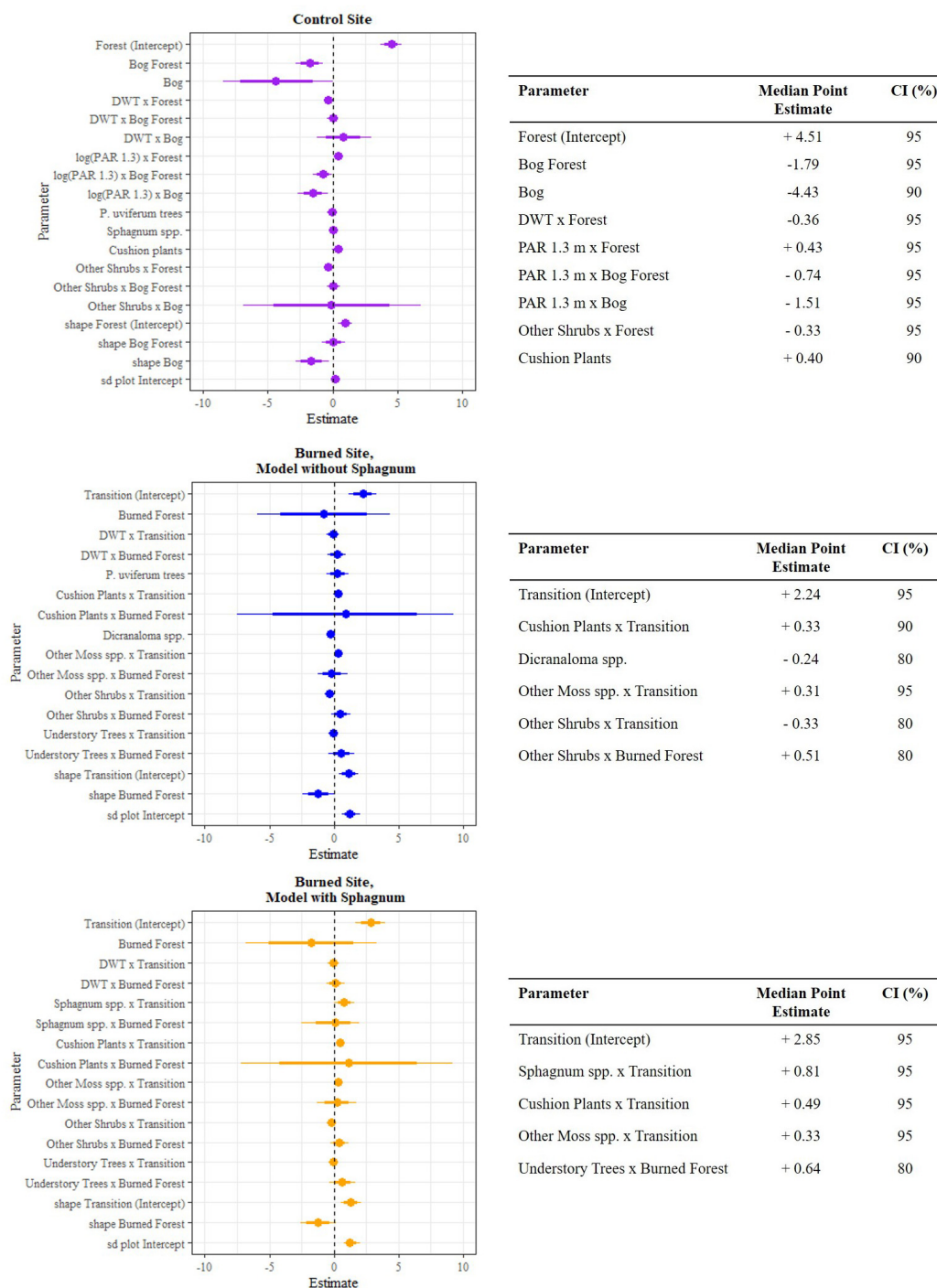


FIGURE 11 Posterior estimates of parameters from final Bayesian hierarchical models of *P. uviferum* seedling counts for the control site (top) and burned site (middle and bottom) with 80% and 95% credible intervals. Parameters with estimates that excluded zero with at least 80% probability (except the shape and plot parameters) are shown in the tables with their widest non-zero credible interval. Estimates are on the log scale.

### 4.1.2 Establishment

Short fire-return intervals relative to the slow growth of *P. uviferum* would seem to be a major limitation to seedling establishment (in the event that seed production is successful). However, direct seedling mortality from fire does not appear to be the sole factor limiting tree recruitment due to the following observations: (1) evidence of historic post-fire cohorts (Holz et al.,

in review; Zaret, 2011), which indicate that *P. uviferum* forests have successfully recovered from fire in the past; and (2) the absence of large-scale fire activity for more than a decade at the time this study was undertaken, but still the lack of widespread seedling establishment. As discussed below, our findings indicate that feedbacks between fire, abiotic conditions and the biotic community together limit *P. uviferum* forest regeneration.

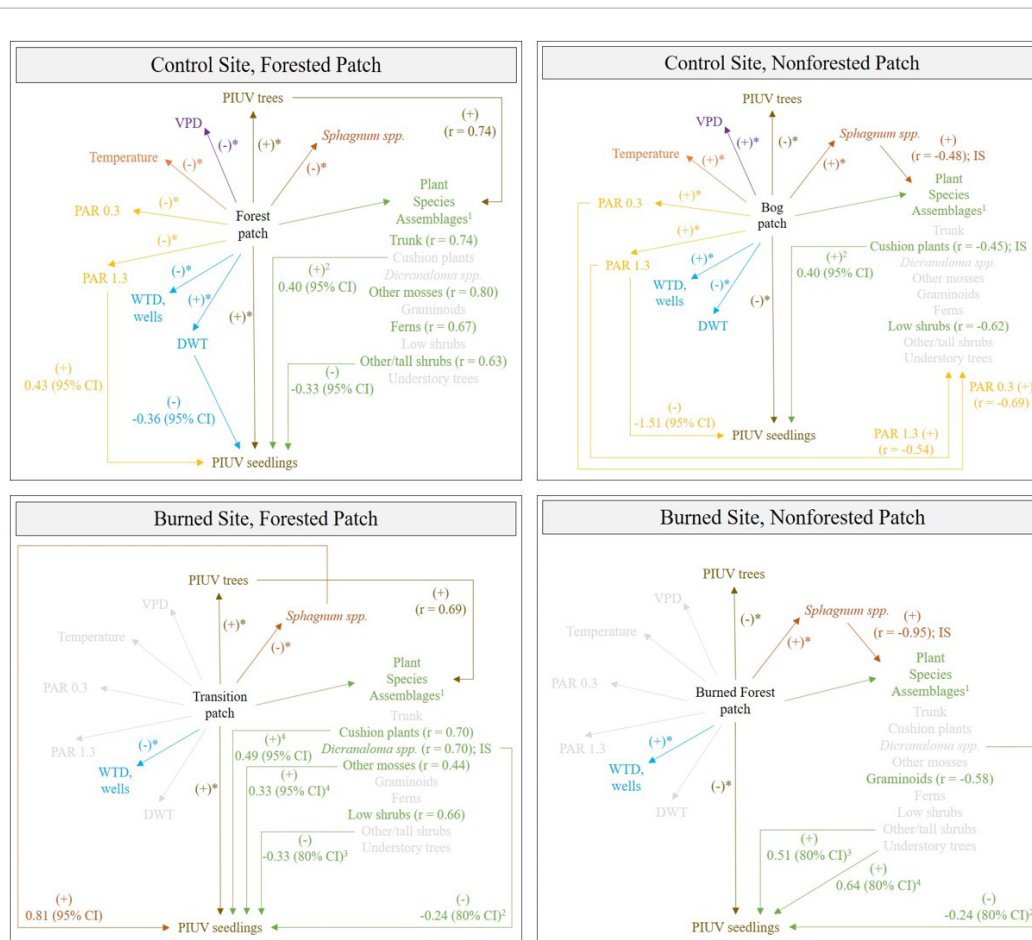


FIGURE 12

Abiotic and biotic factors associated with patch, plant species assemblages and *P. uviferum* (PIUV) seedling abundance at the control and burned site. Significantly different median (tree and seedling counts) or mean (vapor pressure deficit [VPD], temperature, photosynthetically active radiation [PAR], water table depth [WTD], distance from substrate tops to the water table [DWT], and *Sphagnum spp.*) values between the forested and non-forested patches at each site separately were determined via one-way analysis of variance and indicated with an asterisk (\* $P \leq 0.05$ ). Plant species assemblages, their predictors and indicator species (IS) were identified via non-metric multidimensional scaling; only the predictors that were also associated with seedling counts via regression analysis were included (1); Pearson's correlations are shown if the predictor was associated with the same region of ordination space as the plant species assemblages for that patch (i.e., same end of axis 1). Parameter estimates and credible intervals (CI) were generated from Bayesian hierarchical linear regression models of seedling abundance; some parameter effects were pooled across patches (2); at the burned site, final models excluded (3) or included (4) *Sphagnum spp.* as a predictor, but only the strongest effect is shown here.

#### 4.1.3 Modification of abiotic conditions

As noted above, repeated burning, through its effects of restructuring the abundance and size classes of *P. uviferum* trees and other co-dominant tree species (likely *Nothofagus spp.*, *Drimys winteri*, *Podocarpus nubigenus*, *Weinmannia trichospera*, etc.; Veblen et al., 1995), appears to have also disrupted some of the gradients in abiotic conditions that were observed across the forest-peatland ecotone at the control site, instead creating uniform conditions across the burned site. Though *P. uviferum* trees ( $\geq 5$  cm DBH) were present in both the regenerating forest patch at the burned site (i.e., the Transition patch) and the old-growth forest at the control site (i.e., the Forested patch), there were substantially fewer trees in the forested patch at the burned site and they were significantly smaller in DBH and height (Figure 7 and Table 1). Because of their very slow growth rate and the relatively recent history of reburns in the site (Holz and Veblen, 2011; Holz et al., 2018), canopies of slow-growing *P. uviferum* individuals in the

forested patch were still sparse and short, and their understory microclimatic and light conditions were similar to those in the non-forested patch (Figures 4, 9, and Supplementary Figures 15–17). As a result, no effect of PAR on seedling abundances was found for either patch within the burned site (Supplementary Table 7). In contrast, light levels decreased with increasing tree density across the forest-peatland ecotone at the control site (which was especially evident when PAR was measured across patches on the same day under consistent weather conditions; Supplementary Figure 21). For the control site, our best-fit model of seedling abundance included a positive parameter estimate for PAR in the forested patch, but negative parameter estimates in the other patches. This finding corresponds with research conducted by Bannister et al. (2013), who documented negative effects of light levels on shoot elongation and foliar phosphorous and nitrogen concentrations in *P. uviferum* seedlings planted in open conditions; it also suggests that relationships between light levels

and *P. uviferum* establishment, growth and/or survival may be non-linear (Supplementary material). Differences in forest structure across the forest-peatland ecotone at the control site were also associated with different distances to the water table (DWT), which increased with increasing *P. uviferum* tree abundance across the three patches. At the burned site, however, DWT did not differ significantly between the forested and non-forested patches (Figure 10), indicating that repeated burning can reduce spatial variability in microtopography, effectively homogenizing that dimension of microsite structure across an entire burned area.

Though evidence from the control site indicates that tree regeneration is lacking in the non-forested patch due to sunnier, warmer, and drier conditions and/or excessive soil moisture (Figure 12), these factors by themselves did not explain why *P. uviferum* seedling abundance was prolific within the Transition patch but not in the adjacent Burned Forest patch at the burned site. Ultimately, seasonal water table depths (WTD) were the only environmental condition that differed significantly between the forested (lower/further from the surface) and non-forested (higher/closer to the surface) patches at both sites, though there tended to be smaller differences in WTD between patches at the burned site. That greater tree densities were associated with lower water tables supports the idea of an evapotranspiration-tree establishment feedback (Figure 1). However, we did not find evidence that microsites characterized by lower distances to the water table were negatively associated with seedling abundance in more exposed patches (Figure 11, Supplementary Table 2); water tables in the forested patches at the burned and control site were usually within 5 cm and 25 cm of the substrate surface, respectively, (well within the rooting zone); and soils were continuously saturated (regardless of water table depth) in both forested patches. Our findings, like those of other researchers, were thus ambiguous regarding the effects of high water tables on *P. uviferum* regeneration and subsequent forest development pathways.

Past research in climatically more moderate (i.e., seasonally warmer and drier) northwestern Patagonia has suggested that waterlogging limits tree regeneration on secondary shrublands (Díaz et al., 2007) or anthropogenic peatlands (Díaz et al., 2008) that develop following logging and/or fire. However, a negative relationship between high water tables and *P. uviferum* has not been demonstrated experimentally or through field observation (e.g., Díaz and Armesto, 2007; Bannister et al., 2013). In fact, of the 12 tree species observed by Díaz and Armesto (2007), only *P. uviferum* seedlings were observed in the middle and most saturated portion of the site under investigation. Rather, *P. uviferum* is often referred to in association with “poorly-drained conditions” (e.g., Rovere et al., 2002), and the species is believed to be found in greatest abundance in lowland sites given its capacity to withstand wet and nutrient-poor conditions better than potential angiosperm competitors (Cruz and Lara, 1981), potentially due to a lack of vessels and associated resource conservation (Bond, 1989; Brodribb et al., 2012; Piper et al., 2019). Bannister et al. (2012) found evidence for continuous *P. uviferum* regeneration in undisturbed upland and wetland forests on Chiloé Island, and Esse et al. (2021) identified two main types of *P. uviferum* forests in the fjords of SW Patagonia, which differed from other forest communities in terms of high water tables. Thus, the species appears to be capable of regeneration under a wide range of

naturally-occurring soil moisture conditions (i.e., regeneration niches; Grubb, 1977). In terms of post-disturbance establishment, Soto and Figueroa (2008) found evidence of post-disturbance cohorts of *P. uviferum* following high disturbance levels (e.g., repeated fire, logging and/or grazing), and they concluded, for its northernmost and warmest/driest populations, that the species needs open sites with wet soils in order to regenerate and persist. On Chiloé Island, Bannister et al. (2012) actually documented greater post-fire seedling density in bog forests compared to upland forests, and Mansilla (2008) observed *P. uviferum* seedlings on burned bogs on the colder and drier Brunswick Peninsula in far southern Patagonia. Rather than high water tables, per se, there may be interactions between water tables and substrate types, especially those that are biotic (e.g., living mosses rather than bare soil or trunks) that most strongly determine the likelihood of *P. uviferum* establishment and ongoing growth and survival, which we explore in more detail below.

#### 4.1.4 Biotic interactions

Differing abundances of *P. uviferum* trees and seedlings across the forest-peatland ecotones at the burned and control site were also associated with distinct understory plant communities (Figures 5, 12). The cool, moist, dark understory of the forested patch at the control site was characterized by species commonly found in temperate rainforests of the area (e.g., Luebert and Plissock, 2017), but the forested patch at the burned site was characterized by species that have been documented in naturally-occurring and disturbance-induced peatlands elsewhere in Chile (Díaz et al., 2008; Supplementary Tables 16–20). The understory communities in the non-forested patches at both sites were also typical of open peatlands, though *Sphagnum spp.* was a more important member of the community at the burned site, and both communities were readily distinguishable in ordination space, as were plant assemblages for each patch across both sites (Supplementary Figure 23). Thus, despite evidence that forest structure may be recovering across a portion of the burned site, understory composition differs notably from that of the control site.

The distinct life forms and individual plant species that characterized the understories of each patch type (and contributed to microsite composition and structure) appeared to affect seedling abundance via facilitative or competitive interactions, thereby having the potential to influence forest development over the long-term. For example, understory trees and taller shrubs were predicted to increase seedling abundance in the non-forested patch of the burned site (Figure 11), perhaps ameliorating any negative impacts of higher light levels, as discussed earlier, and supporting findings of shrub-nursery effects on *P. uviferum* seedlings in disturbed, open areas further north (Bannister et al., 2019). In contrast, taller shrubs were negatively associated with seedling abundance in the patches in which woody plants were more abundant or under an already-established tree canopy, as in the forested patches at both sites. That the direction of these interactions are mediated by light levels (PAR had a relatively strong correlation with understory plant assemblages; Figure 5), highlights the importance of biotic-abiotic feedbacks in determining dynamics across the forest-peatland ecotones under investigation.

When we took a closer look at interactions between *P. uviferum* seedling abundance and microsite composition to determine

whether they were mediated by DWT, we found that the majority of microsites in the non-forested patch of the burned site (where few seedlings were observed) were dominated by *S. magellanicum*, while those in the forested patch were composed of a diversity of plants (often including cushion species, *Dicranoloma* spp., *S. magellanicum* and other mosses, with no one type covering more than 50% of the area; [Supplementary Figure 24](#)). These results align with previous work on *P. uviferum* regeneration with regard to substrate type and Sphagnum mosses in particular. [Bannister et al. \(2013\)](#) observed significantly higher survival rates of seedlings planted on artificially created mounds of moss as compared to those planted on naturally-occurring Sphagnum spp. lawns or on swaths of mineral soil created by removing Sphagnum mosses. [Galindo et al. \(2021\)](#) found significantly greater numbers of *P. uviferum* seedlings on substrates dominated by cushion plants (i.e., *Donatia* spp. and *Astelia* spp.) and accompanied by a small percent cover of mosses and the least number of seedlings on microsites dominated by Sphagnum spp. Likewise, our regression models for the burned site predicted positive effects of other mosses, cushion species and Sphagnum spp. on seedling abundances in the forested patch ([Figure 11](#), Transition patch results). Thus, it may be that the presence of Sphagnum spp. can facilitate *P. uviferum* establishment, growth and/or survival under conditions that limit the moss species' growth rate or lateral spread (e.g., drier or darker microsites or via competition with other ground-covering plants), but when peat moss cover predominates, i.e., under wetter and/or more open conditions, it will likely have detrimental effects on tree seedlings via overtopping or competition for nutrients.

Unlike at the burned site, there did appear to be interactions between seedling abundance, microsite diversity and DWT at the control site ([Supplementary Figure 25](#)). In the non-forested patch, the microsites with the greatest DWTs were composed almost exclusively by *Sphagnum* spp., while microsites with more intermediary DWTs were associated with relatively diverse assemblages of biotic substrates (most including both cushion species and *Sphagnum* spp.) and also the greatest numbers of *P. uviferum* seedlings. This relationship was more notable in the intermediary (i.e., Bog Forest) patch of the control site: microsites were generally composed by either a variety of substrates (e.g., other non-*Sphagnum* mosses, trunks and/or pools) or *S. magellanicum*. The former tended to be closer to the water table and to have greater numbers of seedlings, while the latter had the opposite relationships (i.e., drier with fewer seedlings), which supports our proposed water table depth—sun exposure—*Sphagnum* feedback ([Figure \[conceptual model\]](#)). This result also supports the idea that the Bog Forest represents an intermediary successional stage in terms of forest structure ([Figures 6, 7](#)), understory composition ([Figure 5](#)) and abiotic conditions ([Figures 4, 10](#) and [Supplementary Figure 21](#)).

In summary, the forest-peatland ecotone at the control site seems to represent a gradient in forest structure, where environmental conditions and biotic interactions are controlled, at least in part, by tree density, and where regeneration-safe microsites tend to be heterogeneous in their composition and structure. In contrast, the forest-peatland ecotone at the burned site seems to represent a gradient in disturbance history, where the current structure and composition of patches have been shaped by fire, which has opened the forest canopy and disrupted gradients in most abiotic conditions. While legacy effects associated with less

frequent or less severe burning (e.g., spatially patchy consumption of trees, understory vegetation and/or microsite features like downed logs or moss hummocks) appear to have supported the regeneration of a new tree cohort in part of the site, almost no tree regeneration is occurring where all older/larger trees were removed by past fires and where microsites are now characterized by a nearly-homogenous cover of *Sphagnum* moss. The regenerating tree cohort will likely recover to a forest similar in structure to that of the control site unless forest development is disrupted by future fires and/or other disturbances. Intensifying drought conditions across western Patagonia may increase that possibility. On the other hand, in these hyperhumid forests warmer, drier conditions in the absence of fire may quicken canopy closure (by increasing *P. uviferum* growth rates), and shift the composition of the understory plant community towards species more representative of temperate rainforests and less like those of non-forested peatlands. Whether trees can recolonize the previously-forested portion of the burned site (that now more closely resembles the bog of the control site) may depend on how climatic patterns simultaneously affect water table dynamics, *Sphagnum* mosses, and their interactive effects on *P. uviferum* establishment, growth and survival. Ultimately, intentional interventions could be needed to restore *P. uviferum* trees to severely- or repeatedly burned patches.

## 4.2 Forest restoration

To date, active post-fire restoration efforts have demonstrated that *P. uviferum* seedlings planted in bog environments have relatively high survival rates after 10 years depending upon the substrates used as growth media and/or the presence of shade plants ([Bannister et al., 2019](#); [Galindo et al., 2021](#)). This is supported by preliminary results from an experimental plantation established at our burned site under the present study: planted seedlings may overcome some limitations of post-reburn abiotic conditions and/or biotic composition, but taller seedlings should be selected to re-forest carpets of *Sphagnum* spp. in order to avoid differences in growth rates that can result in overtopping by the peat moss ([Supplementary Figures 26, 27](#)). The prospects for *P. uviferum* restoration to burned sites in western Patagonia are encouraged by relatively widespread recognition of the tree species as an important part of natural and cultural heritage, which could be leveraged to foster support for community-based restoration efforts on private and state-owned lands.

## 4.3 Limitations and opportunities

As with other investigations based on space-for-time substitutions (e.g., [Lovell et al., 2023](#)), our study was limited by its timing relative to the onset of disturbance and its short-term duration.

Stochastic factors like legacy effects (e.g., the preservation or generation of a diverse spatial array of microsites), priority effects (e.g., immediate post-fire colonization by *Sphagnum* mosses), and rare events (e.g., abnormally wet or dry climatic conditions coupled with a mast year) may have important roles in determining the likelihood of successful *P. uviferum* regeneration. This suggests

that the best approach for investigating the forest-peatland ecotone of western Patagonia should be longitudinal and include field data collection that begins directly following disturbance and continues through early succession and into late succession. Given the extended time frame (especially with a focal species as slow-growing and long-lived as *P. uviferum*), the logistics for supporting this type of investigation could be modeled on Long-term Ecological Research efforts (e.g., Carmona et al., 2010).

Long-term study would contribute toward understanding how dynamic interactions between top-down factors like climate and bottom-up factors like local environmental conditions affect tree regeneration at ecotonal boundaries. Climate differentially affects the growth of *P. uviferum* trees across the species' extensive range (39°35'–54°20' S, ca. 1600 km; Holz et al., 2018), and recent work suggests similar effects on the conifer's establishment: high precipitation was associated with higher establishment of *P. uviferum* on more temperate Chiloé Island and in the Baker River watershed, but the opposite trend was suggested in the colder and wetter Pascua River watershed (Holz et al., in review). Climate may have direct effects on reproduction (e.g., through influencing mast cycles and seed rain). It may also interact with soil moisture and substrate types to promote asexual over sexual reproduction, such as through the formation of adventitious roots and layering, which is more likely under harsh and wet conditions (Cooper, 1911; Del Tredici, 2001) and has been observed previously in *P. uviferum* (Bannister et al., 2012) and in the present study. Future research on *P. uviferum* should include careful quantification of sexually- vs. vegetatively-produced stems to determine how the importance of legacy trees to the process of post-disturbance reproduction changes under varying climatic and local conditions.

Finally, long-term, fine-scale quantitative measurements of *P. uviferum* habitat hydroperiods (e.g., 'flood duration' or 'flood frequency'; Mitsch and Gosselink, 2015) are needed to fully understand the species' regeneration dynamics on edaphically wet sites. That is, such habitats should be investigated using methods appropriate for forested wetlands rather than simply saturated forests. Determining ongoing interactions between climate and hydroperiod on all aspects of *P. uviferum* establishment (e.g., germination, growth, and survival) is key to identifying the conservation and restoration needs of this threatened species, the world's southernmost conifer, and anticipating future shifts in vegetation dominance across the forest-peatland ecotone of western Patagonia.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

KZ: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing—original draft, Writing—review and editing. AH: Conceptualization, Funding acquisition, Methodology, Supervision, Writing—review and editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2024.1385506/full#supplementary-material>

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