RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Using gravel pits as novel fire refugia for the threatened Tasmanian paleoendemic conifer *Athrotaxis cupressoides*

Lynda D. Prior[1,2], Scott C. Nichols[1], Ben J. French[1], Herbert Staubmann[3], David M. J. S. Bowman[1]

***Athrotaxis cupressoides* is an endemic conifer restricted to montane areas of Tasmania. It is slow-growing and vulnerable to the increasing wildfire activity associated with climate change. We explored the novel idea that disused gravel pits could serve as artificial fire refugia for transplanted populations. We compared survival, growth, and response to fertilizer of nursery-grown *A. cupressoides* transplants in these artificial refugia, which had mineral soils, and in burnt and unburnt sites in wilderness areas, which had organic soils. Survival over the 16-month trial increased with initial transplant height and was slightly higher in the gravel pits (97%) than the wilderness areas (89%). Height growth of unfertilized plants was slow, especially in the unburnt wilderness sites and gravel pits. However, fertilizer boosted growth most strongly in the gravel pits, to rates similar to those of fertilized plants in unburnt wilderness sites. Our results show that it is feasible to reintroduce *A. cupressoides* into populations eliminated by wildfire. They also demonstrate the capacity to reclaim gravel pits by creating new localized populations of this iconic species. Thus, denuded gravel pits can be re-imagined as fire refugia to help maintain populations of *A. cupressoides* and other long-lived but fire-sensitive plants in the wild.**

Key words: fertilizer, conservation gardening, plant growth, plant mortality, restoration planting, threatened plants, translocation, wildfire

Implications for Practice

- *Athrotaxis cupressoides* is a slow-growing, Tasmanian endemic conifer of high conservation value with populations vulnerable to wildfire.
- Nursery-grown transplants, if protected against herbivores, can reinforce wild populations of *A. cupressoides*. In wild areas, planting soon after fire is preferred because growth is faster in recently burnt than in long-unburnt areas.
- Fertilizer was found to increase growth, especially in gravel pits. Disturbed environments such as restored gravel pits can be used as novel fire refugia for vulnerable species such as *A. cupressoides*.
- Trials, however, are critical to identify biophysical factors other than fire (soils, herbivores, and climate) that may limit the establishment and growth in artificial fire refugia.

Introduction

Wildfires are expected to increase in frequency and intensity as a result of anthropogenic climate change in many areas globally (Jolly et al. 2015; Cunningham et al. 2024a), including in Australia (Sharples et al. 2016; Cunningham et al. 2024b). As a result, some areas that have been infrequently exposed to fire will be more frequently burnt by severe wildfire. In Australia, the Tasmanian Wilderness World Heritage Area (TWWHA) is a prime example of an area where, until recently, severe fire weather has been rare, but is expected to become more frequent with climate change. The combination of less summer rainfall and rising temperatures in this area (Grose et al. 2010) will cause fuels to become drier and more frequently available to burn following lightning and anthropogenic ignitions (Fox-Hughes et al. 2014; Di Virgilio et al. 2020). Indeed, the area burned annually in the TWWHA by lightning-ignited fires has steadily increased since the 1990s (Styger et al. 2018). Associated increases in fire frequency and severity will adversely affect the many fire-sensitive plant species in the area, which are poorly adapted to fire. This is especially problematic for slow-maturing, fire-sensitive species that rely on a source of viable seed and suitable conditions to reestablish populations after

Author contributions: DB, BF, LP conceived and designed the research; BF, SN, HS performed the fieldwork; SN entered the data; LP analyzed the data; LP, DB wrote and edited the manuscript; all authors reviewed the manuscript prior to submission.

[1]School of Natural Sciences, University of Tasmania, Hobart, Tasmania 7000, Australia
[2]Address correspondence to L. D. Prior, email lynda.prior@utas.edu.au
[3]Habitat Plants, 240 Jones Road, Liffey, Tasmania 7301, Australia

© *2025 The Author(s).* Restoration Ecology *published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.*
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.70003
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70003/suppinfo

severe fire (Bowman et al. 2014; Enright et al. 2015; Harris et al. 2018).

The area protected within the TWWHA contains many fire-sensitive, paleoendemic plant species (Jordan et al. 2016). Paleoendemic clades are ancient clades that are geographically restricted and were probably more widespread in the past. They provide a unique window into biogeographic and evolutionary history, illuminating factors associated with species persistence and speciation. In Tasmania, paleoendemism is associated with alpine and subalpine vegetation in areas experiencing little or no fire and climates that have been constantly moist and without temperature extremes (Jordan et al. 2016). Pencil pine (*Athrotaxis cupressoides*) is a paleoendemic conifer from central and western Tasmania (Worth et al. 2016). It is classed as vulnerable in the wild (Farjon 2013), despite almost all of its range being reserved in the TWWHA, a conservation area with the highest level of legislative protection in Australia. This is because it has a narrow geographical niche and is increasingly at risk from wildfire as the climate becomes warmer and less predictable (Jordan et al. 2016; Mariani et al. 2019). It is readily killed by crown fire and lacks reliable mechanisms to recover from it (Bliss et al. 2021). Because *A. cupressoides* is fire-sensitive, slow-growing, and long-lived, with stems that can be over 1000 years old, it has been assumed to be a late-successional species unable to compete with species adapted to post-fire environments (Bowman 2000). Genetic analyses have shown that *A. cupressoides* is a clonal species and that individual genets were potentially established in the early Holocene (Worth et al. 2016), and thus the species could feasibly have been involved in a primary succession on glacial deposits (Fletcher et al. 2018).

Extensive fires during the exceptionally dry summer of 1960/1961 killed *A. cupressoides* trees in an estimated one-third of its range (Corbett 1995; Johnson & Marsden-Smedley 2002), with almost no recovery evident (Holz et al. 2015). In 2016, large lightning-ignited fires burnt approximately 85 ha of *A. cupressoides* forest (0.7% of that remaining) near Lake Mackenzie, on Tasmania's Central Plateau (DPIPWE 2017). Stem mortality in the areas burnt by the 2016 fires was estimated at 69%, with 42% of the survivors having canopy damage, and there has been minimal natural regeneration since (Bliss et al. 2021).

Translocations of organisms will be essential to maintain biodiversity in the future (Corlett 2016). Where natural regeneration fails, interventions such as artificial seeding or transplanting nursery-grown seedlings or cuttings can be required to maintain populations in the fire-affected area (Guerrant 2012; Bassett et al. 2015). A recent study (French et al. 2024) showed that transplanting nursery-grown cuttings or seedlings can potentially reestablish stands of *A. cupressoides* in Tasmanian wilderness areas. Tube stock were transplanted into stands either killed by recent fire (in 2016) or into areas unburnt since 1961. During the first 20 months after transplanting, 74% of transplants survived if protected from herbivory, but only 9% of open transplants survived, indicating that protection from herbivores is essential for successful reestablishment of the species (French et al. 2024). While survival was promising, growth was extremely slow, consistent with findings of other studies (Cullen & Kirkpatrick 1988; Prior et al. 2018). Transplants will therefore be vulnerable to herbivory (primarily macropod herbivory) for a long period, and it will take many decades for them to reach maturity and for populations to be self-sustaining (Ogden 1978; Holz et al. 2015; French et al. 2024).

One likely factor contributing to the slow growth of *A. cupressoides* is low nutrient availability in the soils where the species is found (Crowden 2005). Applying fertilizer could be a simple and practical way to enhance growth rates and help them mature more quickly. Restoration plantings often include various irrigation, herbicide, and fertilization treatments intended to enhance seedling survival and growth (Hau & Corlett 2003; Devine et al. 2007; Campoe et al. 2010), but studies testing their effects are relatively rare (Guerrant 2012). The results of such treatments appear idiosyncratic; for example, effects of fertilizer application depend on species (Hau & Corlett 2003), but there have also been positive (Campoe et al. 2010; Ruthrof et al. 2010; Kim et al. 2014), negative (Pareliussen et al. 2006), and inconsistent (Devine et al. 2007) results reported within the same species. Fertilizer responses, therefore, need to be tested for the particular species and environment of the planting.

To date, there has been little consideration of managing wildfire in restored vegetation (Bowman & Legge 2016). An unexplored idea is leveraging the inherent low fire risk of denuded land surfaces to create "fire refugia," which are landscape settings that have lower flammability than surrounding areas due to topo-edaphic factors (Meddens et al. 2018). Fire refugia are critical for the persistence of fire-sensitive plants such as *A. cupressoides* (Bowman et al. 2019). Potentially suitable fire refugia are the gravel pits excavated during the development of the hydroelectric scheme at Lake Mackenzie in the 1960s. From these pits, almost the entire regolith had been removed, leaving skeletal mineral soils and very limited plant cover. As well as offering fire protection, these gravel pits could be more cost-effective restoration sites than the wilderness areas of the TWWHA because they are more accessible, with infrastructure such as roads, power, and water channels nearby, and are easier to defend from fire. Additionally, these areas have already been severely disturbed and are not subject to the same stringent criteria as would be areas in the TWWHA if similar interventions were undertaken. We had the opportunity to test the suitability of the gravel pits because hundreds of *A. cupressoides* seedlings and cuttings surplus to the requirements of French et al.'s (2024) establishment trial became available to us. Using the same plant material grown under the same nursery conditions allowed us to compare *A. cupressoides* plantings in the gravel pits with those in the wilderness areas. Plantings into the fire-affected wilderness areas can be considered as restoration sensu stricto, in which areas are restored to their original composition and function (Corlett 2016). By contrast, the plantings into denuded gravel pits near natural populations of *A. cupressoides* can be considered ecological reclamation (sensu Gerwing et al. 2022), which establishes ecosystems similar to surrounding, natural ecosystems in highly degraded areas.

Here, we extended the study of growth and survival of nursery-grown *A. cupressoides* transplanted into the wild to 4 years and tested whether there were benefits in adding fertilizer. We also explored the potential of using gravel pits at Lake Mackenzie for restoration plantings of *A. cupressoides*. Specifically, we (1) extended the monitoring period of survival of transplants in the wild to 4 years and also reported growth; (2) compared the survival and growth of *A. cupressoides* transplanted into these gravel pits, from which the entire regolith had been removed and on which there has been limited plant cover for decades, with *A. cupressoides* plantings on organic soils in wilderness areas burnt recently (2016) or burnt over 60 years ago; and (3) measured whether fertilizer could enhance growth and survival of nursery-grown *A. cupressoides* juveniles used in restoration plantings in the gravel pits and wilderness areas. This study not only illuminates the potential for using restoration plantings to help conserve this relict species but also provides important ecological insights into the role of relict species in primary and secondary succession.

Methods

Study Area

The study area was in the far north of the Tasmanian Wilderness World Heritage Area, near the edge of Tasmania's Central Plateau. Our eight study sites were near Lake Mackenzie (41.7°S, 146.4°E), within and adjacent to the area burnt by wildfire in 2016 (Fig. 1). The sites not burnt in 2016 had been burnt by extensive wildfires in the summer of 1960/1961, with standing bleached dead trees a testament to how destructive those fires were to *Athrotaxis cupressoides* populations on the Central Plateau (Fig. S1).

The sites were at an elevation of approximately 1100 m, and experienced a cool to cold, wet climate (Koppen code Cfc; Kottek et al. 2006). Mean annual precipitation at Lake Mackenzie is 1983 mm, with a winter maximum (data from Bureau of Meteorology 2024 for 1969–1992 for discontinued station no. 96066 and Hydro Tasmania from 1992 to April 2024). Temperatures at Liawenee, the nearest weather station at a similar altitude, range from a mean monthly minimum of −1.5°C in July to a mean monthly maximum of 19.1°C in January, with a mean annual temperature of 6.9°C (Bureau of Meteorology 2024). Sub-zero temperatures are possible in any month. Most months since transplanting occurred were drier than average, with a notable exception in October 2022 (Fig. 2). Total precipitation over the 18-month period of the fertilizer trial was only 79% of the long-term average (Fig. 2). The summers were particularly dry, with precipitation only 50% of the average in the first summer and 66% in the second.

The geology of Tasmania's Central Plateau is dominated by the Jurassic dolerite that intruded into the pre-existing Permian and Tertiary sediments and was exposed after these softer overlying rocks eroded away (Corbett 2019). Repeated glaciation has scoured the dolerite bedrock and covered fringing areas with moraine, producing numerous small lakes and tarns. Extremely shallow, rocky rudisols with very low levels of K and Ca typically occur on more elevated parts of the doleritic landscape, while organosols predominate on lower slopes and depressions (Kirkpatrick et al. 2014). Although the Jurassic dolerite is potentially rich in nutrients, it weathers slowly, and the soils derived from it are shallow and of only moderate fertility (Crowden 2005). Furthermore, heavy rainfall leaches cations from the soil, acidifying and reducing the fertility of the soils (Crowden 2005).

Study Species

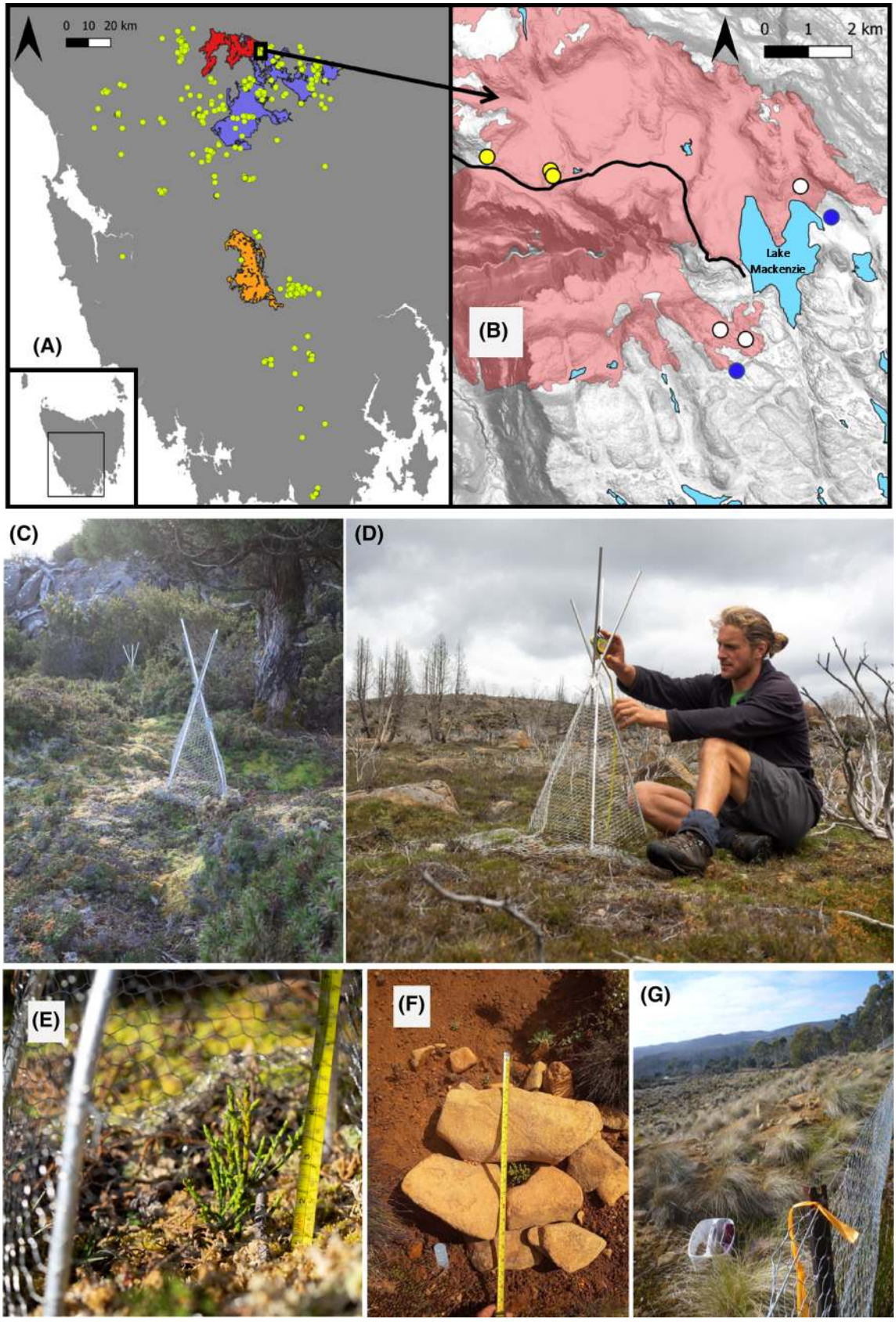
Athrotaxis cupressoides is a slow-growing, long-lived endemic Tasmanian conifer in the Cupressaceae family. It is a mast seeder, producing vast quantities of seed about every 5–6 years (Cullen & Kirkpatrick 1988). However, the seed is poorly dispersed and is viable for only about 4 months, so it is only rarely available (Cullen & Kirkpatrick 1988; Holz et al. 2015). Clonal reproduction through root suckering is important for the persistence of stands (Worth et al. 2016), and suckers can be present over 50 m from a parent plant (Cullen & Kirkpatrick 1988). However, fire does not appear to stimulate root suckering from surviving plants, although plants can weakly resprout from stems and branches after mild fire (Bliss et al. 2021). Herbivory is important in restricting regeneration of *A. cupressoides* (Holz et al. 2015), but there are also other factors that could not be identified (Bowman et al. 2019). Stem mortality in the areas burnt in 2016 was estimated at 69%, with 42% of the survivors having canopy damage (Bliss et al. 2021). Furthermore, the fire scars on the stems of the survivors will render them more vulnerable to being killed by future fires (Bowman et al. 2019).

Trial Design

The fertilizer trial was conducted at three categories of site: "wilderness areas" where organic soils predominated, and (1) those that had been burnt by the 2016 fires, or (2) those that were long unburnt (since 1961); and (3) gravel pits just outside the wilderness area, which had mineral soils. A total of eight study sites were established (Supplement S1), as described below.

Wilderness Area Plantings

This trial was originally established to determine whether it is feasible to reestablish populations of *A. cupressoides* in the Central Plateau of Tasmania, particularly in areas damaged by wildfire (French et al. 2024). Conditions here are harsh, so growth is slow, and the effects of fire, such as a decrease in sphagnum and shrub cover, can persist for years (Kirkpatrick et al. 2010; Prior et al. 2023a). Briefly, the trial examined the survival and health of *A. cupressoides* juveniles in relation to (1) whether seedlings or cuttings perform better after being transplanted into the field; (2) protection from herbivory (caged vs. open); (3) recently burnt (fire in 2016) versus long unburnt areas (fire in 1960/1961); (4) topographic position; and (5) provenance (Prior et al. 2023b; French 2024). Five study sites were used: three that were burnt by the 2016 fires and two that were not but contained dead *A. cupressoides* trees burnt by fire in the



(Figure legend continues on next page.)

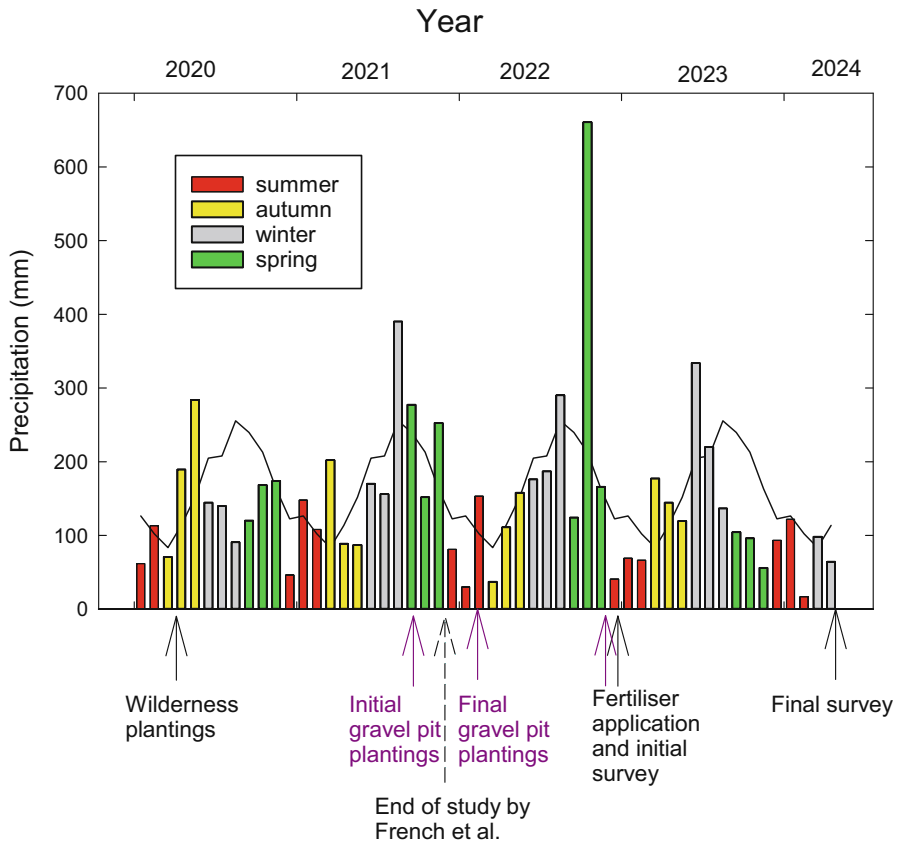


Figure 2. Experimental timeline and monthly precipitation at Lake Mackenzie. Bars indicate actual, and the line, average monthly precipitation, with austral seasons indicated by bar color. Data from Hydro Tasmania. Times of planting, fertilizer application, and surveys are indicated by arrows, with black for wilderness areas and dark pink for gravel pits. The resurvey by French et al. (2024) is also indicated by the dashed arrow.

summer of 1960/1961. Tube stocks were propagated from seed (six provenances, of which one was local) or cuttings (five provenances, of which three were local), as listed in box 4.1 of Prior et al. (2023b). In March and April 2020 (about 4 years after the most recent fire), a pair of nursery-grown plants, one a cutting and the other a seedling, was transplanted to each of 1007 plots (190–227 plots per site; Supplement S1). Tube stock from each provenance was spread randomly across the sites; provenance had a minimal effect (Prior et al. 2023b) and was not considered in our study. Seedlings averaged 123 mm in height, cuttings 132 mm, at the time of transplanting. Half the plots were caged to protect plants from herbivores. Transplants were re-surveyed in November/December 2021, as reported by French et al. (2024). While survival of caged plants was high, growth of these transplants was so slow that at the end of the 20 months, they had not regained the small amount of height they lost when pushed firmly into the soil at planting; hence, French et al. (2024) considered survival and health but not growth.

The fertilizer experiment described here started in December 2022. We found that 575 caged transplants (282 cuttings and 293 seedlings) and 15 open transplants were still alive at this time, corresponding to an overall survival during the initial 32 months from planting of 57% for caged transplants and only 1.5% for open ones. Of the surviving 575 caged transplants, 189 were single plants per plot, and 386 were paired (Supplement S1). The plants were small enough that we considered competition between pairs of plants would be minimal, so fertilizer was applied at a plot rather than a plant level. We used

(Figure legend continued from previous page.)
Figure 1. (A) Map of Western Tasmania showing the global range of *Athrotaxis cupressoides* (green points are observations from the Natural Values Atlas), footprints of fires that have burnt pencil pines since 1960 (purple is 1960/1961, red is 2016, and green is 2018), and the location of the study area (black box). (B) Map of the study area showing the 2016 fire footprint (red) and locations of the eight study sites; sites on gravel pits are shown by yellow circles, and in wilderness areas, recently burnt sites are indicated by white circles, and long unburnt sites by blue. (C) Tree guard in long unburnt area, (D) measuring transplants in recently burnt area, with a stand of dead *A. cupressoides* in the background. Also shown are *A. cupressoides* transplants in a (E) wilderness site and (F) gravel pit; and (G) partly rehabilitated gravel pit at the time of planting. Photo credits: (C–E) A. Szollosi, (F) and (G) S. Nichols.

a slow-release fertilizer formulated for Australian native plants (Scotts Osmocote Native Gardens: Evergreen Garden Care, Bella Vista, NSW) specially formulated for phosphorus-sensitive plants (23% N, 0.49% P, 6.3% K, 11% S with additional minor and trace elements). Three levels of the fertilizer were used: 20 g per plot (whether there were two or one surviving plants), 10 g per plot, and the untreated control. The fertilizer was broadcast in an area approximately 30 cm in diameter surrounding each plant or pair of plants. The higher rate (20 g Osmocote per location) is less than the 60 g recommended on the label for a 30 cm diameter pot, but is equivalent to about 283 g/m^2. We were very conservative in our chosen application rates, because the trial was located in the TWWHA, and an earlier experiment had suggested that even low rates of fertilizer (80 g/m^2 Osmocote) could be harmful to *Sphagnum* (Prior et al. 2023a). However, these low rates can be effective in promoting the growth of woody plants in infertile Tasmanian ecosystems; for example, applying 20 g of Osmocote fertilizer to *Leptospermum scoparium* seedlings transplanted into infertile sedgeland soils led to a 2.5 times faster growth rate (Prior et al. 2024). Fertilizer was applied in December 2022. In total, 314 plants were unfertilized controls, 129 were in plots to which 10 g fertilizer was applied, and 132 received 20 g per plot (Table 1).

For the fertilizer trial, initial plant height was measured in December 2022, at the time of fertilizer application. Because the plants had been growing in the field for about 32 months, these initial heights reflect microsite conditions as well as demonstrating the effect of plant size per se on subsequent growth. Plant survival and height were remeasured in April 2024. Despite intensive searching, we were unable to find 21 of the 575 plants. We present overall survival rates excluding these plants, and our statistical analyses are based on the plausible assumption these plants were all dead.

Soil depth to a maximum of 1 m was measured at three locations around each plot with a stainless steel probe and averaged.

Table 1. Numbers of plants in the wilderness areas (organic soils) and gravel pits (mineral soils) according to site and fertilizer treatment. Sites PB, BN, and EV were burnt in the 2016 fires, while UBN and UBS were long unburnt.

	Fertilizer (g/plot)			
Site	*0*	*10*	*20*	*Total*
Wilderness areas				
PB	103	27	28	158
BN	41	26	27	94
EV	72	28	28	128
UBN	29	23	24	76
UBS	69	25	25	119
Sub-total	314	129	132	575
Gravel pits				
HEC1	98	86	96	280
HEC2	32	30	32	94
HEC3	27	40	30	97
Sub-total	157	156	158	471
Total	471	285	290	1046

Gravel Pits

The nursery-grown plants that were surplus to requirements for the establishment trial were used to test whether sites formerly quarried for gravel could be suitable habitat for *A. cupressoides*. These plants were from the same batches as used in the wilderness sites and comprised seedlings and cuttings and a similar mix of provenances. We note that these individuals spent an additional 18–25 months in the nursery environment compared to those transplants in the wilderness sites, and there were minor differences in planting methods.

Three partly rehabilitated gravel pits were chosen for these plantings. In 2014, the sites were "shaped" with a small excavator, then spread with NPK 14:16:11 at 350 kg/ha and seeded with local native species at approximately 6 kg/ha (A. D'Andrea, Hydro Tasmania, 2024, personal communication). Some brush matting was also applied. At these sites, we used large exclosures rather than individual tree guards for protection against herbivores. Fencing was professionally installed and 1 m high, consisting of metal star pickets every 15–20 m, with six galvanized straining wires with galvanized "hex mesh chicken wire" attached. A video of this transplanting program can be found at https://youtu.be/Dh9oK5IG9rk?si=4Wj3H9k4eTsQtfoT.

For logistical reasons, the first 292 plants were transplanted into all three sites in October 2021, followed by a further 300 plants added to the three sites in May 2022. Plants were placed singly, rather than in pairs. No fertilizer was applied until November 2022, when the three fertilizer treatments were imposed on a total of 471 plants across the three sites: 157 plants were untreated controls, 156 received 10 g, and 158 received 20 g of Osmocote fertilizer, applied as for plants in the wilderness areas (Table 1). Plant height was measured immediately after transplanting, again after fertilizing, and finally in April 2024. Preliminary analyses showed there were no differences between the two transplanting dates in survival and growth during the fertilizer experiment, although at its start, plants that had been transplanted in October 2021 were taller than those transplanted in May 2022 (Supplement S2).

Soil Nutrient Analyses

To characterize the soils in the three site categories, we sampled soils at each site. Prior to fertilizing, we took samples from 5 to 10 cm depth adjacent to 11 transplants from each of the five wild sites and from a total of 108 transplants in the gravel pit plantings (73 from HEC1, 19 from HEC2, and 16 from HEC3). Wet sample weights averaged 133 g for mineral soil from the gravel pits and 45 g for organic soil from the wilderness sites; water content averaged 187 g/100 g dry soil for organic soils compared to 37 g/100 g dry soil for mineral soils. Large roots and debris were removed, and soils were dried and then passed through a 0.5 mm sieve, and the coarse fraction (>0.5 mm) was discarded. Each sample was divided into two subsamples, one for determination of the organic matter concentration and the other for nutrient analysis. Analyses were performed on a subset of these subsamples, as follows: (1) Organic matter concentration (%weight/weight) was determined by loss on ignition

for 66 soil subsamples drawn from all eight sites (20 gravel pit and 46 wilderness site subsamples). First, the soil was redried at 105°C for 24 hours to remove any reabsorbed moisture. Approximately 5 g of soil was then weighed into a crucible and placed in a 550°C furnace for 2 hours, cooled, and reweighed. (2) Total nutrient concentrations were determined on one pooled sample from each site. These pooled samples comprised 10 subsamples from each of the five wilderness sites and 2–3 subsamples randomly selected from each of the gravel pits. The soil samples were sent to a commercial laboratory (LabWest Minerals Analysis, Malaga, Western Australia) for analysis. After pulverization and aqua regia-microwave digestion, these were analyzed by ICP-MS/ICPOES (inductively coupled plasma mass spectrometry/ inductively coupled plasma optical emission spectroscopy) for 50 elements, including P, K, Mg, Mn, and Fe. Total C and total N analyses were performed by CSBP Soil and Plant Analysis Laboratory (Bibra Lake, Western Australia) using the Dumas high-temperature combustion method (Leco analyzer).

Statistical Methods

Our statistical approach was based on generalized linear modeling and model selection using Akaike's Information Criterion for small sample size (AICc) and multi-model inference (Burnham & Anderson 2002). Analyses of initial height and height growth and survival analyses used binomial generalized linear models. Explanatory variables were "Fertilizer" (0, 10, or 20 g per plot), "Site category" (burnt wilderness, unburnt wilderness, or gravel pit), and "Initial height" (at the start of fertilizer experiment, in November/ December 2022). Where possible, site was used as a random effect to account for spatial correlation in the data. To evaluate the statistical importance of the explanatory variables, the function "dredge" of the R package MuMIn (Bartoń 2023) was used to generate a candidate set of models containing all possible combinations of explanatory variables, without interactions, and calculate their AICc weight. We used full model averaging, whereby coefficients were set to zero in models that did not contain the term (Galipaud et al. 2017). The continuous variable "Initial height" was scaled in R (using the default setting, in which centered values are divided by the standard deviation) to allow direct comparison of the magnitude of all model variables. Weighted model average coefficients and 95% CI were calculated from the AICc weights. Variables were considered statistically important if these intervals did not overlap zero (Galipaud et al. 2017). Summed AICc weights were also calculated for each variable to augment this approach; although these have been criticized (Galipaud et al. 2017), they are useful in gaging support across the full set of models (Burnham & Anderson 2002; Giam & Olden 2016).

Preliminary modeling demonstrated that there were important interactions between site category and fertilizer and site category and initial height for height growth but not for survival (Supplement S3). We therefore modeled survival for all sites combined, using site category as a factor, but growth responses were modeled separately for each site category. For survival, we were able to use site as a random effect, but for the growth models, there were insufficient sites within each category to do this, so site was specified as a fixed effect.

Additional analyses, using the above approach, were conducted (1) to determine whether initial height, survival or growth were influenced by the additional variables measured only at the wilderness sites, namely whether the plant was a seedling or a cutting, a single or paired, and soil depth (Supplement S4); and (2) whether initial height, survival and growth in the gravel pits during the fertilizer experiment were influenced by planting date (October 2021 vs. May 2022) (Supplement S2).

Results

At the time of fertilizer application, the initial height of *Athrotaxis cupressoides* plants differed among site categories and averaged 113 mm for unburnt wilderness sites, 143 mm for burnt wilderness sites, and 132 mm for gravel pits. There was statistical support for plants at the unburnt wilderness sites being significantly shorter than those at the other sites (Fig. 3A). Our height growth modeling included initial height as an explanatory variable and therefore allowed for these differences.

Survival of *A. cupressoides* plants between December 2022 and April 2024 was significantly higher in the gravel pits than the wilderness sites, but there was no difference in survival between the burnt and unburnt wilderness sites (Figs. 3B & 4). At the gravel pits, overall survival between December 2022, when fertilizer was applied, and April 2024 was 96.6%. For the wilderness sites, survival was 88.9%, assuming all missing plants were dead (92.2%, excluding the 21 missing plants). Overall survival of caged plants in the wilderness areas in the 4 years since transplanting was 51% (Supplement S1). Survival was strongly correlated with initial height, increasing from an average of 55% for plants ≤50 mm tall to 100% for plants taller than 200 mm (Fig. 4). The initial height model explained 15% of the deviance in survival.

In April 2024, unfertilized plants were, on average, 240 mm tall in the burnt wilderness sites, 147 mm in the unburnt wilderness sites, and 157 mm in the gravel pits. Height growth between December 2022 and April 2024 varied significantly with initial height, fertilizer treatment, and site category (Fig. 5). There was a strong, statistically supported interaction between site category and fertilizer (Supplement S3), such that fertilizer had a stronger effect in the gravel pits than the wilderness areas (Figs. 5 & 6). In the unfertilized treatment, average height growth in the burnt wilderness sites was 94 mm, compared with 33 mm in the unburnt wilderness sites and 29 mm in the gravel pits (Fig. 5D). For all site categories, there was little difference between applying 10 or 20 g of fertilizer per plot (Figs. 5 & 6). On average, fertilizer boosted growth rates by 20 mm in the burnt wilderness sites, 31 mm in the unburnt wilderness sites, and 83 mm in the gravel pits. Thus, while fertilizer application had a small, positive effect on growth in the wilderness sites, in the gravel pits, the effect was strong enough to increase growth to rates similar to those in the burnt wilderness sites (Fig. 5D). Growth of fertilized plants in unburnt wilderness

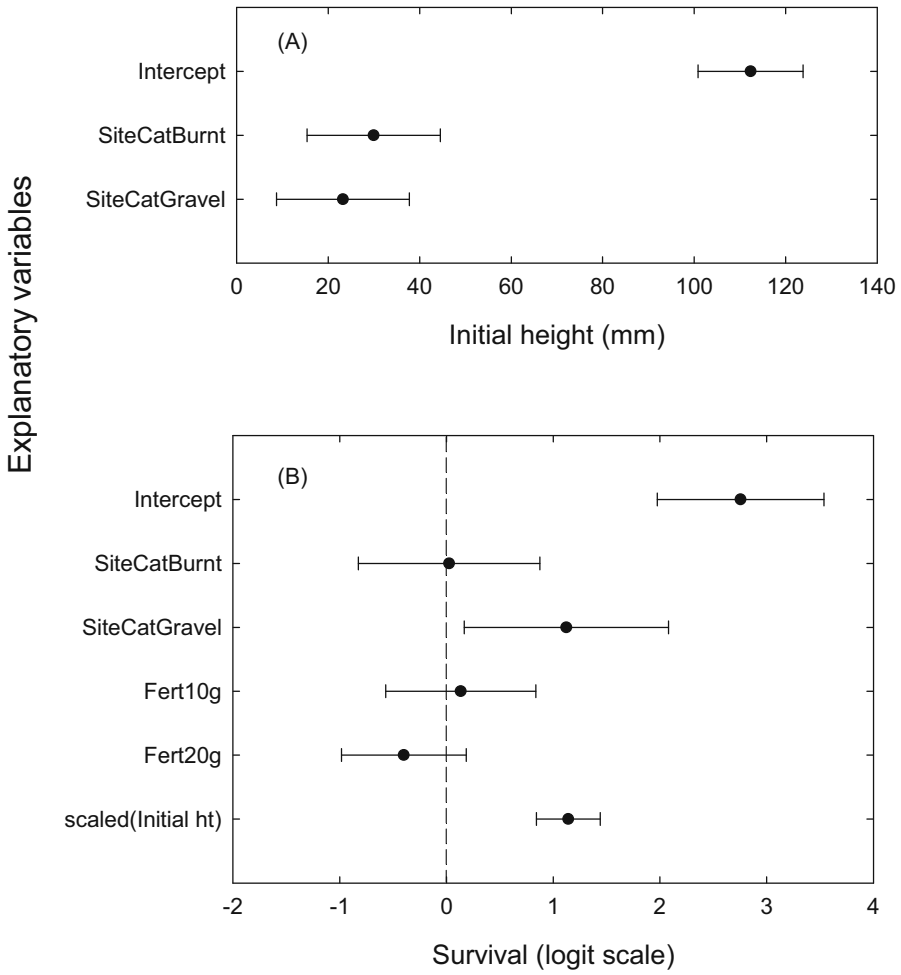


Figure 3. Weighted model average coefficients and associated 95% CIs for (A) the linear mixed effects model describing differences in initial height among site categories. The coefficients for the burnt wilderness sites and gravel pits are relative to the unburnt wilderness sites, and (B) the binomial mixed effects models of survival in relation to site category, fertilizer (0, 10, or 20 g per plot) treatment, and initial height, which was scaled so that effect size could be compared with those of the other (categorical) variables. Values are relative to unfertilized plants in unburnt wilderness sites. Site was a random effect in these analyses. Effects were considered statistically supported where the confidence interval did not include zero.

sites was only about half as fast as for the other site categories. There was also a statistically supported interaction between site category and initial height (Supplement S3), such that initial height had an important, positive effect on growth in the wilderness sites, but not in the gravel pits (Figs. 5 & 6).

The additional data collected for the wilderness sites showed that, relative to transplants in plots where only one transplant survived, transplants in plots where both survived were initially taller and had better survival and growth (Supplement S4). There were no differences between seedlings and cuttings, and we could not detect an effect of soil depth.

Soil Nutrient Levels

Soils in the wilderness areas averaged 69% organic matter (range 59–80%), compared with 13% (11–18%) in the gravel pits. There was an almost perfect correlation between soil organic matter and carbon concentration ($r = 0.99$; Supplement S5). Soil nutrient levels differed strongly between the wilderness sites and gravel pits (Table 2). As well as being higher in carbon, soils from wilderness sites had significantly higher concentrations of total N, P, Ca, and S. They had significantly lower concentrations of total Fe, Al, and Mg. There were insufficient samples to detect significant differences in any nutrient concentrations between soils from recently burnt and long unburnt wilderness sites. With so few soil nutrient measurements, we were unable to detect any significant correlations between the growth of unfertilized plants and the total concentration of any nutrient.

Discussion

In this study we explored a novel idea that degraded gravel pits can serve as fire refugia for the ancient conifer *Athrotaxis cupressoides*, which is increasingly at risk from wildfire as the climate becomes warmer and less predictable. Artificial fire refugia may be required for this species to persist in much of

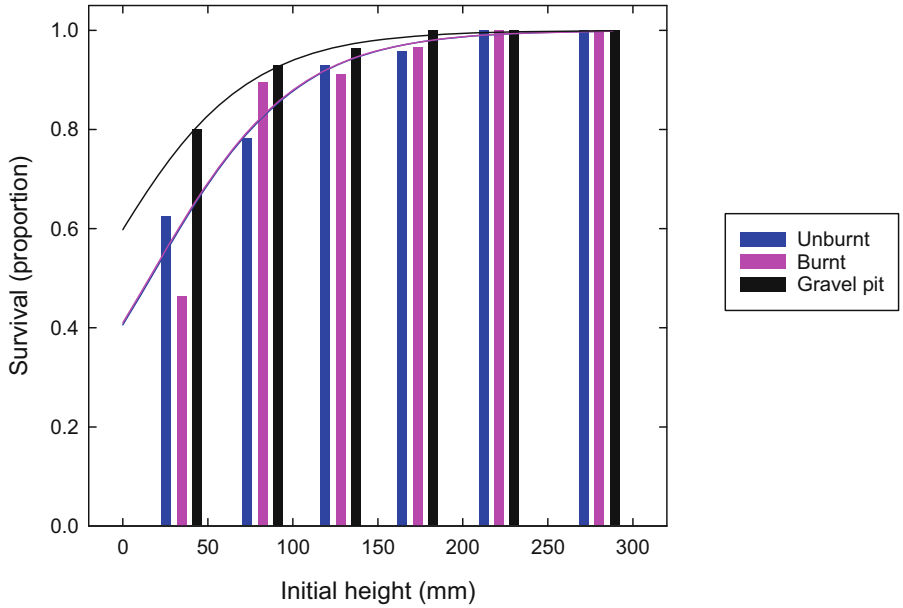


Figure 4. Survival of *Athrotaxis* transplants between December 22 and April 24 in relation to initial height for the three site categories. Bars show actual data and lines, the model predictions. Note that the model predictions for the unburnt and burnt wilderness sites are so close as to be indistinguishable here. Data were binned into 50 mm height classes for presentation, but individual values were used in the modeling.

its current range. We were able to compare the survival and growth of *A. cupressoides* in artificial fire refugia and in recently burnt and long unburnt sites in wilderness areas by extending an earlier trial by French et al. (2024). More broadly, our findings invite discussion of the broader practical and theoretical issues around restoration programs of long-lived trees.

Our study found good survival (89–97%) of *A. cupressoides* transplants during the 16-month experimental period, noting that they were all protected from herbivores. Combined with the data of French et al. (2024), survival of caged transplants was calculated as 51% in the wilderness areas over the 4 years since transplanting. This indicates restoration plantings using nursery-grown tube stock could be valuable in helping secure the future of *A. cupressoides* in the wild. It is important to note that French et al. (2024) documented the overriding importance of herbivore protection for the success of the *A. cupressoides* plantings. This was highlighted at our study site, where there was a temporary breach of the fences at additional plantings in nearby gravel pits; here, survival of *A. cupressoides* transplants was only about 50%, compared with the 97% in the gravel pits with intact fences (these areas were not included in our analyses). French et al. (2024) found substantial effects of fine-scale topography, with better survival in *Sphagnum*-dominated and well-drained positions than in moderately or poorly drained ones. Our results also suggest an important effect of microsite. Seedlings and cuttings were transplanted into the field 32 and 14 months before the fertilizer treatments were imposed at the wilderness and gravel pit sites, respectively. Therefore, it is likely that plants growing in favorable microsites were already taller when fertilizer was applied and continued to grow faster, with better survival, than those at less favorable microsites, especially at the wilderness sites. Future work could explore this effect of microsite on growth.

We found a substantial response of height growth to applied fertilizer, especially in the gravel pits. The response was non-linear; there was little additional benefit in adding 20 g rather than 10 g of fertilizer. Importantly, growth was slow, even with fertilizer. With our top rate of fertilizer, at the end of the study (5–6 years after propagation in the nursery and 16 months after fertilizer treatments were applied), heights were 275, 187, and 244 mm for the long unburnt and recently burnt wilderness areas and the gravel pits, respectively. One field study found even slower growth rates, with the average age of 1-m tall *A. cupressoides* plants being 55 years (Ogden 1978). Therefore, even with fertilizer, it will require decades without severe wildfire to reestablish self-sustaining populations, with long-term ongoing maintenance, such as replacing tree guards and/or protecting the integrity of fencing to provide protection from herbivores.

The difference in fertilizer response among the three site categories can be partly explained in terms of ecological succession. Plantings in the gravel pits represent primary succession; those in wilderness areas, secondary succession, with the long unburnt sites further along the successional gradient than the recently burnt sites. The soils in the gravel pits were less fertile, and there was little vegetation present to compete with the seedlings for resources such as water and light. Therefore, growth rates of unfertilized plants were low, but there was a strong, positive growth response to fertilizer. By contrast, at the long unburnt wilderness sites, the soils were more fertile, but there was abundant cover of shrubs and grasses to compete with the transplanted *A. cupressoides* (French 2024), restricting the

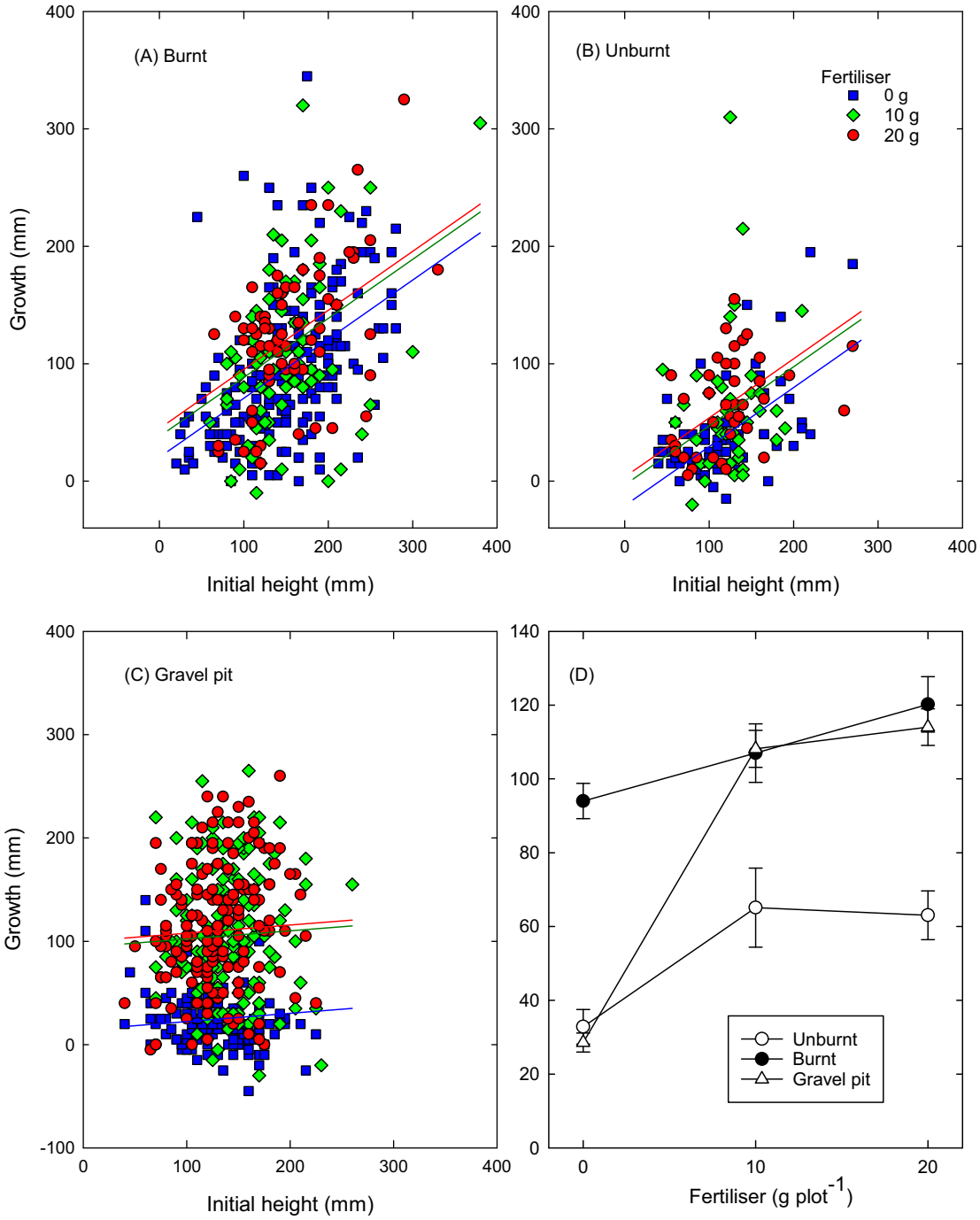


Figure 5. Height growth of *Athrotaxis* juveniles between December 2022 and April 2024 in relation to initial height and fertilizer treatment in (A) recently burnt and (B) long unburnt wilderness areas and (C) gravel pits (mineral soils). Lines are predicted values from linear models with terms site category, fertilizer, and initial height. (D) Average fertilizer responses for the three site categories. There were interactions between site category and fertilizer, and site category and initial height, so models were fitted separately for each site category.

response to applied fertilizer. The recently burnt sites had less vegetative cover than the long-unburnt wilderness sites, enhancing the growth response to fertilizer. These faster growth rates mean that in wilderness areas it is preferable to establish restoration plantings of *A. cupressoides* soon after wildfire.

In general, plant species with short life spans are more likely to establish large populations than long-lived plants (Bellis et al. 2024), such as *A. cupressoides*. There is also a greater need for interventions to maintain populations of rare species like *A. cupressoides* that persist in small, fragmented ecosystems

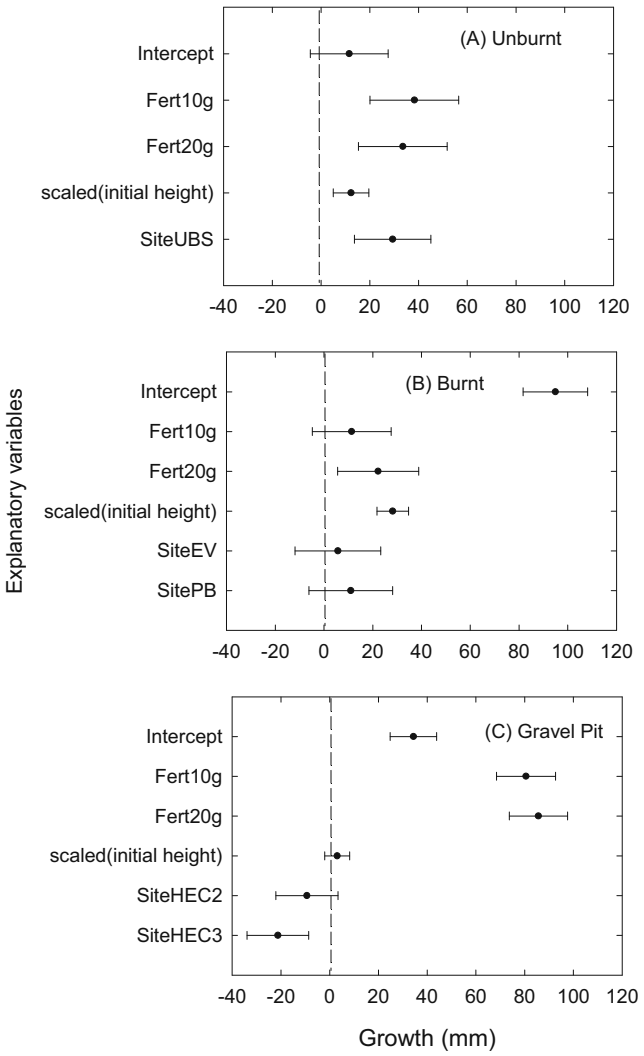


Figure 6. Weighted model average coefficients and associated 95% CIs for linear models describing height growth of *Athrotaxis* transplants in relation to fertilizer (0, 10, or 20 g per plot) treatment, initial height, and site within (A) unburnt wilderness sites, (B) burnt wilderness sites, and (C) gravel pits. Values are relative to unfertilized plants at sites UBN (unburnt), BN (burnt), and HEC1 (gravel pit). Models were fitted separately for the three site categories because of interactions of site category with fertilizer treatment and initial height. Effects were considered statistically significant where the confidence interval did not include zero. The continuous variable "initial height" was scaled so that effect size could be compared with those of the other (categorical) variables.

Table 2. Average total concentrations (mg/g) of elements at our eight sites, according to whether the soil was organic or mineral. The significance of the difference between them is indicated: *** is p less than 0.001; ** is p less than 0.01; * is p less than 0.05 and NS is not significant.

Element	*Organic*	*Mineral*	*Significance*
Higher in organic soils			
C	341	27	***
N	15.0	1.6	***
Ca	4.1	0.4	*
Mn	3.50	1.53	NS
S	1.30	0.52	***
P	0.9	0.5	*
Higher in mineral soils			
Fe	20.3	105.9	***
Al	13.9	84.3	***
Mg	1.22	2.27	*
K	0.7	0.9	NS
Co	0.042	0.061	NS
Zn	0.040	0.106	**
Mo	0.0005	0.0008	NS

compared with those found in large, well-connected ones (Corlett 2016). Planting nursery-grown material to reestablish long-lived tree populations represents a major, long-term investment of scarce conservation resources and should involve careful experimentation, long-term monitoring, especially of second-generation recruitment, ongoing maintenance, and protection from fire (Dillon et al. 2018; Silcock et al. 2019). However, while there have been many tree restoration programs globally (Silcock et al. 2019; Beckmann & Soorae 2022), relatively few have been properly evaluated and monitored, and then usually only for a short period (typically years rather than decades) (Godefroid et al. 2011; Silcock et al. 2019; Fenu et al. 2023).

To illustrate how well-designed restoration programs can conserve populations of biogeographically significant and long-lived tree species, we use two contrasting cases involving Cupressaceae species in the United Kingdom. *Juniperus communis* subsp. *communis* (lowland juniper) is the world's most widespread woody plant, yet it is declining across the United Kingdom. Some populations have dwindled to such an extent as to be functionally extinct, and it has been lost completely from some lowland counties (Wilkins & Duckworth 2011). Notably, lowland juniper habitats include old quarries, and persistence there has been attributed to factors such as abundant bare ground offering protection from fire and minimal grazing. To save England's lowland juniper, a project has been implemented that includes establishing an ex situ seed bank, seed collection, and propagation from cuttings to allow reintroductions and reinforce isolated and edge of range populations (Wilkins & Duckworth 2011). A very different case is that of *J. communis* subsp. *hemisphaerica*, which is native to Sicily, but occurred in several very small populations in Cornwall, probably from accidental introductions centuries ago (Griffiths & McClenaghan 2010). Over the last 150 years, all except one of these populations have disappeared, likely as a result of fire and grazing. Seeds from the remaining population have low viability, and there is no current natural regeneration. A small planting established in 1982 was destroyed by accidental fire soon after. More recently, about 200 plants were grown from cuttings and seeds and planted near the existing wild population to establish a new colony (Trelonk Wellbeing 2021). These programs underscore that careful design, substantial investment of resources, and ongoing monitoring and maintenance, including protection from wildfire, are essential for effective conservation of biogeographically significant conifers.

An important dimension of these programs is that they are seeking to preserve a species, not restore a specific ecosystem. We suggest such a pragmatic "conservation gardening" (Hobbs 2007) approach is warranted for *A. cupressoides* given its globally significant deep evolutionary roots, restricted distribution, and esthetic and cultural importance of these iconic long-lived Gondwanan trees that can be aptly described as "living fossils" (Jordan et al. 2016; DCCEEW 2024).

Our findings demonstrate the capacity to reclaim gravel pits by creating localized populations of a vulnerable endemic Tasmanian conifer species. These denuded gravel pits can be re-imagined as fire refugia. Restoring fire-damaged populations of *A. cupressoides* in wilderness areas using nursery-grown plants is a viable in situ conservation approach, particularly if implemented soon after burning. However, the creation of new *A. cupressoides* populations in artificial fire refugia has advantages from a species conservation perspective, not only because of the reduced fire risk but also because of accessibility for planting, fencing, and ongoing monitoring and management, including firefighting. As the climate continues to warm, future management may include irrigation to sustain the planting and reduce fire risk.

Acknowledgments

We thank Hydro Tasmania, especially A. D'Andrea, for assisting with planting the gravel pits and for rainfall data for Lake Mackenzie. We are grateful to the many volunteers who assisted in planting the wilderness areas and to F. Bird, M. Harding, and T. French. We thank M. Porter for field assistance and project management. Seeds were donated by the Royal Tasmanian Botanical Gardens. S. Staubmann and staff at Habitat Plants took great care in growing all plant material. The initial wilderness area plantings and plant propagation were funded by the Department of Natural Resources and Environment Tasmania, as part of the Lake Mackenzie Alpine Restoration Project, and we thank the many staff involved in the planning phase. B.J. F. was supported by a Research Training Program (RTP) scholarship from the Australian Government and a Future Leaders Scholarship from the Westpac Scholars Trust. This phase of the project was supported by an Australian Research Council grant (FL220100099) to D.M.J.S.B. The authors declare no conflicts of interest. Open access publishing facilitated by University of Tasmania, as part of the Wiley - University of Tasmania agreement via the Council of Australian University Librarians.

LITERATURE CITED

Bartoń K (2023) MuMIn: multi-model inference. R package version 1.47.5. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf (accessed 10 Feb 2025)

Bassett OD, Prior LD, Slijkerman CM, Jamieson D, Bowman DMJS (2015) Aerial sowing stopped the loss of alpine ash (*Eucalyptus delegatensis*) forests burnt by three short-interval fires in the Alpine National Park, Victoria, Australia. Forest Ecology and Management 342:39–48. https://doi.org/10.1016/j.foreco.2015.01.008

Beckmann KM, Soorae PS (2022) Conservation translocations from the 'Global reintroduction Perspectives' series: disease and other biological problems. Ecological Solutions and Evidence 3:e12163. https://doi.org/10.1002/2688-8319.12163

Bellis J, Osazuwa-Peters O, Maschinski J, Keir MJ, Parsons EW, Kaye TN, et al. (2024) Identifying predictors of translocation success in rare plant species. Conservation Biology 38:e14190. https://doi.org/10.1111/cobi.14190

Bliss A, Prior LD, Bowman DMJS (2021) Lack of reliable post-fire recovery mechanisms makes the iconic Tasmanian conifer *Athrotaxis cupressoides* susceptible to population decline. Australian Journal of Botany 69:162–173. https://doi.org/10.1071/bt20117

Bowman DMJS (2000) Australian rainforests: islands of green in a land of fire. Cambridge University Press, Cambridge, United Kingdom

Bowman DMJS, Bliss A, Bowman CJW, Prior LD (2019) Fire caused demographic attrition of the Tasmanian palaeoendemic conifer *Athrotaxis cupressoides*. Austral Ecology 44:1322–1339. https://doi.org/10.1111/aec.12789

Bowman DMJS, Legge S (2016) Pyrodiversity – why managing fire in food webs is relevant to restoration ecology. Restoration Ecology 24:848–853. https://doi.org/10.1111/rec.12401

Bowman DMJS, Murphy BP, Neyland DLJ, Williamson GJ, Prior LD (2014) Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. Global Change Biology 20:1008–1015. https://doi.org/10.1111/gcb.12433

Bureau of Meteorology (2024) Climate data online. Climate Services, Bureau of Meteorology. http://www.bom.gov.au/climate/data/ (accessed 14 Oct 2024)

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach. Springer, New York

Campoe OC, Stape JL, Mendes JCT (2010) Can intensive management accelerate the restoration of Brazil's Atlantic forests? Forest Ecology and Management 259:1808–1814. https://doi.org/10.1016/j.foreco.2009.06.026

Corbett S (1995) Vegetation of the Central Plateau: Tasmanian wilderness world heritage area. Report 95/3. National Parks and Wildlife Service, Hobart, Tasmania, Australia

Corbett K (2019) Child of Gondwana – the geological making of Tasmania. Forty South Publishing, Hobart, Tasmania, Australia

Corlett RT (2016) Restoration, reintroduction, and rewilding in a changing world. Trends in Ecology & Evolution 31:453–462. https://doi.org/10.1016/j.tree.2016.02.017

Crowden RK (2005) Alpine vegetation. Pages 333–356. In: Reid JB, Hill RS, Brown MJ, Hovenden MJ (eds) Vegetation of Tasmania. Australian Biological Resources Study, Canberra, Australia

Cullen PJ, Kirkpatrick JB (1988) The ecology of *Athrotaxis* D Don (Taxodiaceae). 1. Stand structure and regeneration of *Athrotaxis cupressoides*. Australian Journal of Botany 36:547–560. https://doi.org/10.1071/bt9880547

Cunningham CX, Williamson GJ, Bowman D (2024*a*) Increasing frequency and intensity of the most extreme wildfires on earth. Nature Ecology & Evolution 8:1420–1425. https://doi.org/10.1038/s41559-024-02452-2

Cunningham CX, Williamson GJ, Nolan RH, Teckentrup L, Boer MM, Bowman D (2024*b*) Pyrogeography in flux: reorganization of Australian fire regimes in a hotter world. Global Change Biology 30:e17130. https://doi.org/10.1111/gcb.17130

DCCEEW (Department of Climate Change, Energy, the Environment and Water) (2024) World heritage places – Tasmanian wilderness. Department of Climate Change, Energy, the Environment and Water, Canberra, Australia

Devine WD, Harrington CA, Leonard LP (2007) Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* Dougl. Ex hook.) seedlings. Restoration Ecology 15:212–222. https://doi.org/10.1111/j.1526-100X.2007.00205.x

Di Virgilio G, Evans JP, Clarke H, Sharples J, Hirsch AL, Hart MA (2020) Climate change significantly alters future wildfire mitigation opportunities in southeastern Australia. Geophysical Research Letters 47:e2020GL088893. https://doi.org/10.1029/2020gl088893

Dillon R, Monks L, Coates D (2018) Establishment success and persistence of threatened plant translocations in south west Western Australia: an experimental approach. Australian Journal of Botany 66:338–346. https://doi.org/10.1071/bt17187

DPIPWE (Department of Primary Industries, Parks, Water, Environment) (2017) Assessment of the ecological impacts of the 2016 Mersey Forest Fire Complex. Nature conservation report no. 17/5. Department of Primary Industries, Parks, Water, Environment, Hobart, Tasmania, Australia

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Frontiers in Ecology and the Environment 13:265–272. https://doi.org/10.1890/140231

Farjon A (2013) *Athrotaxis cupressoides*. The IUCN Red List of Threatened Species 2013: e.T32054A2810019. http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T32054A2810019.en

Fenu G, Calderisi G, Borsic I, Kharrat MBD, Fernández AG, Kahale R, Panitsa M, Cogoni D (2023) Translocations of threatened plants in the Mediterranean Basin: current status and future directions. Plant Ecology 224:765–775. https://doi.org/10.1007/s11258-023-01303-7

Fletcher MS, Bowman DMJS, Whitlock C, Mariani M, Stahle L (2018) The changing role of fire in conifer-dominated temperate rainforest through the last 14,000 years. Quaternary Science Reviews 182:37–47. https://doi.org/10.1016/j.quascirev.2017.12.023

Fox-Hughes P, Harris R, Lee G, Grose M, Bindoff N (2014) Future fire danger climatology for Tasmania, Australia, using a dynamically downscaled regional climate model. International Journal of Wildland Fire 23:309–321. https://doi.org/10.1071/wf13126

French B (2024) Advancing ecological restoration in flammable systems: insights from a simulation and two field studies. PhD thesis. University of Tasmania, Hobart, Australia.

French BJ, Prior LD, Bowman DMJS (2024) Transplanting interventions could help conserve the living fossil *Athrotaxis cupressoides* under climate-change induced fire regimes. Frontiers in Conservation Science 5: e1491062. https://doi.org/10.3389/fcosc.2024.1491062

Galipaud M, Gillingham MAF, Dechaume-Moncharmont FX (2017) A farewell to the sum of Akaike weights: the benefits of alternative metrics for variable importance estimations in model selection. Methods in Ecology and Evolution 8:1668–1678. https://doi.org/10.1111/2041-210X.12835

Gerwing TG, Hawkes VC, Gann GD, Murphy SD (2022) Restoration, reclamation, and rehabilitation: on the need for, and positing a definition of, ecological reclamation. Restoration Ecology 30:e13461. https://doi.org/10.1111/rec.13461

Giam XL, Olden JD (2016) Quantifying variable importance in a multimodel inference framework. Methods in Ecology and Evolution 7:388–397. https://doi.org/10.1111/2041-210X.12492

Godefroid S, Piazza C, Rossi G, Buord S, Stevens AD, Aguraiuja R, et al. (2011) How successful are plant species reintroductions? Biological Conservation 144:672–682. https://doi.org/10.1016/j.biocon.2010.10.003

Griffiths A, McClenaghan R (2010) Survey, conservation and propagation of *Juniperus communis* subsp. *hemisphaerica* on the Lizard, Cornwall. Eden Project, Cornwall, United Kingdom. https://www.plant-talk.org/documents/JuniperStudyEdenProject.pdf (accessed 21 Oct 2024)

Grose MR, Barnes-Keoghan I, Corney SP, White CJ, Holz GK, Bennett JB, Gaynor SM, Bindoff NL (2010) Climate futures for Tasmania: general climate impacts technical report. Climate Futures, Hobart, Tasmania, Australia.

Guerrant EOJ (2012) Characterizing two decades of rare plant reintroductions. Pages 9–30. In: Maschinski J, Haskins KE (eds) Plant reintroduction in a changing climate. Promises and perils. Island Press, Washington, D.C. https://doi.org/10.5822/978-1-61091-183-2_2

Harris RMB, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, Perkins-Kirkpatrick SE, et al. (2018) Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8:579–587. https://doi.org/10.1038/s41558-018-0187-9

Hau BCH, Corlett RT (2003) Factors affecting the early survival and growth of native tree seedlings planted on a degraded hillside grassland in Hong Kong, China. Restoration Ecology 11:483–488. https://doi.org/10.1046/j.1526-100X.2003.rec0279.x

Hobbs RJ (2007) Managing plant populations in fragmented landscapes: restoration or gardening? Australian Journal of Botany 55:371–374. https://doi.org/10.1071/bt06088

Holz A, Wood SW, Veblen TT, Bowman DMJS (2015) Effects of high-severity fire drove the population collapse of the subalpine Tasmanian endemic conifer *Athrotaxis cupressoides*. Global Change Biology 21:445–458. https://doi.org/10.1111/gcb.12674

Johnson KA, Marsden-Smedley JB (2002) Fire history of the northern part of the Tasmanian Wilderness World Heritage Area and its associated regions. Papers and Proceedings of the Royal Society of Tasmania 136:145–152

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:e7537. https://doi.org/10.1038/ncomms8537

Jordan GJ, Harrison PA, Worth JRP, Williamson GJ, Kirkpatrick JB (2016) Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. Global Ecology and Biogeography 25:127–140. https://doi.org/10.1111/geb.12389

Kim YS, Byun JK, Kim C, Park BB, Kim YK, Bae SW (2014) Growth response of *Pinus densiflora* seedlings to different fertilizer compound ratios in a recently burned area in the eastern coast of Korea. Landscape and Ecological Engineering 10:241–247. https://doi.org/10.1007/s11355-012-0208-1

Kirkpatrick JB, Bridle KL, Dickinson KJM (2010) Decades-scale vegetation change in burned and unburned alpine coniferous heath. Australian Journal of Botany 58:453–462. https://doi.org/10.1071/bt10138

Kirkpatrick JB, Green K, Bridle KL, Venn SE (2014) Patterns of variation in Australian alpine soils and their relationships to parent material, vegetation formation, climate and topography. Catena 121:186–194. https://doi.org/10.1016/j.catena.2014.05.005

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Koppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263. https://doi.org/10.1127/0941-2948/2006/0130

Mariani M, Fletcher MS, Haberle S, Chin H, Zawadzki A, Jacobsen G (2019) Climate change reduces resilience to fire in subalpine rainforests. Global Change Biology 25:2030–2042. https://doi.org/10.1111/gcb.14609

Meddens AJH, Kolden CA, Lutz JA, Smith AMS, Cansler CA, Abatzoglou JT, Meigs GW, Downing WM, Krawchuk MA (2018) Fire refugia: what are they, and why do they matter for global change? Bioscience 68:944–954. https://doi.org/10.1093/biosci/biy103

Ogden J (1978) Investigations of the dendrochronology of the genus *Athrotaxis* D. Don (Taxodiaceae) in Tasmania. Tree Ring Bulletin 38:1–13. http://hdl.handle.net/10150/260392

Pareliussen I, Olsson EGA, Armbruster WS (2006) Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. Restoration Ecology 14:196–203. https://doi.org/10.1111/j.1526-100X.2006.00121.x

Prior LD, French B, Bowman DMJS (2018) Effect of experimental fire on seedlings of Australian and Gondwanan trees species from a Tasmanian montane vegetation mosaic. Australian Journal of Botany 66:511–517. https://doi.org/10.1071/bt18124

Prior L, French B, Williamson G, Nichols S, Bliss A, Porter M, Bowman D (2023*b*) Tasmanian Wilderness World Heritage Area (TWWHA) bushfire recovery: Lake Mackenzie rehabilitation trials. Final report. January 2023. Nature conservation report 23/4. Department of Natural Resources and Environment, Hobart, Tasmania, Australia. https://nre.tas.gov.au/Documents/TWWHA%20Bushfire%20Recovery%20-%20Lake%20Mackenzie%20Sphagnum%20and%20Pencil%20Pine%20Rehabilitation%20Trials.pdf (accessed 14 Oct 2024)

Prior LD, Nichols SC, Foyster SM, Ondei S, Bowman DMJS (2024) Soil not fire: field, glasshouse and dendrochronology studies show how edaphic factors control post-fire woody plant growth across a sedgeland – forest boundary in Tasmania. Forest Ecology and Management 553:e121639. https://doi.org/10.1016/j.foreco.2023.121639

Prior LD, Nichols SC, Williamson GJ, Bowman DMJS (2023*a*) Post-fire restoration of *Sphagnum* bogs in the Tasmanian wilderness world heritage area, Australia. Restoration Ecology 31:e13797. https://doi.org/10.1111/rec.13797

Ruthrof KX, Douglas TK, Calver MC, Barber PA, Dell B, Hardy GES (2010) Restoration treatments improve seedling establishment in a degraded Mediterranean-type *Eucalyptus* ecosystem. Australian Journal of Botany 58:646–655. https://doi/org/10.1071/bt10211

Sharples JJ, Cary GJ, Fox-Hughes P, Mooney S, Evans JP, Fletcher MS, Fromm M, Grierson PF, Mcrae R, Baker P (2016) Natural hazards in Australia: extreme bushfire. Climatic Change 139:85–99. https://doi.org/10.1007/s10584-016-1811-1

Silcock JL, Simmons CL, Monks L, Dillon R, Reiter N, Jusaitis M, Vesk PA, Byrne M, Coates DJ (2019) Threatened plant translocation in Australia: a review. Biological Conservation 236:211–222. https://doi.org/10.1016/j.biocon.2019.05.002

Styger J, Marsden-Smedley J, Kirkpatrick J (2018) Changes in lightning incidence in the Tasmanian wilderness world heritage area, 1980–2016. Fire 1:e38. https://doi.org/10.3390/fire1030038

Trelonk Wellbeing (2021) Cornwall: home of the rarest juniper plant. https://www.trelonkwellbeing.com/blogs-juniper-cornwall (accessed 14 Oct 2024)

Wilkins TC, Duckworth JC (2011) Breaking new ground for juniper – a management handbook for lowland England. Plantlife, Salisbury, United Kingdom. https://www.plantlife.org.uk/wp-content/uploads/2023/03/ManagingJuniper.pdf (accessed 14 Oct 2024)

Worth JRP, Sakaguchi S, Rann KD, Bowman CJW, Ito M, Jordan GJ, Bowman DMJS (2016) Gondwanan conifer clones imperilled by bushfire. Scientific Reports 6:e33930. https://doi.org/10.1038/srep33930

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Photos of study area.
Supplement S1. Counts of *A. cupressoides* transplants in wilderness areas according to propagation method, fertilizer treatment and site, and survival through time.
Supplement S2. Modeling effects of transplanting date on initial height, survival, and growth of *A. cupressoides* on mineral soils in gravel pits.
Supplement S3. Modeling of site category interactions for growth and survival of *A. cupressoides*.
Supplement S4. Modeling of effects of additional variables (fertilizer treatment, soil depth, and transplant type) on initial height, survival, and growth of *A. cupressoides* transplants in wilderness areas.
Supplement S5. Characterizing soils at the eight study sites.

Coordinating Editor: Klára Řehounková

Received: 23 October, 2024; First decision: 24 December, 2024; Revised: 28 January, 2025; Accepted: 30 January, 2025