Climatic warming strengthens a positive feedback between alpine shrubs and fire

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Climate change is expected to increase fire activity and woody plant encroachment in arctic and alpine landscapes. However, it is unknown whether increases in woody species and fire will interact to exacerbate changes in structure, function and composition of these ecosystems. Here we use field surveys and experimental manipulations to examine warming and fire effects on recruitment, growth and survival of seedlings of evergreen obligate seeding alpine shrubs. We find that fire substantially increased shrub seedling establishment (up to 32–fold) and that warming doubled tall shrub seedling growth rates and could increase survival. Warming had limited or no effect on shrub recruitment, post-fire gap-infilling by grass, or competitive effects of grass on shrub seedling growth and survival. These findings indicate that rising temperatures coupled with more frequent or severe fires will likely exacerbate increases in tall evergreen shrubs by increasing recruitment, doubling growth rates, and potentially increasing shrub survival.

Accurately forecasting the effects of climatic warming on vegetation dynamics requires an understanding of the mechanisms by which climate and vegetation interact. Most forecasting models include the direct effects of climatic conditions on species distributions, but largely ignore biotic interactions and the type, frequency and severity of disturbances that are also likely to change[1–3]. Because disturbance strongly influences recruitment opportunities, and thus, composition and structure of plant communities and biomes worldwide[4,5], it has the capacity to exacerbate or diminish how climate affects vegetation. Seedlings are the life stage most vulnerable to climate and disturbance, and the life stage which determines the long-term persistence of a species and its capacity to establish in new areas. Consequently, it is imperative to understand how seedlings

35 respond to both changing climate and disturbance regimes[6,7].

36 Field manipulative experiments have been widely used to investigate the effects of climate

37 change on plant communities. These experiments have provided invaluable information on how

38 climate change directly influences plant phenology[8,9], reproduction[10], morphology[11], growth[12],

39 floristic composition[13] and biotic interactions[14]. However, because disturbances vary both spatially

40 and temporally, most have focused on mature plant responses in relatively undisturbed vegetation[7].

41 As such, few field climate experiments have been conducted on seedlings or vegetation in post-

42 disturbance conditions (but see[15–17]). Consequently, little is known about how climate change in-

43 fluences seedling demographic rates[7] and thus, vegetation recovery in post-disturbance conditions.

44 We consider these issues in Australian alpine heathland.

45 In alpine and arctic ecosystems, warming experiments and long-term monitoring have doc-

46 umented significant increases in the growth and cover of woody species[18–20]. The frequency and

47 extent of wildfires have also increased in these environments over recent decades, a trend expected

48 to continue[21–24]. In alpine and tundra ecosystems, current evidence from long-term and experimen-

49 tal studies indicate that shrub recruitment and encroachment is highest in disturbed areas[25–27], that

50 climatic warming is likely to increase woody species growth rates[20,28,29], and that shrubs are the

51 most flammable component of these ecosystems[30–32]. The combination of this evidence indicates

52 that more frequent or severe fire may increase recruitment opportunities for woody species, which

53 when coupled with higher growth and survival rates caused by rising temperatures, will exacerbate

54 shrub expansion[33,34] and ultimately increase the likelihood of fire[20,31,32]. In effect, warming could

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strengthen an existing feedback loop that not only has the potential to cause rapid changes in the composition and structure of alpine and arctic vegetation, but also has serious social, biodiversity and carbon sequestration consequences[35].

While paleoecological studies have indicated that such a feedback may exist[31,32], there is a paucity of information on multiple mechanisms that may strengthen, mitigate or break this feedback loop (Fig. 1a). For example, we have little information on whether fire will stimulate shrub seedling recruitment in alpine or tundra ecosystems, nor do we know how rates of seedling growth and survival will be affected under warmer, more exposed, post-fire conditions. Furthermore, we do not know how tussock grasslands (the other dominant community in these ecosystems) will respond to warmer post-fire conditions, whether grasses have competitive, facilitative or no effect on shrub seedling vital rates, or whether such effects are altered by warmer post-fire conditions.

We examine these unknowns and their impacts on the feedback between climatic warming, shrubs and fire in Australian alpine vegetation. As with tundra ecosystems, the Australian Alps have experienced rapid changes in climate. Since 1979, mean growing season temperatures have risen by approximately 0.4°C and annual precipitation has fallen by 6%[36], with a consequent decline in snow pack depth[37]. These climatic changes have been correlated with a 10 to 20% increase in shrub cover and a 25% decline in graminoids cover[36]. Much of the Australian Alps has also been burnt by recent wildfires, the frequency and severity of which are expected to increase[24,38].

We took advantage of recent fires in alpine open heathland, a plant community that occupies ca. 25% of the Australian alpine landscape[38]. Under global warming, this plant community is likely

75 to encroach upon grasslands and is itself susceptible to shrub thickening[39]. To determine drivers

76 of shrub establishment and how warmer post-fire conditions affect shrub cover, we combined field

77 observations with a warming experiment that used seedlings of four Australian evergreen obligate

78 seeding shrubs: *Grevillea australis* (Proteaceae; a tall shrub), *Asterolasia trymalioides* (Rutaceae;

79 a prostrate shrub), *Phebalium squamulosum* (Rutaceae; a tall shrub) and *Prostanthera cuneata*

80 (Lamiaceae; a tall shrub). This combination of data sources allowed us to examine: 1) landscape

81 scale drivers of shrub seedling establishment; 2) how warmer post-fire conditions influence rates

82 of grass recovery and shrub seedling recruitment, growth and mortality; 3) how proximity to grass

83 affect shrub seedling demographic rates; and 4) whether such grass effects change under warmer

84 post-fire conditions.

85 **Drivers of shrub seedling establishment.** We first investigated how altitude, Topographic Wet-

86 ness Index (TWI), adult density, fire and fire severity (as measured by post-fire twig diameters—see

87 Supplementary Methods) influenced the density of *Grevillea* and *Asterolasia* seedlings (the two

88 dominant shrubs of alpine open heathland). In 2011-12, we estimated seedling density for both

89 species across 40 alpine sites and found that the abundances of *Grevillea* (Fig. 2) and *Asterola-*

90 *sia* (Supplementary Fig. S1) seedlings were strongly influenced by the occurrence of fire. Sites

91 burnt in 2003 had seedling densities between 14 and 32 times higher than unburnt sites. The mean

92 seedling density of *Grevillea*, was $1.3/m^2$ at burnt sites and $0.04/m^2$ at unburnt sites. *Asterolasia*

93 had similar mean densities: 1.63 and 0.12 seedlings/m^2 at burnt and unburnt sites, respectively. For

94 both species, seedling density was also higher in severely burnt sites (i.e. sites with larger post-

95 fire twig diameters). As expected, pre-fire adult density positively influenced *Grevillea* seedling

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96 density. For both shrub species, we detected no change in seedling density along a 190 m altitu-

97 dinal range (equivalent to a 1.5°C change in mean temperature[40]). The field warming experiment

98 (see below) indicates that this lack of elevation response in *Grevillea* is due to rates of recruitment

99 (Supplementary Fig. S2) and mortality (see below) largely being insensitive to a 1°C change in

100 temperature. We detected no strong effect of Topographic Wetness Index for either species.

101 **Experimental warming effects on shrub seedling growth.** As shrub seedlings were more abun-

102 dant in burnt vegetation, we investigated how warmer post-fire conditions affected seedling growth

103 and mortality rates. Seedlings of *Grevillea*, *Asterolasia*, *Phebalium* and *Prostanthera* emerging

104 after a wildfire were transplanted into experimentally burnt plots. These plots were either enclosed

105 in Open Top Chambers (OTCs) whose temperature was 1°C warmer than control plots subjected to

106 current ambient conditions. After 1813 days (1087 growing season days) or 5 years' growth, mean

107 seedling heights of the tall shrubs (*Grevillea*, *Phebalium* and *Prostanthera*) growing in post-fire

108 bare ground were greater in warmed plots relative to controls by 9.7, 3.8 and 13.8 cm, respectively

109 (Fig. 3a). Warming increased heights of both *Grevillea* and *Prostanthera* seedlings in all years,

110 while *Phebalium* did not respond to the warming treatment until the second growing season. By

111 contrast, seedlings of the prostrate shrub, *Asterolasia*, showed no difference in growth rate between

112 warmed and control plots in any year. For each species, we also observed similar treatment trends

113 with stem diameter growth (Supplementary Fig. S3). Accounting for initial height and assuming

114 logistic growth, the rates of change in mean annual predicted height of *Grevillea*, *Phebalium* and

115 *Prostanthera* were 2.4, 1.4 and 1.9 times that observed in control plots, respectively. According to

116 this model, a 6 cm seedling (the mean initial height of seedlings used in this experiment) attains

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maximum height 39 years sooner 38 (*Grevillea*) or 17 years sooner (*Phebalium* and *Prostanthera*) when warmed by 1°C (Fig. 3b). *Asterolasia* was predicted to reach its maximum height in approximately 22 to 24 years, irrespective of warming treatment.

We validated the *Grevillea* and *Asterolasia* growth responses observed in experimentally warmed plots by examining the effect of elevation on maximum heights of post-fire recruits across 30 open heathland sites burnt in 2003. Here, a 190 m altitudinal range is equivalent to a mean ambient temperature difference of approximately 1.5°C[40], which is comparable to that observed between experimentally warmed and control plots (1°C). In response to shifts in temperature, the maximum height of *Grevillea* post-fire recruits was expected to decrease with elevation, whereas *Asterolasia* seedlings were not expected to show this pattern. Our experimental predictions were verified (Supplementary Fig. S4). Mean maximum height of *Grevillea* seedlings in burnt open heathland were 8 cm taller at 1670 m a.s.l compared to seedlings at 1860 m a.s.l. (22 cm vs 14 cm; a difference comparable to our experimental findings). In contrast, mean maximum height of *Asterolasia* seedlings did not vary significantly with elevation. Topographic Wetness Index and fire severity had no detectable influence on maximum seedling heights in either species.

Experimental warming on shrub seedling mortality. After five years and across all plots, 34% (172 out of 511) of all seedlings growing in burnt bare ground patches had died. Most deaths occurred in *Asterolasia* (65) followed by *Phebalium* (63), *Grevillea* (31) and *Prostanthera* (13). *Prostanthera* showed the largest treatment effect (Fig. 4), with annual mortality rates estimated to be near 0% in warmed plots and 4% in control plots. This significant decrease in mortality may

137 be a consequence of OTCs reducing the severity of spring frosts by rising minimum ambient and

138 soil temperatures by 0.9°C and 1.6°C, respectively (see Supplementary Fig S5-7). Warming also

139 reduced mean seedling mortality in *Grevillea* and *Phebalium* (Fig. 4); however, for both species,

140 the effect was highly uncertain (i.e. credible intervals overlap). By contrast, annual mortality rates

141 in the prostrate shrub, *Asterolasia*, were marginally higher in warmed plots, but again this effect

142 was highly uncertain (Fig. 4).

143 **Effects of tussock grass proximity on shrub seedling growth and mortality rates.** Climate

144 change is expected to alter biotic interactions because their strength and direction depend strongly

145 on climatic conditions, particularly in alpine and arctic ecosystems[14,41]. Here, we assess the inter-

146 active effects of warming and grass proximity on the growth and survival of *Grevillea* seedlings

147 transplanted into various sized inter-tussock gaps (Fig. 5). We detected a strong positive effect

148 of warming treatment on growth rates and a marginal, yet not significant, decrease in mortality.

149 However, we did not detect significant inter-tussock gap size effects or an interaction between gap

150 size and warming treatment on either growth or mortality rates (i.e. coefficient credible intervals

151 overlap zero).

152 **Experimental warming and rates of gap infilling by tussock grass.** Despite having little impact

153 on shrub seedling growth and mortality rates, tussock grass may still limit shrub recruitment, and

154 thus, shrub expansion, by infilling post-fire bare ground gaps (whether by vegetative growth or

155 seedlings) faster under warmer conditions. Using five years of post-fire inter-tussock gap size

156 changes in warmed and unwarmed plots we found that gaps were being infilled by tussock grasses

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157 (Fig. 6). However, the rate at which this occurred was very slow, with a 10 cm radius gap predicted

158 to decrease by approximately 2 cm over a ten year period. We also detected no significant effect

159 of a 1°C temperature rise on the rate of infilling.

160 **Strengthening of the warming-shrub-fire feedback.** Here we quantified several unknown inter-

161 actions between fire, shrub-grass relationships and climate to extend a conceptual model of alpine

162 shrub dynamics under climate change (Fig. 1b). We showed how these interactions strengthen a

163 hypothesized feedback loop that can rapidly increase shrub cover in alpine and tundra ecosystems[31].

164 The combination of rising temperatures and more frequent or severe fire creates conditions that

165 allow shrub seedlings to establish in greater densities, and for tall shrubs, double their growth

166 rates and potentially increase their survival. These demographic effects will ultimately result

167 in shrub thickening and expansion into grasslands. Coupled with field[30], experimental[42] and

168 paleoecological[31] evidence, which indicate that shrubs are the most flammable component of alpine

169 and tundra ecosystems, our results suggest that flammable fuel loads will accumulate faster and

170 cover a larger proportion of the alpine and arctic landscapes under a warmer environment. This

171 further strengthens the feedback[31,32] by potentially increasing the frequency or severity of fires,

172 which then creates further recruitment opportunities for shrubs with little demographic impact of

173 neighbouring tussock grass.

174 While we have addressed several unknowns associated with this feedback between climatic

175 warming, shrubs and fire, there are others we have not addressed that may also strengthen, weaken

176 or break this feedback. The most obvious mechanism that will break this cycle involves shorter

177 fire intervals that prevent obligate seeding shrubs reaching reproductive age and thereby exhausting

178 the seedbank. However, this scenario is unlikely for the majority of alpine (or tundra) landscapes,

179 including in Australia, where current fire intervals of 50 to 100 years would need to decrease to less

180 than 20 years—the time estimated for the species in this study to reach reproductive maturity[43].

181 Furthermore, if reproductive output is related to plant size[44], then climatic warming may allow

182 obligate seeding species to reach reproductive maturity sooner, and consequently, may increase

183 species resilience to short fire intervals. Nevertheless, these factors and others such as changes in

184 snow pack[45], soil moisture[46] or herbivory[47] require further research because they are likely to be

185 altered by the interactive effects of climate and disturbance in unpredictable ways[20].

186 Our findings provide mechanistic understanding as to why shrub cover has increased, of-

187 ten at the expense of grasslands, in many alpine and arctic ecosystems[20, 27, 33, 34]. But more im-

188 portantly, our results provide evidence for underlying processes that could result in a warming-

189 fire-shrub feedback that has been hypothesized in paleoecological studies[31, 32]. Based on current

190 observations and predictions, average global temperature has already increased by 0.85°C since

191 1880 and is expected to rise by as much as 4.8°C by 2100[48]. In alpine and tundra environments,

192 temperatures[49], shrub cover[20] and the frequency and severity of fire[21–24] have all increased in the

193 last few decades. These changes mean that the warming-shrub-fire feedback loop identified here

194 has already strengthened, which could cause grasslands and other non-woody communities to tran-

195 sition to an alternative state with more shrubs and more fire, both of which are likely to have

196 consequences for carbon sequestration, water supply and biodiversity.

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Methods

We investigated shrub dynamics in open heathland because it is a common and highly flammable plant community in the Australian Alps above 1600 m a.s.l[30]. It is also an ecotone between closed heathland (>70% shrub cover) and tussock grassland consisting of *Grevillea australis* shrubs interspersed among a *Poa hiemata* sward. Aerial photography has revealed that the plant community has acted as an invasion front of shrub expansion into grassland and has itself experienced shrub thickening by closed heathland dominants such as *Prostanthera cuneata*[39].

Open Top Chamber Experiment. In March 2010, at 1750 m a.s.l, we burnt 32 randomly selected mature (60 cm tall and 1.5 m^2) *Grevillea australis* shrubs in open heathland to create patches of bare ground approximately 0.7 m^2 surrounded by burnt tussock grass, simulating disturbance in open heathland burnt by wildfire. After creating the bare ground patches we collected seedlings of dominant alpine shrub species from a nearby (<2 km) site of similar altitude burnt by a late 2006 wildfire. We collected shrub seedlings of two dominant open heathland species *Grevillea australis* (Proteaceae; a tall shrub) and *Asterolasia trymalioides* (Rutaceae; a prostrate shrub), a dominant closed heathland species *Prostanthera cuneata* (Lamiaceae; a tall shrub) that typically grows on warmer aspects and a species common to both open and closed heathland *Phebalium squamulosum* (Rutaceae; a tall shrub). All four species are killed by fire[50].

A total of 640 seedlings, 256 *Grevillea* (half used in *Poa* inter-tussock experiment—see below) and 128 for each of *Asterolasia*, *Prostanthera* and *Phebalium* were used. Four seedlings per species were randomly selected and transplanted into a 4×4 square grid in the center of each

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burnt patch, with 14 cm between individuals and the edge of the patch dominated by resprouting tussock grass *Poa hiemata*. To examine interactions between tussock grass and shrub seedlings we also randomly transplanted four additional *Grevillea australis* into various sized inter-tussock gaps between burnt *Poa hiemata* immediately surrounding the bare ground (Supplementary Fig. S8). The experimental site was fenced to prevent grazing by deer and horses. We detected no obvious signs of rabbit or invertebrate herbivory within our plots.

To simulate near-term warmer conditions indicated by the IPCC[48], we randomly assigned Open Top Chambers (OTCs) to half (16) the plots, with the remainder treated as unwarmed controls. OTCs were placed over plots, ensuring all seedlings (including inter-tussock shrub seedlings) occurred within the 1.1 m^2 open top to minimise edge effects. OTCs were placed out at the start of the growing season (October) where they remained until snowfall (early June). This procedure was repeated for five growing seasons from May 2010 to May 2015.

Microclimatic conditions were measured hourly using Onset Micro Stations (Onset Computer Corporation, Bourne, MA, USA) at four control and four OTC plots. Across 5 growing seasons (1087 growing season days), OTCs simulated warmer conditions at the lower end of IPCC projections[48] (Supplementary Fig. S5-7). OTCs passively increased average ambient and soil temperatures by 1°C, and 0.9°C, respectively. Minimum and maximum temperatures were also raised in both ambient air (min: 0.9°C; max: 2.4°C) and soil (min: 1.6°C; max: 1°C). Chambers only marginally decreased soil moisture by 0.2% and relative humidity by 1.2%.

Seedling survival, maximum height and stem diameter (nearest mm measured with Vernier

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237 calipers) were initially recorded in May 2010 and then subsequently re-measured at the end of each

238 growing season (May-June). At the same time, we recorded the distance to the nearest tussock or

239 grass seedling in each of four cardinal directions for shrub seedlings growing in inter-tussock

240 gaps. Thus, changes in inter-tussock gap size could be due to either vegetative growth or seedling

241 establishment. We did not measure individual characteristics (e.g. height and basal diameter) of

242 surrounding tussock grass because we could not distinguish individuals, and because height varied

243 throughout the season. Numbers of natural *Grevillea australis* recruits establishing within the plots

244 were also recorded for the first two seasons.

245 **Seedling gradient study.** We used 40 long-term open heathland sites established after the 2003

246 fires[50] consisting of 30 burnt sites and 10 sites thought to be unburnt for over 70 years. In the

247 summer of 2011-12, at each site, seedling density/m^2 was estimated using 40 quadrats, each 1 m^2,

248 that were evenly distributed in groups of 10 along four 50 m transects, with 10 m between transect

249 lines, subsampling an area of 2000 m^2. Within plots we recorded the number and maximum

250 height of *Grevillea* and *Asterolasia* seedlings. For unburnt sites we counted the number of mature

251 *Grevillea* plants (>0.5 m^2) within 5 m of each transect. In burnt sites, this required counting the

252 number of skeletons (there were no living adults at any burnt site) that still persisted post-fire. We

253 were unable to estimate numbers of adult *Asterolasia* because this species does not have a persistent

254 woody skeleton post-fire. Site level data, elevation and Topographic Wetness Index (TWI) were

255 obtained from a 30 m resolution digital elevation model. Lastly, for burnt sites, fire severity was

256 estimated by twig diameters, collected immediately after the 2003 fires[50].

257 **Data analysis.** In total we built 11 hierarchical models to examine factors influencing post-fire

258   recovery of tussock grass and shrub seedling establishment, growth and mortality. For each model

259   we used Bayesian inference and fitted models in R 3.2.2 using package `rstan` 2.8.1. Data and

260   source code for reproducing analysis and figures are available at: `https://github.com/`

261   `jscamac/Alpine_Shrub_Experiment`. Additional information about experimental design

262   and analysis can be found in Supplementary Methods.

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Author contributions

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276 J.C. conceived, designed and performed the experiments, field surveys and analysis; C-H.W, R.W,

277 A.H and P.V. supervised the development of this work, aided in data collection and provided sta-

278 tistical advice. All authors contributed to the writing of this manuscript.

Competing financial interests

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280 The authors declare that they have no competing financial interests.

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398 **Figures**
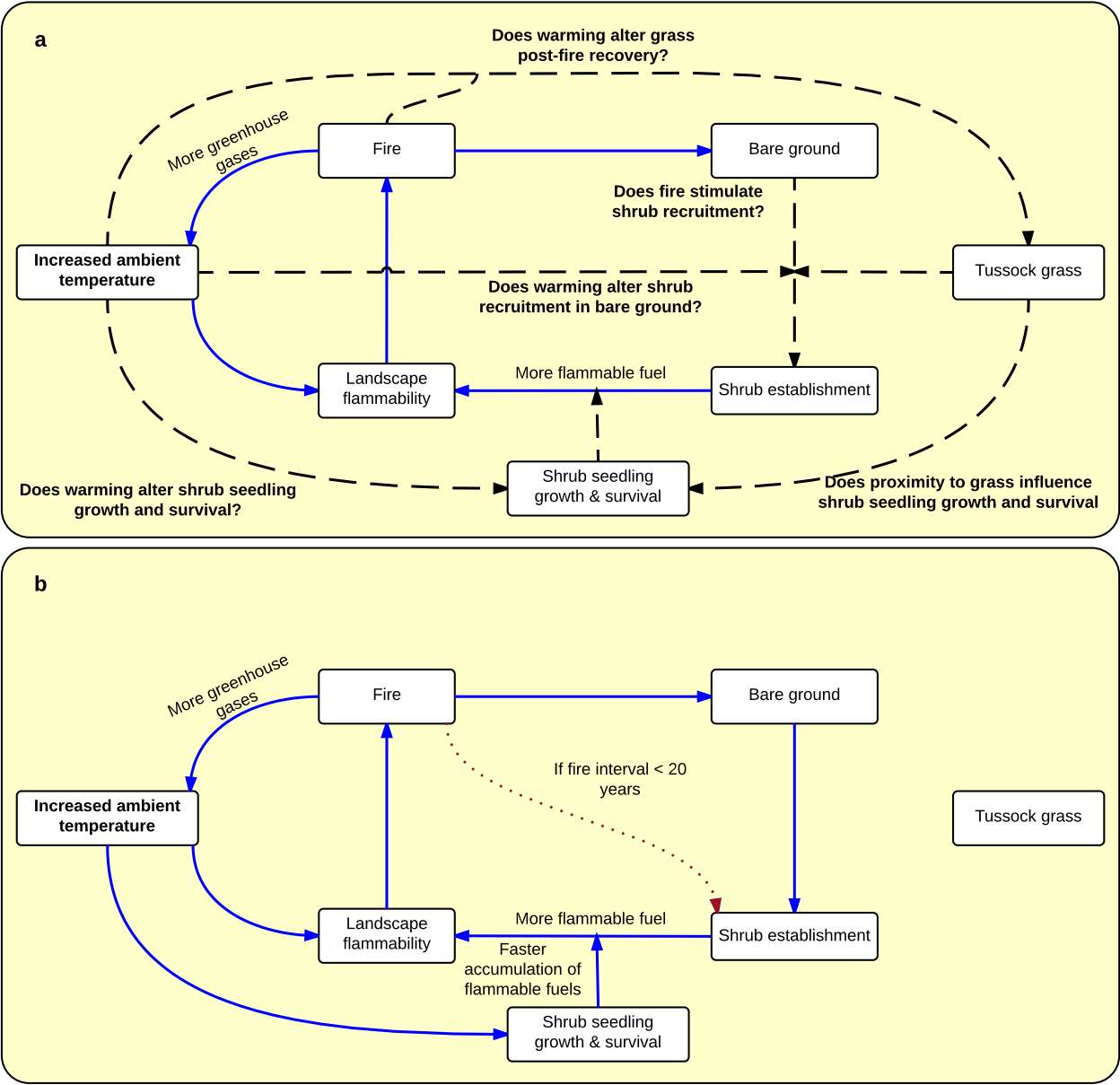
Figure 1   Conceptual diagram illustrating positive warming-shrub-fire feedback loop. (**a**) Hypothesised positive feedback loop between fire, climatic warming and landscape flammability. Solid blue lines = known mechansims; Dashed black lines = mechansims that may exacerbate or diminish this feedback loop but which we have a paucity of information on. (**b**) Feedback loop based on new evidence obtained from experimental and field surveys conducted in this study. Also includes an example of a potential, but unlikely, effect (red dotted line) that could break this feedback.

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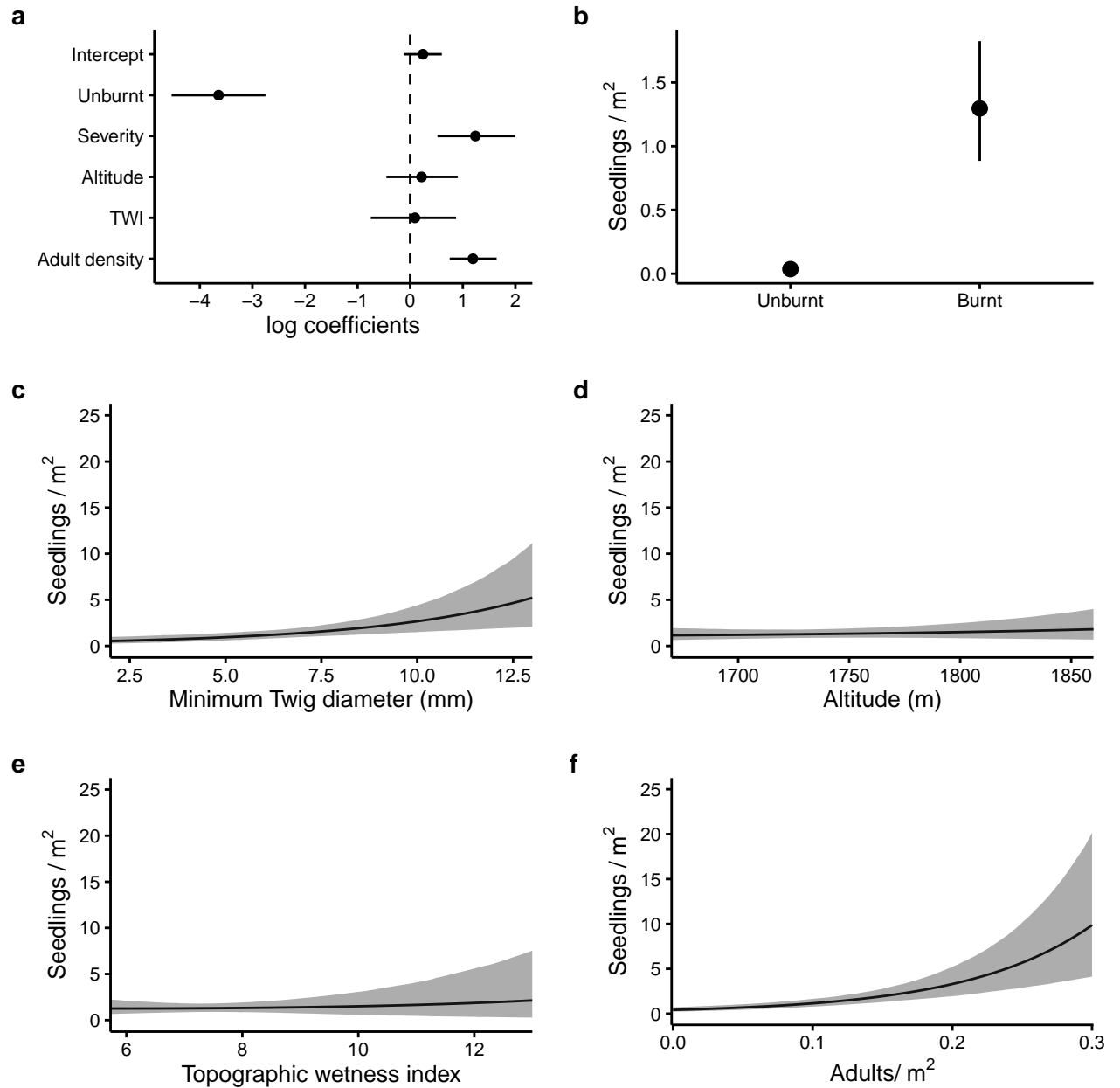
Figure 2   Mean *Grevillea australis* seedling density along gradients of burning, fire severity (twig diameter), altitude, Topographic Wetness Index (TWI) and adult density. (**a**) Centered and standardized model coefficients (on the log scale); and effects of: (**b**) burning, (**c**) fire severity, (**d**) altitude, (**e**) topographic wetness and (**f**) adult density, in areas burnt by the 2003 fires. All bars and shaded areas indicate 95% Bayesian Credible Intervals.
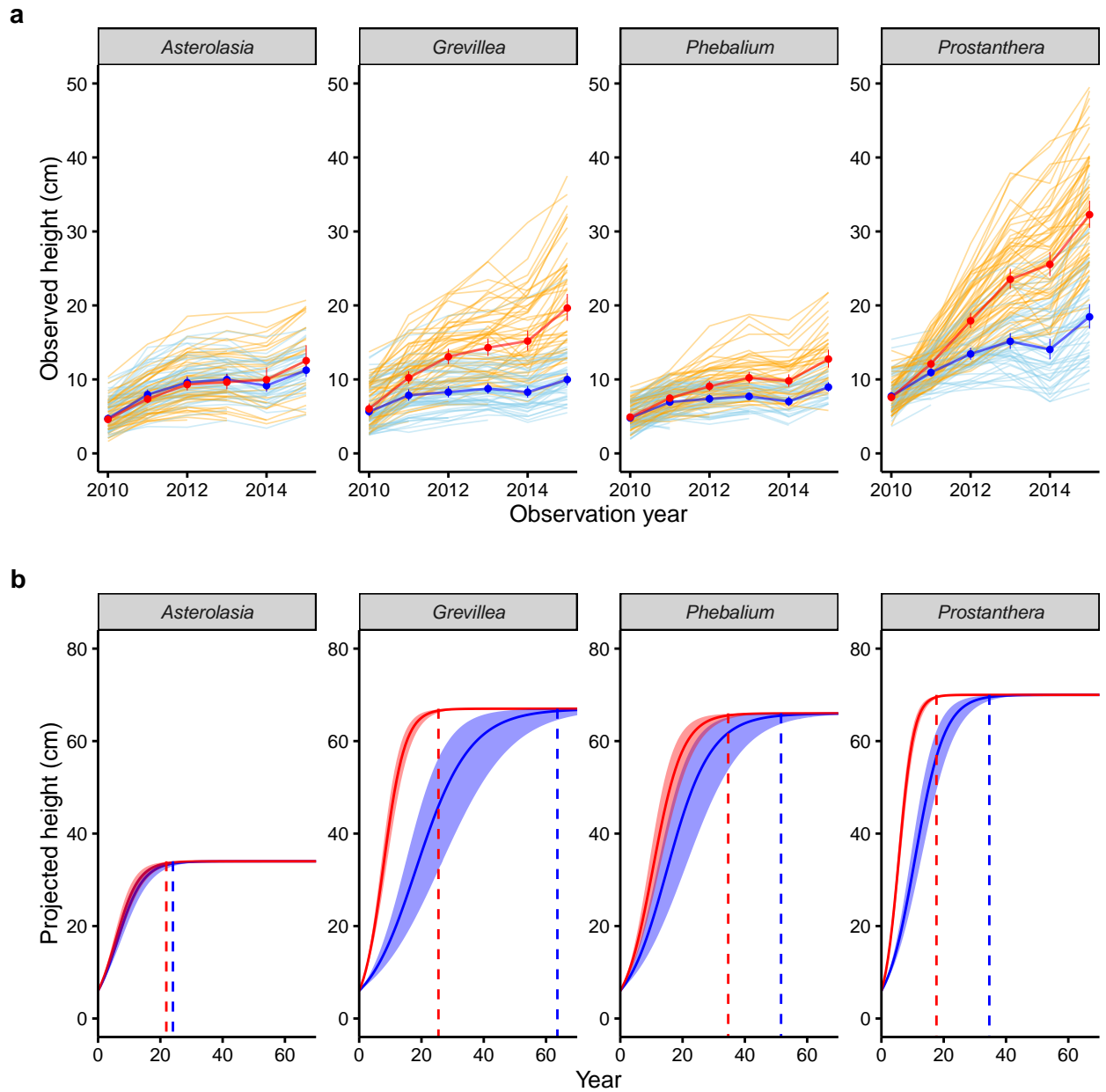
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Figure 3 Observed and projected growth trajectories of four dominant Australian alpine shrubs. (**a**) Observed height growth: Thick lines with error bars represent mean (± 95% confidence intervals) observed heights at each May census. Thin lines represent individual growth trajectories. (**b**) Mean (± 95% Bayesian Credible Interval) projected growth trajectories. In all cases, red and orange lines = seedlings growing in warmed (OTC) conditions and blue and light blue lines = seedlings growing in control conditions. Projections were based on an logistic growth model using initial seedling size of 6 cm (the mean initial height observed in the OTC experiment) and mean maximum heights observed in long-unburnt sites (i.e. 34, 67, 66 & 70 cm for *Asterolasia*, *Grevillea*, *Phebalium*, & *Prostanthera*, respectively).
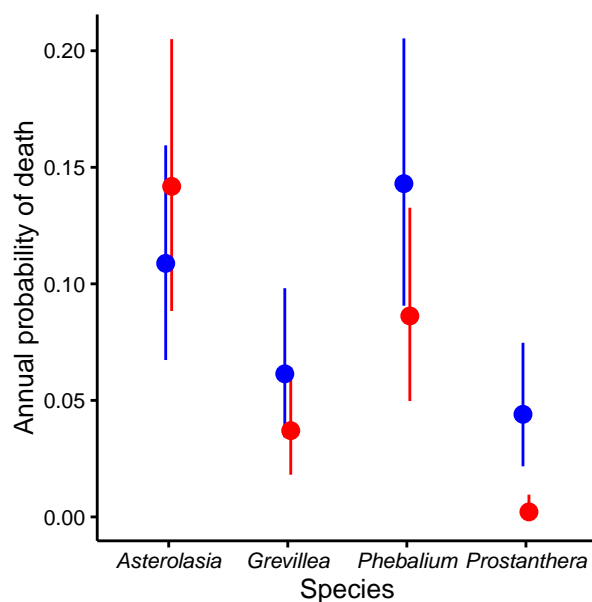
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Figure 4   Mean ($\pm$ 95% Bayesian Credible Interval) annual probability of death for each species growing in control (blue) and warmed (red) conditions.
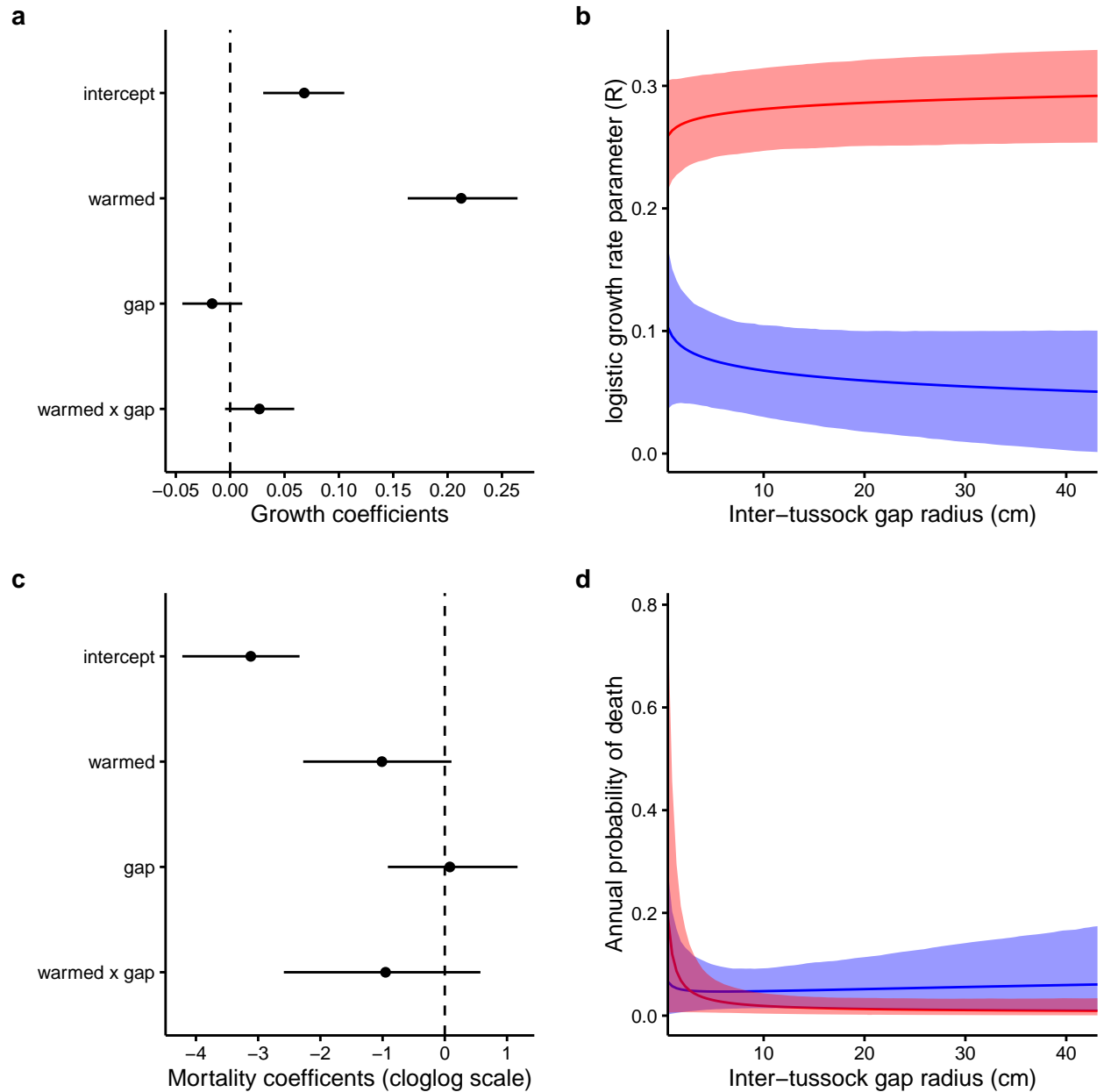
Figure 5 **Experimental warming and inter-tussock gap size effects on *Grevillea australis* seedlings.** Top rows = Growth rate effects, Second row = Mortality effects. (**a** & **c**) Centered and standardized model coefficients; (**b** & **d**) growth and mortality rate response curves along an inter-tussock gap size gradient in warmed (red) and control (blue) conditions. All error bars and shading are 95% Bayesian Credible Intervals.
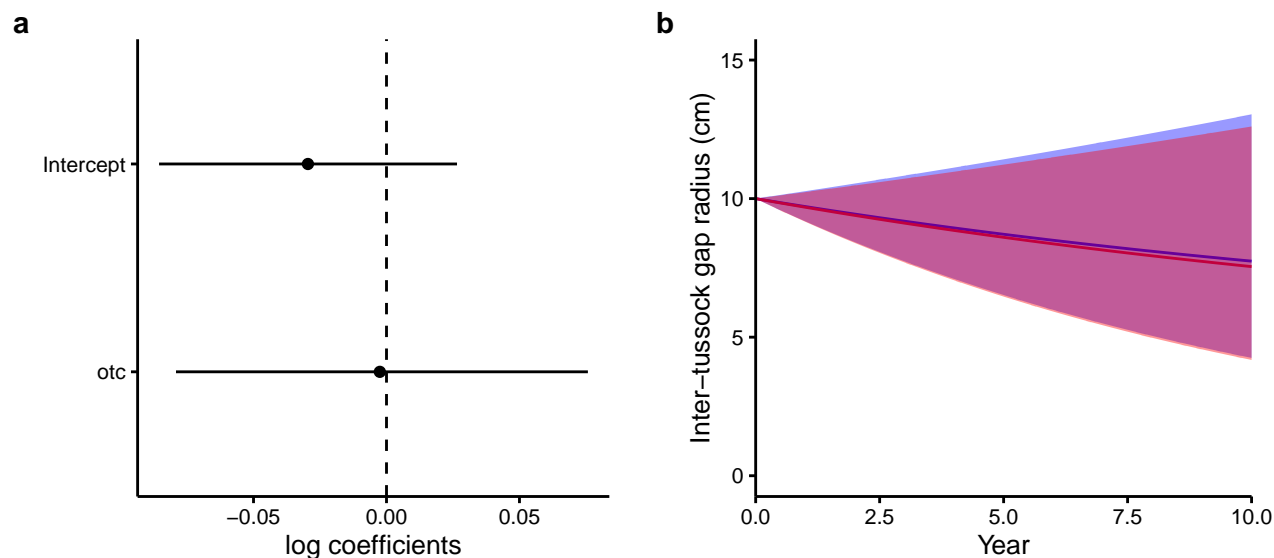
Figure 6   Effects of warming on rates of gap infilling by tussock grass. (**a**) Model coefficients and (**b**) projected temporal change in size for an average 10 cm inter-tussock gap in warmed (red) and unwarmed (blue) conditions. All error bars and shading are 95% Bayesian Credible Intervals.