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**Article:**

Joshi, AA, Ratnam, J and Sankaran, M [orcid.org/0000-0002-1661-6542](https://orcid.org/0000-0002-1661-6542) (2020) Frost maintains forests and grasslands as alternate states in a montane tropical forest–grassland mosaic; but alien tree invasion and warming can disrupt this balance. *Journal of Ecology*, 108 (1). pp. 122-132. ISSN 0022-0477

<https://doi.org/10.1111/1365-2745.13239>

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# Journal of Ecology

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Article type : Research Article

**Handling Editor: Natalia Norden**

**Frost maintains forests and grasslands as alternate states in a montane tropical forest-grassland mosaic; but alien tree invasion and warming can disrupt this balance**

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2745.13239

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**Abstract**

1. Forest-grassland mosaics, with abrupt boundaries between the two vegetation types, occur across the globe. Fire and herbivory are widely considered primary drivers that maintain these mosaics by limiting tree establishment in grasslands, while edaphic factors and frosts are generally considered to be secondary factors that reinforce these effects. However, the relative importance of these drivers likely varies across systems. In particular, although frost is known to occur in many montane tropical mosaics, experimental evidence for its role as a driving factor is limited.

2. We used replicated in-situ transplant and warming experiments to examine the role of microclimate (frost and freezing temperatures) and soil in influencing germination and seedling survival of both native forest trees and alien invasive Acacia trees in grasslands of a tropical montane forest-grassland mosaic in the Western Ghats of southern India.

3. Seed germination of both native and alien tree species was higher in grasslands regardless of soil type, indicating that germination was not the limiting stage to tree establishment. However, irrespective of soil type, native seedlings in grasslands incurred high mortality following winter frosts and freezing temperatures relative to native seedlings in adjoining for-

ests where freezing temperatures did not occur. Seedling survival through the tropical winter was thus a primary limitation to native tree establishment in grasslands. In contrast, alien *Acacia* seedlings in grasslands incurred much lower levels of winter mortality. Experimental night-time warming in grasslands significantly enhanced over-winter survival of all tree seedlings, but increases were much greater for alien *Acacia* than for native tree seedlings.

4. Synthesis: Our results provide evidence for a primary role for frost and freezing temperatures in limiting tree establishment in grasslands of this tropical montane forest-grassland mosaic. Future increases in temperature are likely to release trees from this limitation and favour tree expansion into grasslands, with rates of expansion of non-native *Acacia* likely to be much greater than that of native trees. We suggest that studies of frost limitation to plant establishment are needed across a range of tropical ecosystems to re-evaluate the general importance of frost as a driver of vegetation transitions in the tropics.

**Keywords:** *Acacia*, abrupt transition, climate change, determinants of vegetation structure, shola-grasslands, Nilgiris, Western Ghats

## **Introduction**

Mosaics of forest and grassland patches, with abrupt transitions between the two, are a recurrent feature of vegetation across the globe (Bond & Parr, 2010; Parr, Lehmann, Bond, Hoffmann, & Anderson, 2014). Such mosaics are found in regions characterized by contrasting climatic and edaphic conditions ranging from the Afromontane forest-grassland mosaics of Malawi and Madagascar, the Shola-grassland mosaics of the Western Ghats in India, the Patanas in Sri Lanka and the South Brazilian Campos, to the grassy balds of Australia and

South Appalachia in North America ( Bond, Silander, Ranaivonasy, & Ratsirarson, 2008; Delcourt & Delcourt, 1997; Meadows & Linder, 1993; Moravek, Luly, Grindrod, & Fairfax, 2013; Overbeck et al., 2007; Pemadasa, 1990; Pemadasa & Amarsinghe, 1982; Thomas & Palmer, 2007; Webb, 1964). The existence of these forest-grassland mosaics has been long debated (Bond et al., 2008; Meadows & Linder, 1993; Moravek et al., 2013; Overbeck et al., 2007; Thomas & Palmer, 2007; Weigl & Knowles, 2014) as their occurrence contradicts the conventional ‘one climate-one biome’ view of a single climax vegetation community for a given climate (Bond, 2005; Clements, 1936; Moncrieff, Bond, & Higgins, 2016; Staver, Archibald & Levin, 2011a). Interestingly, most of these mosaics occur under climates where global biome distribution models predict the existence of forests and not grasslands (Bond, 2008; Bond, Woodward, & Midgley, 2005; Olson et al., 2001; Whittaker, 1975). Why, then, are trees unable to establish in these grasslands?

Ecologists have invoked a range of different explanations for the absence of trees in the grasslands of these mosaics. A historical view has been that these grasslands are anthropogenic in origin, having arisen as a result of human clearing of forests, resulting in the mosaics observed today (Bond & Parr, 2010; Joshi, Sankaran & Ratnam, 2018; Thomas & Palmer, 2007). However, paleo-ecological evidence and the levels of endemism in these grasslands indicate that many of these mosaics are in fact ancient ecosystems that pre-date human presence and so are unlikely to be anthropogenic in origin (Bond et al., 2008; Dumig, Schad, Rumpel, Dignac, & Kogel-Knabner, 2008; Karunakaran, Uniyal, & Rawat, 1998; Meadows & Linder, 1993; Overbeck et al., 2007; Parr et al., 2014; Pemadasa & Amarasinghe, 1982; Premathilake, 2012; Sukumar, Ramesh, Pant, & Rajagopalan, 1993). An alternate mechanism frequently invoked to explain the maintenance of mosaics of closed forests and open grassy vegetation is fire (Bond et al., 2005; Bond & Parr, 2010; Hirota, Holmgren, Van Nes, &

Scheffer, 2011; Staver et al. 2011a; Staver, Archibald & Levin, 2011b). Fires are a common occurrence in grasslands, but rarely spread into forests. By killing tree seedlings and promoting grasses, fires can generate a feedback loop that limits tree seedling establishment only to forest patches and not grasslands, thereby reinforcing boundaries between these vegetation types (Blanco et al., 2014; Bond, 2008 ; Bond & Parr, 2010; Bor, 1938; Delcourt & Delcourt, 1997; Fairfax et al, 2009; Fensham & Fairfax, 1996; Meadows & Linder, 1993; Overbeck et al., 2007; Parr et al., 2014; Phipps & Goodier, 1962; Weigl & Knowles, 2014). However, the notion that ‘natural’ self-sustaining fire regimes of sufficient magnitude and frequency to maintain open grasslands can emerge in the absence of any human intervention remains debated (Veenendaal et al., 2018).

Besides humans and fires, frost has also been previously invoked as a potential factor maintaining forest-grassland mosaics (Meher-Homji, 1965, 1967; Ranganathan, 1938). Tropical woody species do not tolerate freezing, and are often killed at temperatures below  $-1^{\circ}\text{C}$  (Sakai & Larcher, 1987). Because the occurrence and impacts of frost are typically greatest in open grassy areas compared to closed-canopy forest patches, frost can act to reinforce existing spatial patterns of tree cover and contribute to the maintenance of forest-grassland or forest-savanna mosaics in landscapes (Devaney, Lehmann, Feller, & Parker, 2017; Hoffmann et al., 2018). Although recent evidence suggests that occasional frosts can reinforce demographic bottlenecks to tree seedling establishment imposed by other drivers such as fire and herbivory (Hoffmann et al. 2018; Holdo, 2006; Wakeling, Cramer, & Bond, 2012), whether and when frosts by themselves can maintain forest-grassland mosaics remains unclear. Frost was first suggested as a potential mechanism maintaining forest-grassland mosaics nearly 80 years ago (Ranganathan, 1938), but to date, there have been no experimental tests of the same that we are aware of.

In addition to frost, it has also been argued that edaphic factors may be important drivers in maintaining forest-grassland mosaics, with grasslands expected to occur on shallow soils with low nutrient levels and low water holding capacity (Fensham & Fairfax, 1996; Jose, Sreepathy, Kumar, & Venugopal, 1994; Meadows & Linder, 1993; Overbeck et al., 2007). There is evidence to suggest that soil nutrients (organic C, total N and P), soil moisture content and soil pH tend to be higher in forest patches compared to adjacent grasslands or savannas (Dantas, Batalha, & Pausas, 2013; Jose et al., 1994; Jose, Gillespie, George, & Kuma, 1996; Raghurama, 2013), but such differences are likely to both result from, and drive, differences in forest and grassland vegetation states. At present, the extent to which edaphic factors act as drivers of the occurrence and maintenance of forest-grassland mosaics remains unclear.

Here, we experimentally examined the role of micro-climate and soils in regulating the establishment of native trees in grasslands of a tropical montane forest-grassland mosaic in the Western Ghats biodiversity hotspot in India. Locally known as shola-grasslands, multiple explanations have historically been invoked for the absence of native trees from the grasslands of these mosaics. Early observers suggested limitation of trees by frosts which were observed to occur in the grasslands (Meher-Homji, 1965, 1967; Ranganathan, 1938). Likewise, fire (Bor, 1938; Chandrasekharan, 1962; Gupta, 1960 a,b; Noble, 1967) and mammalian herbivory (Bor, 1938), both of which were associated with the grassland state, were implicated in the maintenance of the mosaic. Potential differences in soil properties were also invoked (Ranganathan, 1938), with more recent work documenting greater soil organic C, total C, total N, available P and soil moisture in sholas relative to grasslands (Jose et al., 1994, Raghurama, 2013). At the current time, these mosaics are severely threatened by the invasion of alien plant species (Arasumani et al., 2019; Thomas and Palmer, 2007; Srinivasan, 2012),

particularly a non-native plantation tree, *Acacia mearnsii*, into the grasslands. Planted for forestry purposes since the early nineteenth century in this landscape (Joshi et al., 2018), these trees are able to establish and survive in grasslands, in contrast to native shola tree species. Specifically, we asked the question: What factors maintain this landscape mosaic where native tree species are unable to establish in adjoining grasslands but an alien invasive tree species is able to do so?

### **Study site**

The study was carried out in the upper plateau (11.2 - 11.4° N and 76.4 - 76.6°E) of the Nilgiri Biosphere Reserve, Tamil Nadu, which is a part of the Western Ghats biodiversity hot-spot in southern India (Fig. 1; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Elevation at the site ranges from 2000 to 2500 m a.s.l. Annual rainfall in the area ranges from 2500-5600 mm (Caner, Seen, Gunnell, Ramesh, & Bourgeon, 2007; Zarri, Rahmani, Singh, & Kushwaha, 2008), the bulk of which falls during the Asian southwest monsoon, between April and September. Mean annual temperature is around 15°C (Range: -2.1 to 29°C; IMD:1969-2005), and frosts are common occurrences in the tropical winter (~15 frost nights with night-time temperatures dropping as low as -4°C in January were observed during the winter in our study).

Soils of the study area are derived from parent rocks which are gneiss, charnockites and schists (Sukumar et al., 1993). Top soils of both shola forests and grasslands vary in colour from pale brown to black. Shola soils have higher total carbon and nitrogen content than grasslands (Raghurama, 2013). Grassland soils are less moist, more compact (Mean bulk

density: Grassland = 0.71g/cm<sup>3</sup>, Shola forest = 0.54g/cm<sup>3</sup>) and slightly lower in their clay content than shola soils (Mean clay content: Grassland = 10.76%, Shola forests = 13.53%; see Table S1 for detailed description of soil properties).

The natural vegetation of the area is a two-phase mosaic comprising patches of stunted tropical evergreen forests, locally referred to as ‘sholas’, embedded in a grassland mosaic. Large-scale planting of alien trees including *A. mearnsii*, *Eucalyptus* spp. and *Pinus* spp. in grasslands during the last century has, however, resulted in large sections of grassland being converted to exotic tree plantations (Joshi et al., 2018). Importantly, of these planted species, *A. mearnsii* has since invaded large tracts of native unplanted grassland.

## **Methods**

Between June 2013 and February 2015, we conducted a series of experiments to investigate how soil, habitat type and micro-climatic differences, specifically temperature, influenced the germination success and seedling survival of native shola tree species as well as the invasive *A. mearnsii* in both grassland and forest patches at our study site.

### **GERMINATION EXPERIMENT**

Between June and August 2013, we carried out a 2×2 factorial experiment involving two habitat treatments (forest patches vs. grassland) and two soil treatments (forest soil vs. grassland soil) to investigate the effects of soil properties and differences in micro-climate between grassland and forest patches on the germination success of a native tree species *Syzygium grande* as well as the alien invasive *A. mearnsii*. We timed our experiment to coincide with

the typical germination period of trees in this system (i.e. during the southwest monsoon from June to August in 2013). Seeds of native *S.grande* as well as the invasive *A. mearnsii* were collected from adjoining sites during the first week of June 2013. Although we would have ideally liked to include more native tree species in this experiment, shola trees display high inter-annual variability in seed production (AA Joshi, personal observation; D Mudappa, personal communication), and we were unable to get sufficient seeds from other species during 2013 to include in our experiment.

We selected 14 replicate forest patches and paired adjacent grassland sites for our experiment. Forest patches were matched for size (~0.4ha) and aspect. At each site, we placed two trays – one filled with soils collected from the grassland and the other with soils collected from within shola forest patches – both inside the forest patch and in the adjacent open grassland. Each tray contained 25 mature seeds of each of the two focal plant species. Seed locations were marked with labels on germination trays for ease of identification during monitoring and all trays covered with a wire mesh to prevent seed predation. Seed germination was monitored weekly for a total of 90 days.

The roles of microclimate and soil on seed germination were analyzed using a mixed effect model with binomial errors and a logit link function in the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2014; R Core Team, 2016). Microclimate and soil were treated as fixed effects and site was included as a random effect. P-values were obtained by likelihood ratio tests of the model with the effect in question against the model without the effect in question.

## SEEDLING SURVIVAL EXPERIMENT

In the next experiment, we evaluated how soil and micro-climatic differences between shola forest and grassland patches influenced subsequent seedling survival of both native and alien tree species. We transplanted seedlings of both native *S.grande* and *A. mearnsii* that had germinated in the previous experiment into six litre black polythene nursery bags containing the same soil medium as their germination trays i.e. either forest or grassland soil. We chose two replicate shola-forest and paired adjacent grassland sites for this experiment. At each site, ten seedlings of each species were transplanted into nursery bags containing either forest or grassland soil media, and placed in grasslands as well as in the adjoining forest patches.

Seedlings of both focal species at one of the sites in grassland were destroyed by elephants (*Elephus maximus*) during the first week of the monitoring period. After reallocation of seedlings, this site had only five seedlings per soil type per microclimate for the rest of the monitoring period. There were no fires at the sites, nor were any signs of mammalian herbivory recorded on seedlings during the monitoring period. Our final sample sizes included 30 seedlings per species per treatment. Seedling survival was monitored every 15 days for eight months, from October 2013 to June 2014, of which October to January were the coldest months.

Kaplan-Meier survival functions were computed to analyze seedling survival over time using the survival package in R. The survival distributions of two focal groups were compared using non-parametric logrank test – a method used to compare survival distributions when data are right skewed and censored (Therneau, 2015).

## FREEZING TEMPERATURE – SEEDLING SURVIVAL EXPERIMENT

During 2014-15, we also carried out an additional manipulative experiment to investigate if freezing temperatures limit the establishment of tree species in these grasslands. Seedlings of five common native tree species – *Cinnamomum wightii*, *Glochidion neilgherrense*, *Syzygium calophyllifolium*, *Syzygium densiflorum* and *S. grande* - and the alien invasive *A. mearnsii* were used for the study. These five species (out of 57 native shola tree species) account for ~20% of tree abundance in sholas across the study area (Mohandass & Davidar, 2009).

Seeds of all species were collected from the field prior to the experiment between (15 May and 30 June), germinated in a greenhouse, and transported to one of the protected shola forests in the field when three to four months old. Transportation was done overnight in a semi-closed vehicle to avoid seedlings becoming heat stressed. Seven days after transportation to the field, seedlings were transplanted into six litre nursery bags at the same site and allowed to acclimatize to the field environment for a month.

We used in-situ experimental night-time warming treatments to examine the role of low temperatures in limiting the establishment of tree seedlings in grasslands. Three replicate grassland blocks, each 10 m × 20 m in size, and separated from one other by at least 100 m, were identified and fenced off. One block was located at the valley bottom, the second at mid-slope, and the third on the hill crest. Within each fenced block, we demarcated eight replicate plots (1.5 m×3 m), four of which were randomly assigned the experimental warming treatment and four of which served as control plots. In each plot, nursery bags containing seedlings of both native tree species and *A. Mearnsii* were placed in 30cm deep pits to ensure that the soil surface in seedling bags matched the ground level. Because of differences in germination success, our final sample sizes differed between species. Each replicate plot, both warmed and control, contained seven *C. wightii*, six *S. calophyllifolium*, four *S. densiflorum*

and seven *A. mearnsii* seedlings. Because of low seedling numbers for *S. grande* and *G. neilgherrense*, we were only able to have four seedlings of each species in two and seven replicate plots of both control and experimental warming treatments, respectively. Experimental night-time warming was achieved through the use of thermal blankets (Coleman Emergency Blanket, 53×32 inch) that were pasted on plastic sheets and placed on scaffolds to cover experiment plots between 5 pm in the evening and 8 am the next morning. However, the seedlings were not covered on two nights during the course of the study: once because of logistical reasons and the second time due to high winds that blew away the blankets. Seedling survival and soil moisture in seedling bags in control and experimentally warmed plots were monitored every alternate day and weekly respectively, during the peak of winter, from 3 December 2014 to 2 February 2015.

Temperature data loggers (DS 1921G-F5 thermochrons, Homechip Ltd.) were deployed to record temperature every 30 minutes in both control and experimental warming plots. In addition, we also measured temperatures in the interior of forest patches, at the forest-grassland edges, and in the open grasslands to quantify natural variation in temperatures across the mosaic.

Kaplan-Meier survival analysis and log rank tests were used for statistical analyses as described in the previous section. All statistical analyses were performed using R statistical computing software (R Core Team, 2016).

## Results

### ROLE OF MICROCLIMATE AND SOIL IN SEED GERMINATION

Contrary to our expectations, germination success of both native *S. grande* and the alien *A. mearnsii* was higher in grasslands when compared to adjoining forest patches (Fig 2a; *S. grande*:  $\chi^2 = 44.642$ ,  $df = 1$ ,  $P < 0.001$ ; *A. mearnsii*:  $\chi^2 = 45.611$ ,  $df = 1$ ,  $P < 0.001$ ). Soil type had no effect on germination success of either species in both grassland and forest habitats (Fig 2b, *S. grande*:  $\chi^2 = 0.32$ ,  $df = 1$ ,  $P = 0.57$ ; *A. mearnsii*:  $\chi^2 = 0.13$ ,  $df = 1$ ,  $P = 0.72$ ). Overall, germination success of *A. mearnsii* was almost three times higher than the native *S. grande*, irrespective of microclimate and soil type (Mean germination: *A. mearnsii* = 13.8% (SE = 1.3), *S. grande* = 4.8% (SE = 0.6)).

### ROLE OF MICROCLIMATE AND SOIL IN SEEDLING SURVIVAL

Over-winter survival of native *S. grande* seedlings in grasslands was extremely low, and nearly all seedlings (89%) were dead by the end of the winter (Fig. 3a). Survival of *S. grande* seedlings within forest patches, on the other hand, was much higher, with nearly 77% of seedlings surviving the winter (Fig. 3a; logrank test:  $P < 0.001$ ). Soil type did not have any effect on survival of *S. grande* in either grasslands or forest patches ( $P = 0.93$ ). In contrast, *A. mearnsii* seedling survival did not differ appreciably between the micro-climates as well as between the soil types (Fig. 3b; microclimate:  $P = 0.236$ , soil:  $P = 0.766$ ).

Overall, *A. mearnsii* seedling survival (50%) was much higher than that of native *S. grande* seedlings in grasslands ( $P < 0.001$ ) as well as in both soil types (grassland soil:  $P = 0.027$ ; shola soil:  $P = 0.039$ ). However, survival within forest patches did not differ between species ( $P = 0.25$ ).

## ROLE OF FREEZING TEMPERATURES IN TREE SEEDLING SURVIVAL IN GRASSLANDS

Night-time temperatures in the experimental warming treatments were approximately 3 to 4°C higher than that of adjacent control plots during the experiment (Mean night-time temperature: Control: 8.1°C, Warming: 11.7°C; Range: Control: -4.5 to 24.5°C, Warming: -2.5 to 24.5°C). In control plots, we noted the occurrence of frost on 15 mornings when temperatures during the previous night had dropped below 0°C (Fig.4a), whereas we observed frost in experimental warming plots only on the two nights when the thermal blankets were not in place (see Methods). In contrast, winter temperatures within forest patches did not fall below freezing, with mean night-time temperatures averaging 9.8°C (range: 5.6 to 14.1°C) across the duration of the experiment. Over the course of the study, temperatures within forests and at forest edges never dropped below 0°C, whereas temperatures below zero were recorded on six nights in adjacent grasslands (Fig. 4b).

### Seedling survival in control and experimental warming treatments

Survival of both native species and *Acacia* was significantly higher in experimentally warmed plots than in control plots (Fig. 5a & b,  $P < 0.001$ ; see supplementary Fig. S1 for responses of each native species individually). In both warmed and control plots, the alien invasive *A. mearnsii* had significantly higher survival rates than native species (Fig. 5a & b; both control & experimental warming:  $P < 0.001$ ).

Although seedling survival of both native species and *A.mearnsii* was higher in warmed relative to control plots across all site locations, seedling survival in control plots was higher at hill-top compared to mid-slope and foot-slope locations ( $P < 0.001$ ; supplementary Fig. S2), consistent with lower frequencies of frost nights and higher minimum temperatures experienced at hill-top sites (supplementary Table S1).

## **Discussion**

Our results demonstrate that frosts and freezing night-time temperatures that occur during the winter kill native tree seedlings in grasslands, and thereby maintain this tropical montane forest-grassland mosaic system. Further, our results suggest that seedling establishment rather than seed germination is likely the primary demographic bottleneck to native tree establishment in these grasslands. Although earlier studies have suggested a role for edaphic differences in maintaining these forest-grassland mosaics (Jose et al., 1994), we found no evidence for this, with germination and seedling survival of native species being comparable across grassland and forest soils within each micro-climate. Although we do not have comprehensive data on soil properties, which limits our inferences, these results suggest that differences in soil texture, bulk density, organic matter content and nutrient availability between forest and grassland patches (Table S1; Jose et al., 1994; Raghurama, 2013) are more likely to be a consequence of differences in aboveground vegetation characteristics between these two habitat types, rather than the underlying driver maintaining forest-grassland mosaics in this system.

In contrast to native seedlings, the higher germination rates and greater tolerance of non-native *A. mearnsii* seedlings to frosts and freezing temperatures underlie the ongoing widespread invasion by this species into the grasslands. Experimentally elevated night-time temperatures enhanced seedling survival of both native tree and alien *A. mearnsii* seedlings, suggesting that climate warming will promote both shola expansion and increased exotic invasion into the grasslands. However, the increase in survival with warming is much greater for *A. mearnsii* relative to native seedlings, and combined with the greater fecundity of this species, suggests that climate warming will disproportionately accelerate grassland invasion by *A. mearnsii*.

The high germination rate of *Syzygium grande*, a dominant native shola species, in grasslands establishes that germination was not the limiting stage for the establishment of this native species in grasslands. We were constrained to this species by lack of fruiting of other species in the year the experiment was conducted. Many shola tree species fruit supra-annually such that only a few species may produce seeds in any given year (see Methods). Anecdotally, across the period of this study, we routinely observed germination and very young seedlings of various shola tree species, typically during and post-monsoon, in the grasslands, whereas we rarely saw established seedlings or saplings. These observations support the results from our experiment with *S. grande*, that germination per se may not be a primary limiting stage for native tree establishment in grasslands.

Studies across a range of tropical forest-grassland mosaics have postulated and/or demonstrated a major role for fires and herbivory in maintaining these mosaics (Bond & Keeley 2005; Bond & Parr, 2010; Bor, 1938; Dumig et al. 2008; Fairfax et al., 2009; Fensham &

Fairfax, 1996; Karunakaran et al., 1998; Meadows & Linder, 1993; Noble, 1967; Overbeck et al., 2007; Srinivasan, 2012). Fires and mammalian herbivory, both of which are frequent in grasslands, but rare in forests, impose mortality on tree seedlings in grasslands and thereby allow the grasslands to persist. In our study system however, the chronological sequence of these disturbances points to frost and freezing temperatures as the primary drivers of native tree seedling mortality in these grasslands. Germination at our site occurs during the southwest monsoon (June -September) and tree seedlings die due to frost during the winter (October-February) that follows the monsoon. Fires, if any, occur in the dry season and summer following the winter (February-May) by which time most seedlings have already perished from winter frost and freezing. Further, while frost occurs predictably during the winter months at this site, fires are both much rarer and less predictable. There were no fires in the grasslands at our study site for five years (2012-2016). Despite this, we found no established native tree seedlings in the grassland during this period, confirming that frost and freezing temperature are the primary limiting factors to native tree establishment in the grasslands of these shola-grassland mosaics.

The sharp difference in minimum temperatures across the forest-grassland edge points to a significant role for temperature regimes in the abrupt transitions between forests and grasslands in this mosaic. Closed forest patches maintain higher interior temperatures such that frosts cannot penetrate, thereby allowing frost-sensitive seedlings to persist. The sharp drop in temperature away from the forest edge results in frost occurring immediately outside the edge, preventing trees from invading the open grassland. These positive feedbacks between closed-canopy forests and warmer temperatures and open grasslands and freezing temperatures potentially maintain and reinforce the abrupt edge between forest and grassland states.

Not surprisingly, the role of frosts and low temperatures as drivers in sub-tropical and temperate forest-grassland transitions and treelines, either by themselves but also in concert with grass competition, fire and herbivory has been well documented (Ball, Hodges & Laughlin 1991; Cairns & Moen, 2004; Coop & Givnish, 2007, 2008; Moore & Williams, 1976; Wardle, 1971). In these systems which experience low and freezing temperatures regularly, trees do display some degree of cold tolerance, but tree seedling growth is nevertheless retarded by low temperatures and frost damage, which then renders them susceptible to elimination by grass competition, fire and herbivory (Coop & Givnish, 2008). In contrast, although frosts and freezing temperatures do occur in many montane and semi-arid tropical ecosystems, they have not received as much attention as drivers of ecosystem boundaries. For most tropical forest-grassland and forest-savanna mosaics, vegetation-disturbance feedbacks with fire and herbivory are widely thought to be the primary mechanisms generating and maintaining the transitions between ecosystem states (Bond, Dickinson & Mark, 2004; Bond & Parr, 2010; Dantas et al., 2013, Dantas, Hirota, Oliveira, Pausas, 2016; Hoffmann et al., 2012; Ratnam et al., 2011; Staver et al., 2011a,b). Where frost does occur, it can reinforce the limiting effects of fire and herbivory on tree establishment (Chafota & Owen-Smith, 2009; Hoffmann et al., 2018; Holdo, 2006; Wakeling et al., 2012). When rare frost events of adequate severity occur, they can reduce tree cover both by slowing tree growth such that trees remain longer within the fire trap, and because frost-damaged trees act as added fuel that intensifies subsequent fires (Hoffmann et al., 2018). In our study system, frosts were both frequent and relatively mild, but nevertheless were the primary driver of tree mortality in grasslands, suggesting that native shola tree species in this ecosystem were highly frost intolerant. This is supported by evidence that most ligneous species in native shola assemblages are derived from tropical lineages, whereas non-native species that can survive in grasslands often show temperate affinities (Meher-Homji, 1967; Sakai & Larcher, 1987). It is apparent that for trop-

ical ecosystems, the importance of frost as a driver of vegetation transitions will hinge on both the frequency and intensity of the frost regime and the frost tolerances of the local species assemblages in question. We suggest that empirical studies examining the role of low temperature and frost across a diverse range of tropical ecosystems will yield a revised and synthetic view on the relative importance of frost as a driver of alternate vegetation states in these regions.

Paleoecological studies have established that the shola-grassland mosaics of southern India are Pleistocene relics that have been in existence for more than 20,000 years (Sukumar et al., 1993; Sukumar, Suresh, & Ramesh, 1995). The relative extents of shola and grassland within these mosaics have naturally contracted and expanded with past climatic changes, with grasslands expanding during periods of lower temperature, precipitation and CO<sub>2</sub> levels (Meher-Homji, 1967; Sukumar et al., 1993, 1995). Here we add to this body of evidence, experimental data on the role of frost and low temperatures in driving the balance between forests and grasslands in this tropical forest-grassland mosaic in the present day. In this context, the introduction of non-native *A. mearnsii* into this ecosystem, a species drawn from temperate origins in south-eastern Australia and New Zealand (Courteau, 2011), has changed the balance between frost and tree recruitment in this ecosystem. With both higher seed germination potential and higher frost tolerance of its seedlings, as demonstrated in our experiments, *A. mearnsii* has successfully recruited and spread into the grasslands, with the result that the grasslands in these mosaics are today severely diminished relative to their extent in the eighteenth century (Joshi et al., 2018). A similar example of invasion by frost resistant *Pinus elliottii* in frost sensitive species assemblages has been reported from the Brazilian savannah biome (Abreu & Durigan, 2011). Furthermore, the enhanced survival of both native and alien *Acacia* tree seedlings with elevated night temperatures in our experiment suggests that the

grasslands in these mosaics will further contract with future climate warming. Unfortunately, the relatively higher survival of non-native Acacias relative to native tree seedlings at elevated temperature indicates that the ongoing Acacia invasion of grasslands will be further exacerbated as the climate warms.

### **Acknowledgements**

We thank the Tamil Nadu Forest Department for permits to carry out the work and for logistical support in the field. We are grateful to AJT Johnsingh, Arundhati Das, Kadambari Deshpande, M O Anand, Nachiket Kelkar, R. Raghunath, Ravi Bhalla, Suhel Quader, Sumanta Bagchi and Varun Varma for their help with the study design and analysis. We are grateful to the National Centre for Biological Sciences (NCBS) for funding support. We thank Aditi, Amol, Balavignesh, Chandan, Chengappa, Hari, Kavita, Manaswi, Manjunatha, Nandita, Navendu, Rutuja, Selva, Siddharth, Susilan, Vijay, Yadugiri, the FERAL field staff, and local personnel for all their help in setting up and carrying out experiments.

### **Data Availability Statement**

Data deposited in the Dryad repository: doi:10.5061/dryad.4n7n883 (Joshi, Ratnam & Sankaran, 2019)

### **Authors' contributions**

AJ, JR and MS conceived the ideas and designed methodology; AJ collected the data; AJ and MS analysed the data; AJ, JR and MS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## **Table and figure titles**

### **Main Manuscript**

Figure 1: a) The distribution of montane forest-grassland mosaics along the upper elevations of the Western Ghats, India, with the study area, the Nilgiri Plateau encircled (Reproduced with modification from Das, Nagendra, Anand & Bunyan, 2015). b) An image of an undisturbed mosaic landscape of stunted shola forests alternating with grasslands, with abrupt transitions between the two vegetation states (Credit: Prasenjeet Yadav).

Figure 2: Germination rates of a) native shola tree species *Syzygium grande* and b) alien invasive *Acacia mearnsii* in different soil types and micro-climates (N = 14 sites). Germination of both species was significantly higher in grasslands than shola forests ( $P < 0.001$ ) but did not differ between soil types ( $P > 0.05$ ). However, in all cases, germination rates of *A.mearnsii* were significantly higher than *S.grande* ( $P < 0.001$ ).

Figure 3: Kaplan Meier survival curves of a) native tree *Syzygium grande* and b) alien invasive *Acacia mearnsii* in forest and grassland micro-climates (Dotted lines denote 95% CI). *S.grande* incurred severe winter mortality in grasslands relative to forests (log rank test:  $P < 0.001$ ), and relative to *A. mearnsii* which incurred lower winter mortality in grasslands (log rank test:  $P < 0.001$ ).

Figure 4: (a) Minimum night-time temperatures in control and experimentally warmed plots during the monitoring period. Freezing temperatures occurred on as many as 15 nights in control plots, whereas experimental warming treatments only experienced freezing on 2 nights when thermal blankets were absent. (b) Minimum night-time temperatures in forest interiors, forest edges and in grasslands across the study period. Temperatures never dropped below freezing in forests and forest edges, whereas grasslands repeatedly experienced freezing temperatures in the coldest month of January.

Figure 5: Kaplan Meier survival curves of a) all native species and b) alien invasive *Acacia mearnsii* (dotted lines denote 95% CI) in control and experimentally warmed plots through the tropical winter (3 December 2015 – 2 February 2016). Experimental warming significant-

ly increased seedling survival of all native species relative to their survival in control plots, but this effect was even greater for invasive *A. mearnsii* which achieved nearly 100% survival in warmed plots. The responses of individual native species are detailed in Supplementary Figure S2.

### Supplementary Material

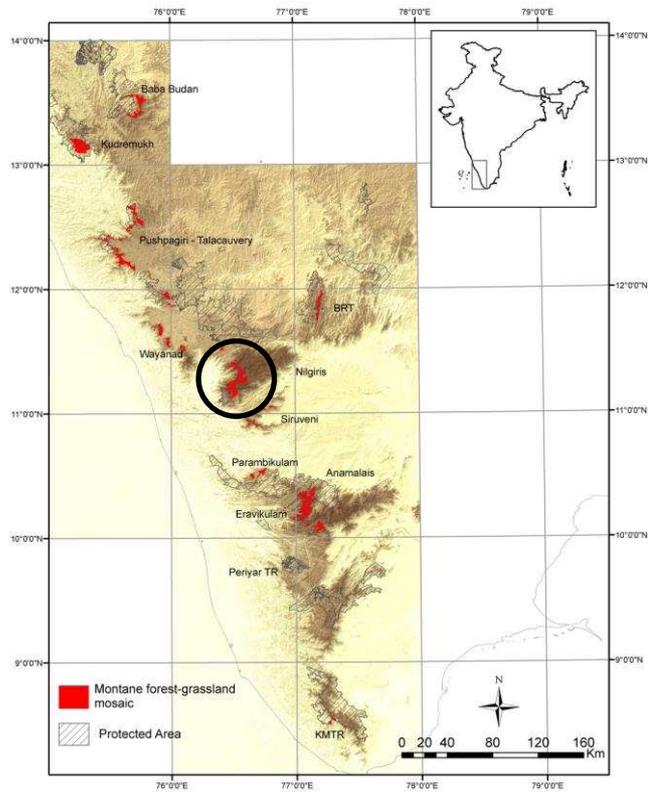
Table S1: Soil properties of grasslands and shola forests at the study site. Shola soils were more moist, had higher total C and N, were less compact and more clayey than grassland soils.

Table S2: Temperature regimes at hill-top, mid-slope and valley locations in the grassland across the duration of the warming experiment. Mean minimum temperatures were higher and the number of nights with freezing temperatures fewer at hill-top relative to mid-slope and valley locations.

Figure S1: Kaplan Meier survival curves of four native species seedlings a) *Cinnamomum wightii* b) *Glochidion neilgherrense* c) *Syzygium calophyllifolium* d) *Syzygium densiflorum* (dotted lines denote 95% CI) in control and experimentally warmed plots. Warming significantly increased seedling survival relative to control plots for all four species. A fifth native species, *S. grande*, showed the same trend but is not shown here due to the limited number of replicates.

Figure S2: Kaplan Meier survival curves of seedlings at hill-top, slope and valley locations in the a) Control and b) experimental warming treatments (dotted lines denote 95% CI).

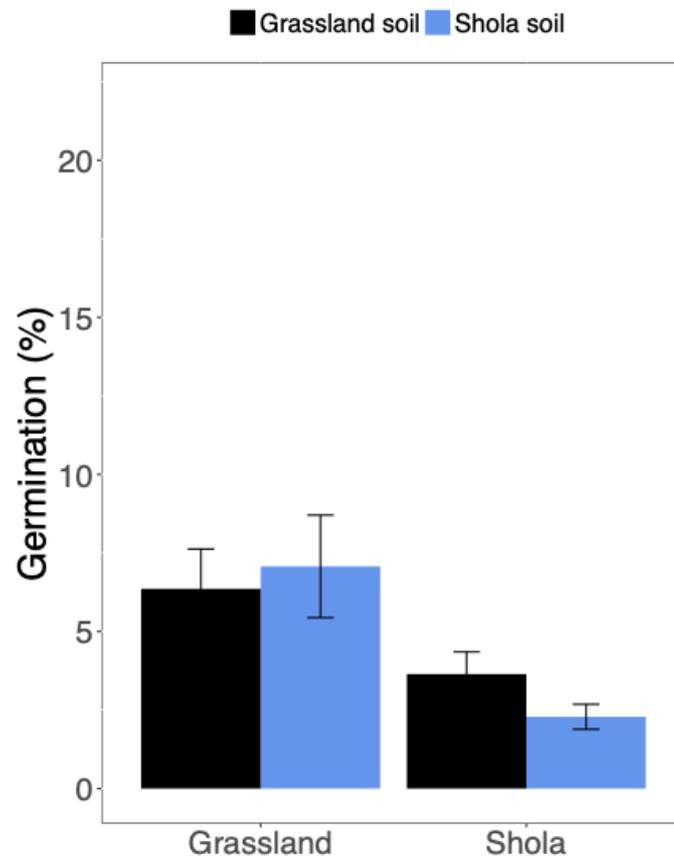
a)



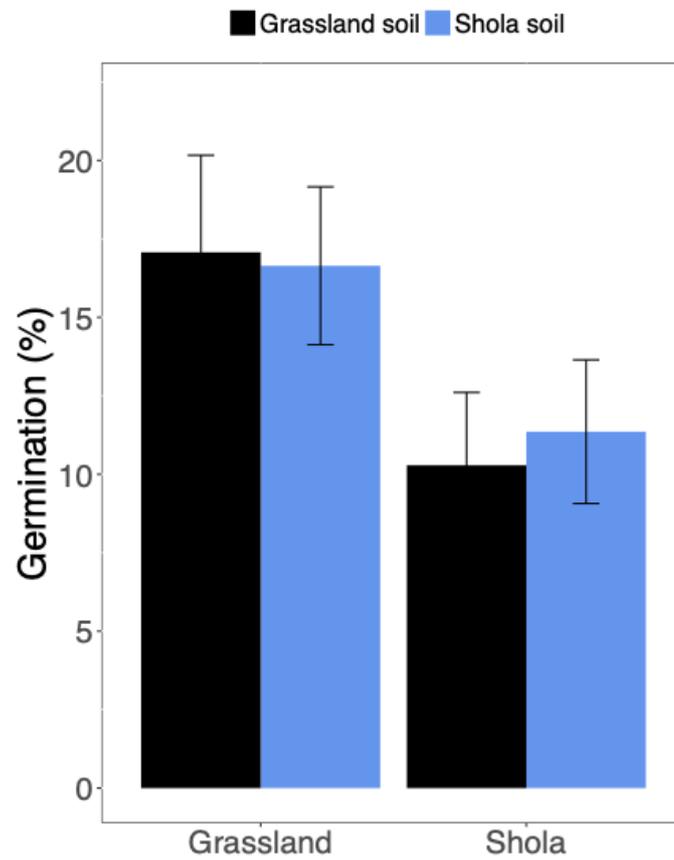
b)



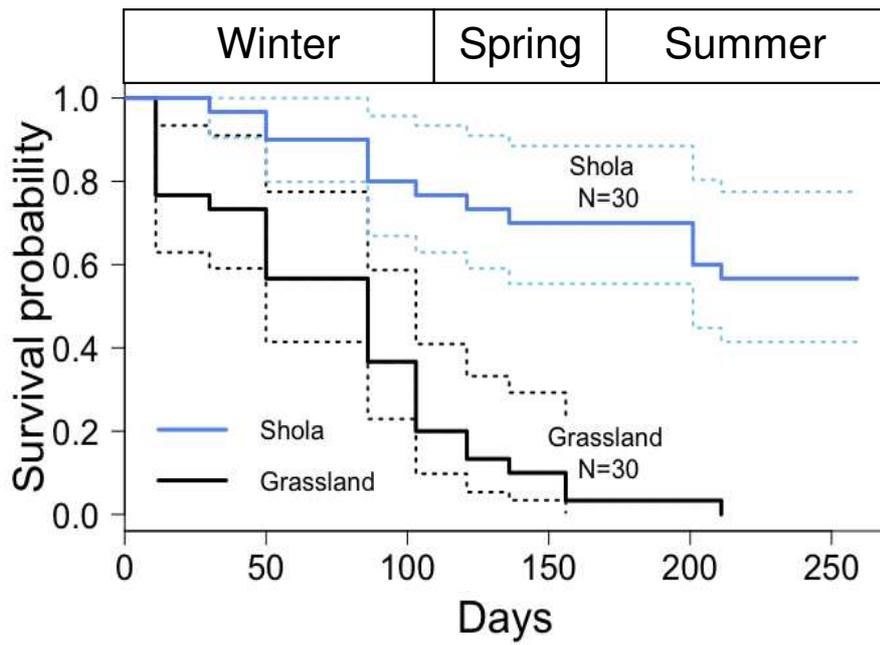
a) *Syzygium grande*



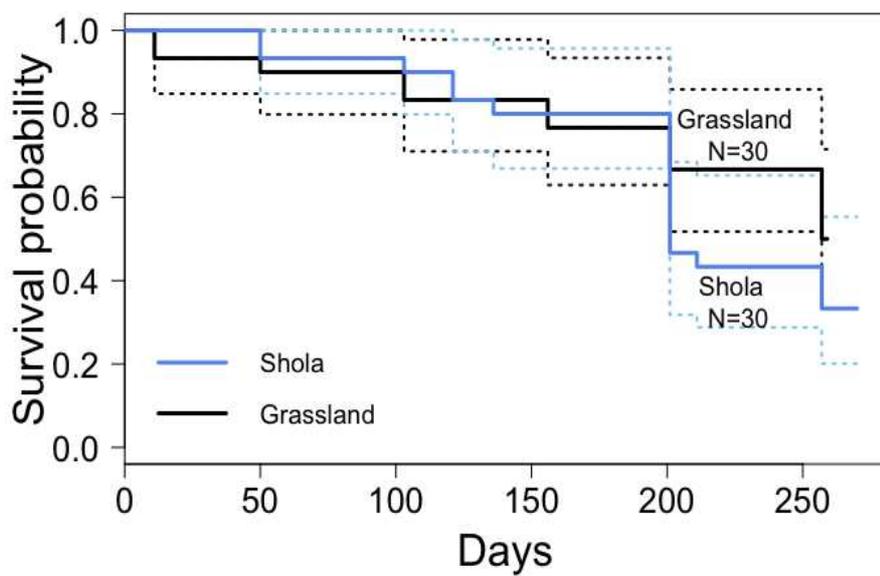
b) *Acacia mearnsii*



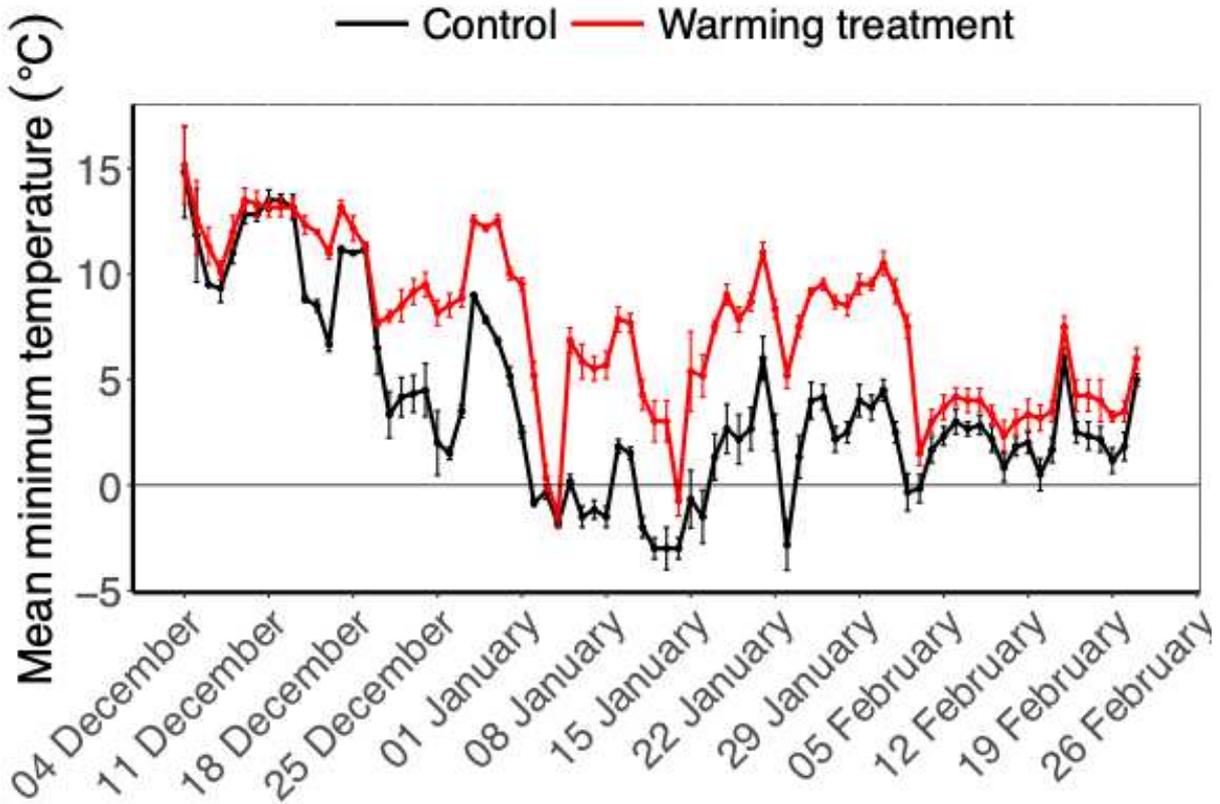
a) *Syzygium grande*



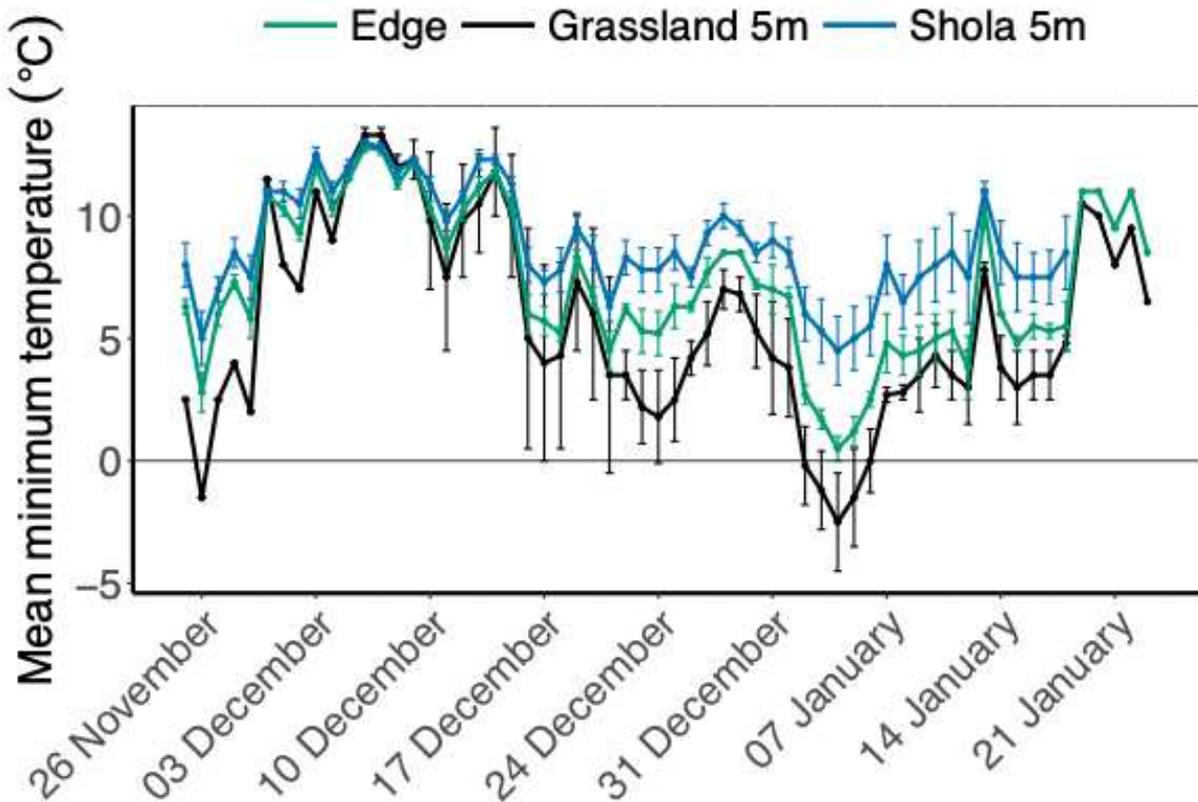
b) *Acacia mearnsii*



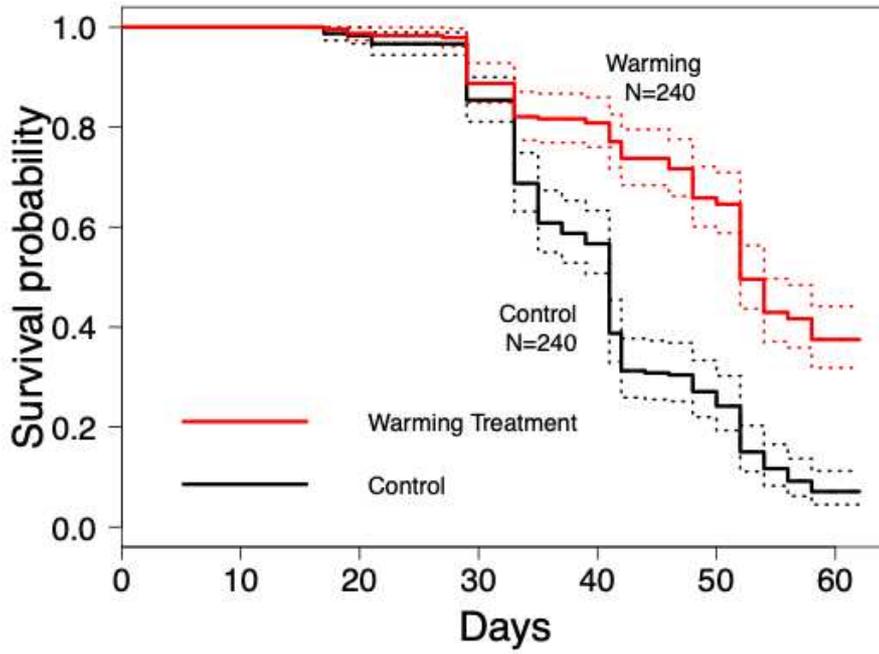
a)



b)



a) All native species



b) *Acacia mearnsii*

