Thermal germination niches of *Persoonia* species and projected spatiotemporal shifts under a changing climate

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**Abstract**

**Aim:** Seasonal germination is critical in synchronizing seedling emergence with optimal conditions for survival but will be disrupted by climate change. Understanding how germination of threatened species with complex dormancy patterns will be affected by climate change is a priority for their management. By exploring the effects of temperature on germination for six *Persoonia* species ranging in rarity, this study aims to improve ex situ plant production and better understand the probable impacts of climate change on persistence of local populations.

**Location:** South-eastern Australia.

**Methods:** The role of temperature on seed dormancy was explored using generalized additive models to predict germination probabilities for six *Persoonia* species ranging in rarity. Embryos were exposed to 24-hr cycles of alternating 12-hr warmer/light and 12-hr cooler/dark combinations of temperatures between 8°C and 45°C. Optimal temperature conditions for germination were determined, and spatiotemporal changes in germination probability were predicted in response to expected temperatures under future climate change scenarios.

**Results:** Unique germination niches representing complex responses across diurnal regimes were identified for each species. Germination probability was predicted to decline in four species in response to warmer day or night temperatures and in two species in response to cooler day or night temperatures. Across bioregions, areas of likely germination largely aligned with species-specific temperature sensitivity, with suitable germination niche declining in four species, one staying roughly the same and one increasing in physical range under predicted climate warming.

**Main conclusions:** In response to increased temperatures associated with climate change, germination probability varied from current rates. These changes were quantified both spatially and temporally and highlight expected challenges for persistence of some populations, particularly range restricted and rare species. Current understanding of extinction threat must consider future conditions, and these results highlight the urgent need to protect populations of these six *Persoonia* species that are currently threatened by habitat destruction and encourage future population persistence through restoration efforts.
1 | INTRODUCTION

Biotic and abiotic factors set the cadence of life histories and population dynamics for plants (Chuine, 2010; Franks & Weis, 2008; Letten, Ashcroft, Keith, Gollan, & Ramp, 2013). Key transitional stages like seed germination and seedling establishment are particularly sensitive to disruptions in resource availability and environmental conditions (Abbott, 1984; Bell, 1999; Lloret, Peñuelas, Prieto, Llorens, & Estiarte, 2009). Delayed germination through dormancy is a typical bet-hedging strategy, synchronizing high-risk seedling emergence with conditions most likely to support sexual maturation (Bell, 1999; Fenner & Thompson, 2005; Whelan, 1995). Often, seed dormancy is primarily regulated by ambient temperatures and availability of light and moisture (Finch-Savage & Leubner-Metzger, 2006; Probert, 2000; Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). The effects of climate change are already evident, and average seasonal temperatures are projected to continue to increase at rates dependant on economic and industrial activities (IPCC, 2014). Changes in patterns of rainfall, drought and fire will also effect conditions in which seedlings will emerge (Benali et al., 2017; Le Page, Oom, Silva, Jónsson, & Pereira, 2010; Williams et al., 2009).

Aside from germination patterns, population persistence depends on factors such as dispersal, phenotypic plasticity, species interactions and geographic barriers (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Fitzpatrick, Gove, Sanders, & Dunn, 2008; Gallagher, Hughes, & Leishman, 2013; Gilman, Urban, Tewsbury, Gilchrist, & Holt, 2010; Parmesan & Yohe, 2006). Often, seed dormancy is primarily regulated by ambient temperatures and availability of light and moisture (Finch-Savage & Leubner-Metzger, 2006; Probert, 2000; Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). The effects of climate change are already evident, and average seasonal temperatures are projected to continue to increase at rates dependant on economic and industrial activities (IPCC, 2014). Changes in patterns of rainfall, drought and fire will also effect conditions in which seedlings will emerge (Benali et al., 2017; Le Page, Oom, Silva, Jónsson, & Pereira, 2010; Williams et al., 2009).

Climate change is disrupting many of these biological processes, and the rate of change in local climates may be too rapid or far reaching for species to adapt too or migrate to more suitable environments (Ackerly, 2012; Duputié, Rutschmann, Ronce, & Chuine, 2002). Climate change is disrupting many of these biological processes, and the rate of change in local climates may be too rapid or far reaching for species to adapt too or migrate to more suitable environments (Ackerly, 2012; Duputié, Rutschmann, Ronce, & Chuine, 2002). Many species will rely on their innate adaptive capacity, partially expressed in the broadness of climatic conditions that support germination, termed the "germination niche" (Donohue et al., 2010; Luna & Moreno, 2010; Slater, Hirst, & Sexton, 2013; Valladares et al., 2014). The realized germination niche is a product of complex trait–environment interactions, and whether they can be comprehensively represented by germination temperatures measured in the laboratory is still unclear (Thompson & Ceriani, 2003). Despite this, temperature as an isolated factor is a primary driver of germination (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006; Probert, 2000; Wagemann et al., 2012; Walck et al., 2011). Quantifying germination rates in response to warmer or cooler temperatures useful in identifying species-specific germination niche, and understanding the effects of warmer temperatures is particularly valuable in predicting the responses of species to future climate scenarios where temperature changes are expected (Cochrane, 2015; Cochrane, Daws, & Hay, 2011; Cochrane, Hoyle, Yates, Wood, & Nicotra, 2014; Fenner & Thompson, 2005; Thuiller, Lavorel, & Araújo, 2005).

Temperature changes are a central factor in the biological effects of future climate scenarios. Seasonal average temperatures are expected to affect the timing of germination, alter geographic ranges—particularly in already restricted species, and modify community compositions (Dirnböck, Essl, & Rabitsch, 2011; Hoyle et al., 2013; Mondini, Rossi, Orsenigo, & Probert, 2012; Orrù, Mattana, Pritchard, & Bacchetta, 2012; Thuiller et al., 2005). Maximum, minimum and diurnal oscillations in temperature and light also work as physiological and germination signals for some species and will be affected by increasing occurrences of extreme temperature events under future climate scenarios (Fenner & Thompson, 2005; Foley, Anderson, Chao, Doğramaci, & Horvath, 2010; IPCC, 2014; Meehl et al., 2007; Vasseur et al., 2014). Simulating a 24-hr diurnal regime with alternating 12-hr light/warmer and dark/cooler periods can then potentially improve model accuracy for germination and climate change predictions (Fernandez-Pascual, Seal, & Pritchard, 2015; Qiu, Bai, Coulman, & Romo, 2006).

Persoonia (Proteaceae) are endemic to Australia, with the greatest species occurring in south-eastern Australia, a region where vegetation clearing and habitat fragmentation is common. Persoonia mostly occur as part of sclerophyllous plant assemblages associated with sandstone-derived soils (Weston, 2003). In these nutrient-poor environments, they produce carbohydrate-rich fruits, nectar and shoots that are a food source for animals (Cannon, 1984; Rose, 1973; Snow, 1981). Nine of the approximately one-hundred Persoonia species in south-eastern Australia are threatened, endangered or critically endangered (IUCN, 2017; Unit, 1999). A number important populations of listed Persoonia species are currently threatened by clearing for mining and development (DEE, 2008; DEC, 2006; OEH, 2012). Yet, an inability to cultivate sufficient plant numbers for reintroduction, either by propagation or seed, has so far excluded Persoonia from restoration programmes (Bauer, Johnston, & Williams, 2004; Cambecedes & Balmer, 1995; Mullins, Koch, & Ward, 2002).

The pyrene or "seed" of Persoonia consists of an embryo with no endosperm, encased in a thick, woody endocard, which is relatively durable compared to other species (Norman & Koch, 2008). The endocard is water permeable, but exerts physical dormancy, with germination occurring after its removal or weakening (Bauer et al., 2004; Chia, Sadler, Turner, & Baskin, 2016; Norman & Koch, 2008). Following endocard removal however, Persoonia species still fail to germinate or germinate at low numbers, suggesting the existence of other germination triggers (Abbott & Van Heurck, 2012).
1988). Fire signals are critical factors in some cases (McKenna, 2007; Nield, Monaco, Birnbaum, & Enright, 2014), but climatic factors and seed burial also affect germination (Chia, Koch, Sadler, & Turner, 2015; Chia et al., 2016; Nancarrow, 2001). Seed bank longevity remains largely undefined with some indication that soil- and Turner, 2015; Chia et al., 2016; Nancarrow, 2001). Seed bank storage and seed burial also affect germination (Chia, Koch, Sadler, 1988). Fire signals are critical factors in some cases (McKenna, 2007; Auld & Ooi, 2008). Long juvenile development but short seed bank persistence suggests that inter-fire germination (occurring independent of fire events) is important in buffering population regeneration during periods of both infrequent and frequent fires. Temperature as an isolated germination signal remains unknown for many species in this genus, and identification of optimal temperatures could improve ex situ germination, predict impacts of future climates and assist in prioritizing conservation efforts.

In this study, we aim to characterize the relationship between germination probability and temperature for six significant and rare Persoonia species (Table 1). We do this by subjecting recently dispersed, dormant Persoonia seeds to ranging temperature regimes using thermogradiant tables. We then modelled the probability of germination against average day temperatures (\(x_{\text{day}}\)), average night temperature (\(x_{\text{night}}\)) and the difference between day and night temperatures (\(x_{\text{day}} - x_{\text{night}}\) or DT) using generalized additive models. Using predicted germination responses and continental-scale surface temperature models, we predict the germination niche for each species under historical (1970–2000) conditions as well as quantify the spatial and temporal shifts under projected climate scenarios (2080). We discuss results with respect to improving and informing current and future conservation efforts for three rare Persoonia species included in this study and provide insights into the challenges faced by the Persoonia genus under future climate conditions.

2 | METHODS

2.1 | Fruit collection

Seeds of six Persoonia species were collected from sites in New South Wales, Australia (Figure 1). These species range in rareness (Table 1) and were chosen because they are currently effected by mining and development, yet are not included in restoration projects due to low levels of ex situ germination. Following the guidelines for seed collection of New South Wales threatened plant species, we collected <5% of available seeds in each population (Offord & Meagher, 2009). These species were thus also chosen as they produced large enough fruit sets for collection of sufficient seeds without endangering wild populations. Persoonia acerosa (Sieber ex Schult. & Schult.f.) is listed as a vulnerable and is restricted to altitudes of around 317-1153m above sea level (ASL) mostly in urbanized areas of the Greater Blue Mountains Region, in Eastern Australia (DEE, 2008). P. nutans (R.Br.) is listed as endangered and grows at 5-158m ASL in the alluvial soils of the Hawkesbury River floodplains of Western Sydney (National Herbarium of NSW, 2018). It’s geographic range is now significantly fragmented, and the majority (roughly 95%) of the population is restricted to an area of <2 km² (DEC, 2006; Robertson, Matthes, & Smith, 1996). P. pauciflora (P.H. Weston) is critically endangered and occurs at two sites (49-95m ASL); however, one population was recently cleared for development (OEH, 2012). P. levis ((Cav.) Domin), P. pinifolia (R.Br.) and P. linearis (Andrews) are all commonly occurring species with broad, overlapping distributions that range in altitude (National Herbarium of NSW, 2018). All six species rely to varying degrees on the formation of a soil-stored seed bank to regenerate following disturbance, but P. acerosa, P. nutans, P. pauciflora and P. pinifolia are obligate seeders, while P. levis and P. linearis are facultative resprouters (Table 1).

2.2 | Seed preparation

We used x-ray imagery, tetrazolium staining, cut tests and germination experiments to quantify the viability of the collections and

| TABLE 1 | Conservation status from the Environmental Protection and Biodiversity Conservation Act (Commonwealth of Australia 1999): critically endangered (CE), endangered (E), vulnerable (V) and not listed (NL), disturbance strategy (Benson & McDougall, 2000): facultative res sprouter (FR), obligate seeder (OB) and flowering time of the six studied Persoonia species (Benson & McDougall, 2000). A number of subregions of the Interim Biogeographic Regions of Australia (IBRA) were visited (Geoscience Australia & Department of the Environment and Energy, 2018): Burrarorang (B), Cumberland (C), Hunter (H), Mona Vale (MV), Sydney Cataract (SC), Wollemi (W), Yengo (Y) and multiple collection location (each with multiple collection sites) were visited within each subregion depending on species range |
| Species | Conservation status | Disturbance strategy | Flowering time | IBRA |
|---------|---------------------|----------------------|----------------|-------|
| P. acerosa | V | OS | December–April | W |
| P. levis | NL | FR | September–February | B,C,H,MV,SC,W,Y |
| P. linearis | NL | FR | December–July | B,C,H,MV,SC,W,Y |
| P. nutans | E | OS | December–January | C |
| P. pauciflora | CE | OS | December–January | H |
| P. pinifolia | NL | OS | December–July | B,C,SC |
FIGURE 1 Collection sites for six Persoonia species, endemic to New South Wales, Australia. Locations have been truncated and dispersed to show the various species collected at singular sites and to protect locations of listed species.
test seed treatment methods as part of preliminary work for our research (Daws, Garwood, & Pritchard, 2006; ISTA, 1985; Leist, Krämer, & Jonitz, 2003). Using these methods, we found that for maximum seed viability, *Persoonia* fruits must remain attached to the parent plant until fully matured, signified by natural abscission. We placed mesh bags around developing fruits and then returned to collect a standardized cohort of fully matured, recently fallen fruits from October 2016 through to February 2017. Within subregions of the Sydney Basin, the number of collection locations varied between species depending on species’ distribution and range size (Geoscience Australia & Department of the Environment and Energy, 2018). We confirmed that environmental conditions at the collection sites for each species were representative of those across the species’ range by directly comparing the mean annual temperature, mean annual rainfall and altitude at collection sites with recorded locations of each species held in the Atlas of Living Australia (Atlas of Living Australia: Geoscience Australia & Department of the Environment and Energy, 2018 accessed on 15.01 2019). We derived mean annual temperature and mean annual rainfall at a resolution of 30 arc seconds from WorldClim and mean altitude from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) database for collection sites and species record locations (CGIAR-CSI, 2008; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Table 2). For *P. acerosa*, *P. nutans* and *P. pauciflora*, fewer than five populations had a large enough seed bank to tolerate collection of seeds. In order to obtain sufficient seeds for germination experiments, particularly from these rare species, we pooled seeds from all collection sites for each of the six species, assuming seeds were representative of seed and climatic variability.

### 2.3 | Experimental preparation

The mass ratio of seed coats to seed is a measure commonly used to predict tolerance of desiccation and orthodox storage conditions (<15% humidity ~ 4°C) (Daws et al., 2006; Gold & Hay, 2008; Hong et al., 1996). Using a routine seed coat ratio test (Appendix 1), seeds of *Persoonia* species were found to be desiccation tolerant, indicating that viability is maintained with orthodox storage (Daws et al., 2006; Gold & Hay, 2008; Hong et al., 1996; International Seed Testing Association, 1985). Fruits were spread on trays, stored at 15% humidity and 15°C for up to six months. Germination trials were run on a feasible subset of fresh seeds and compared to stored seeds (Baskin, Thompson, & Baskin, 2006), for which germination rates did not differ significantly when compared to seeds post-storage. We acclimatized seeds to laboratory conditions for 24 hr before initiating the germination protocols. The seeds, still encapsulated in fruit, were soaked in water with Ultrasound® (0.3 g/L) for approximately 24 hr before separating the mesocarp from the pyrene, consisting of a woody endocarp encasing an embryo (Tieu, Turner, & Dixon, 2008). While intact, the fleshy mesocarp and woody endocarp exerts a mechanical constraint restricting moisture to the seed (Chia et al., 2016) and

### TABLE 2

Mean annual (± standard deviation) temperature, diurnal range in temperature, rainfall (Hijmans et al., 2005) and altitude above sea level (SRTM, 2008) for collection sites and for species occurrence records held at the Atlas of Living Australia (ALA 2019)

| Species       | Temperature (°C) | Diurnal range (°C) | Rainfall (mm) | Altitude (m) |
|---------------|------------------|--------------------|---------------|--------------|
|               | Mean (±SD)       | Range              | Mean (±SD)    | Range        |
| *P. acerosa*  |                  |                    |               |              |
| Collection sites | 12.4 (±0.3) | 11.6–13.1 | 10.5 (±0.3) | 9.7–11.1 | 140.1 (±1.5) | 133.3–141.5 | 837 (±65) | 702–986 |
| All records   | 12.8 (±0.7)     | 11–15.4            | 10.8 (±0.6)   | 9.5–12.5 | 135.7 (±7.4) | 93.4–147.7 | 773 (±138) | 317–1153 |
| *P. levis*    |                  |                    |               |              |
| Collection sites | 15.3 (±0.9) | 12–16.5            | 11 (±0.5)     | 10.1–12.9 | 124 (±11.6) | 93.6–173.9 | 335 (±144) | 149–911 |
| All records   | 16 (±1.7)       | 10.4–18.9          | 10.5 (±1)     | 6.6–13.4 | 122.5 (±16.5) | 66.1–198.3 | 250 (±255) | 0–1178 |
| *P. linearis* |                  |                    |               |              |
| Collection sites | 15.4 (±1) | 12.3–17.5          | 10.8 (±0.9)   | 10–12.4 | 132.3 (±27.4) | 80.6–180.5 | 345 (±137) | 95–850 |
| All records   | 15.7 (±1.7)     | 9.8–18.8           | 11.3 (±1.3)   | 6.7–14.2 | 105.4 (±20.6) | 59.8–195.6 | 361 (±292) | 2–1489 |
| *P. nutans*   |                  |                    |               |              |
| Collection sites | 17.1 (±0) | 17.1–17.1          | 12.9 (±0)     | 12.9–12.9 | 89.8 (±0.2) | 89.6–90.1 | 31 (±1) | 30–33 |
| All records   | 17.2 (±0.1)     | 16.6–17.6          | 12.2 (±0.8)   | 10.3–13 | 90.4 (±3.2) | 82.9–119.5 | 36 (±14) | 5–158 |
| *P. pauciflora* |               |                    |               |              |
| Collection sites | 17.5 (±0) | 17.5–17.5          | 12.4 (±0)     | 12.4–12.4 | 80.6 (±0.1) | 80.6–81.1 | 95 (±2) | 85–95 |
| All records   | 17.6 (±0.1)     | 17.4–17.7          | 12.5 (±0.1)   | 12.3–12.5 | 79.2 (±0.7) | 78–81.1 | 61 (±11) | 49–95 |
| *P. pinifolia* |                |                    |               |              |
| Collection sites | 15.5 (±0.5) | 11.7–16.9          | 10.8 (±0.4)   | 9.7–12.8 | 128.6 (±11.1) | 89.7–152.7 | 298 (±83) | 62–956 |
| All records   | 16.5 (±0.7)     | 13.5–17.7          | 10.3 (±0.7)   | 8.8–13.1 | 126.3 (±12.8) | 83.2–162.2 | 178 (±101) | 3–646 |
therefore minimizing exposure of the seed to the Ultrazyme® treatment. Previous germination trials indicated that extremely strong mechanical restriction is exerted by the endocarp and therefore would need to be overcome to observe the effects of temperature on germination. The endocarp was detached by first creating fissures with a scalpel and then using a vice to gently apply pressure across the longitudinal axis. The endocarp fragments were then carefully removed, and the condition of the exposed embryo was assessed for viability, indicated by healthy, plump, undamaged embryo tissue surrounded by an intact testa. Only viable embryos were then included in the experiment, eliminating the need for retrospective adjustments of results. Prior observation indicates that removal of the seed from natural soil microbial communities tends to allow for pathological microbial overgrowth in laboratory grown *Persoonia* seed. Therefore, embryos were sterilized using 1% bleach for 5 min, rinsed in sterilized water three times and set separately in sterile vials on a 0.7% agar media substrate containing 250 μM/L gibberellic acid (GA3). Seeds of *Persoonia* species are physiologically dormant, responding to GA3 in some studies, but not others (McIntyre, 1969; Mullins et al., 2002; Nancarrow, 2001). Taking into account that GA3 may enhance germination, it was included to isolate and explore the role of temperature on germination, with the assumption that all other conditions required for optimal germination have been met.

In order to extrapolate realistic germination responses from laboratory based studies, any pre-treatment of seeds must resemble preparatory processes for germination in natural contexts (Baskin et al., 2006). In line, each of these steps does so; the application of Ultrazyme® representing the natural breakdown of fruit through ingestion by animals or microbes; the removal of the endocarp resembling the breakdown of the endocarp through repeated wet and drying or microbial degradation (Chia et al., 2016); and the application of GA3, resembling the build-up of naturally occurring growth hormones in order to optimize germination conditions. Likely required conditions, including the provision of natural growth hormones, such as GA3 that stimulate germination, moisture and removal of physical dormancy in the form of the endocarp, were therefore met to isolate and observe the effects of temperature on germination (Mullins et al., 2002; Norman & Koch, 2008).

### 2.4 | Germination

For each species, 630 embryos were sown individually into sterile glass vials with 0.7% agar media substrate infused with gibberellic acid, except *P. pauciflora*, for which 357 embryos were sown due to a smaller seed collection. Each species was tested on a bidirectional thermogradient plate (Grant Instruments, UK, model GRD1; Figure 2). Along both gradient axes, temperatures ranged from 8 to 45°C. Photoperiods alternated between light and dark every 12 hr coupled with a reversal along one temperature gradient axis. The thermogradient table was partitioned into 36 compartments of 9 cm², and average light ($\bar{X}_{\text{day}}$) and dark ($\bar{X}_{\text{night}}$) temperatures characterized each compartment with a unique thermo-photoperiod. The temperature within each compartment was recorded by a Thermochron iButton every 10 min throughout the duration of the experiment and used to calculate $\bar{X}_{\text{day}}$ and $\bar{X}_{\text{night}}$ temperatures.

**FIGURE 2** Schematic of the bidirectional diurnal thermogradient table, with a 12-hr light/dark cycle. One axis showing the temperature gradient occurring during the 12-hr photoperiod and the other axis showing the dark period temperature gradient. Half of the thermogradient had relatively warmer dark periods and so was not utilized.
The 12-hr light/warmer and 12-hr dark/cooler regimes simulated diurnal conditions over 24-hr cycles (Cochrane, 2019; Fernandez-Pascual et al., 2015). Available testing equipment is incapable of simulating a more realistic, gradual ramping up and down of temperature and light in true diurnal patterns, possibly affecting extrapolation to ecological contexts. Half of the table had relatively warmer dark periods and cooler light periods and were therefore excluded, leaving 21 active thermo-period combinations. Aside from simulating an ecologically implausible scenario, this also minimized our use of seeds from rare species. Seeds were set on top of firm agar medium, exposed to air temperature for the most part. For each species, 30 vials, each containing one embryo, were placed within each compartment, except for P. pauciflora, for which 17 vials were used in each compartment. Germination was recorded every two or three days, and the test was terminated after at least two weeks of no recorded change, but the experiment was continued for a minimum of 89 days for comparability between species.

2.5 Statistical analysis

We used generalized additive models (GAMs) to examine associations between germination probabilities and the DTA vectors of $\vec{X}_{\text{day}}$, $\vec{X}_{\text{night}}$, and the range of difference between them (DT6), with each model postulating these vectors as singular or additive explanatory variables. GAMs are a non-parametric extension of a generalized linear model (GLM) that do not require pre-specification of non-linear relationships. In GAMs, predictors depend linearly on unknown smoothing functions of some of the covariates (Hastie & Tibshirani, 1990). The degree of smoothing was selected by minimum GCV/UBRE scores, controlling for over-fitting with a gamma multiplier of 1.4 (Wood, 2011). To avoid over-fitting and ease of interpretation, the number of knots (i.e. polynomial level) was limited in the GAMs to three. As third-order polynomial models, they are sufficient in contouring to three-dimensional response variables. While being flexible, they are restrained as additives, allowing for conventional regression analysis (Hastie & Tibshirani, 1990; Yee & Mitchell, 1991).

We used the "gam" function in the "mgcv" package with a binomial link function (Wood, 2017) in the R environment (R Development Core Team, 2014). Prior to modelling, we evaluated the correlation between the three explanatory variables ($\vec{X}_{\text{day}}$, $\vec{X}_{\text{night}}$ and DT6) and those to be less than $r = .5$. We developed a unique model for each of the six species, only considering possible main effects of the three potential predictors without interactions. We examined two response models. The first, at the individual level, a Binomial response model of germination success of each seed. The second, at the population level, a Poisson response model of the number of seeds germinated within each compartment (i.e. from a pool of 30 seeds with the exception of P. pauciflora which had 17 seeds). For each examined model (six species, two response levels), we considered the full model space, examining all eight possible explanatory variable combinations using the "dredge" function in the "MuMln" package (Barton, 2018). The corrected Akaike’s information criterion (AICc) was used to identify plausible models having AICc scores not greater than two relative to the lowest score (Appendix 2; Burnham & Anderson, 2002; White & Burnham, 1999). We then used a model averaging approach, weighted by model AICc scores, to quantify the average strength of association between the two response models, that is, germination probability and number of seeds, and the three explanatory variables. We also evaluated the fit of averaged models by calculating Efron’s pseudo $R^2$ (Efron, 1978).

2.6 Current and future germination predictions

Soil temperature models do not currently exist given the complex interactions between soil and air temperature (Parton & Logan, 1981; Zheng, Hunt, & Running, 1993); therefore, in concurrence with our experimental design, we used modelled continental-scale air temperature to predict germination–temperature responses (Cochrane, 2019; Fernandez-Pascual et al., 2015). Using model-averaged responses of binomial models, we predicted the geographic distribution of seed germination probability ($P_{\text{germ}}$) under historic (1970–2000) conditions using monthly $\vec{X}_{\text{day}}$, $\vec{X}_{\text{night}}$ and DT6 (Bureau of Meteorology, 2018) at a spatial resolution of 30 arc seconds. To minimize commission errors predicting to areas outside of the species’ ecological potential (Peterson, 2006), calculations of potential range for each species were based on the Biogeographic Regionalisation for Australia (Geoscience Australia & Department of the Environment and Energy, 2018), a classification of geographically distinct bioregions that is the basis of systematic conservation planning that depends on common climate, geology, landform, native vegetation and species compositions (Commonwealth of Australia, 2009). Predictions of germination probability were confined to subregions where each species was recorded at least five times in the Atlas of Living Australia (Atlas of Living Australia; Geoscience Australia & Department of the Environment and Energy, 2018, accessed on 15.01.2019). The only exception was for P. nutans, predominantly occurring within the Cumberland subregion, but with 27 records recorded <700 m from the boundary of the Cumberland subregion in a neighbouring subregion which we did not warrant the inclusion of an additional subregion (1,539 km$^2$). This exclusion was based on the notion of continuous transitional zone between subregions rather than a representation of amenable environmental conditions throughout the additional subregion. The future (year 2080) distribution of germination probability was predicted using $\vec{X}_{\text{day}}$, $\vec{X}_{\text{night}}$ and DT6 values, under the pre-established Representative Concentration Pathways (RCPs) (Van Vuuren et al., 2011), depicting scenarios of total radiative forcing produced by human greenhouse gas emissions resulting from different combinations of economic, demographic and institutional futures (IPCC, 2018). RCP 2.4 scenario assumes least change in radiative forcing and thus climate conditions resulting from implementation of policy and economic
action to mitigate fossil fuel emissions, RCP 6.0 assumes moderate increase in radiative force and changed climate conditions, and RCP 8.5 assumes highest increase in radiative force and associated change in climate conditions obtained from the HadGEM2-ES model (Hijmans et al., 2005; Jones et al., 2011). The HadGEM2-ES model was chosen as it accounts for measures of interest, such as surface soil temperature, it has suitable resolution for the region of interest in this study and it is considered to be one of the best performing models for climate in Australia (Commonwealth Science Industrial Research Organisation & Bureau of Meteorology, 2015). Germination probabilities were predicted at a spatial resolution of 30 arc seconds under three RCP climate change scenarios and then compared to germination probabilities predicted under averages of historic (1970–2000) climatic conditions (Bureau of Meteorology, 2018). The Sydney Basin Bioregion has the highest population density in Australia, reflected in continuing urbanization and dynamic land-use patterns (Commonwealth of Australia, 2017a). To provide a more realistic indication of protected habitat, we also examined the predicted germination area within protected areas.

3 | RESULTS

Germination niches for the six Persoonias were species-specific, presenting complex responses across diurnal regimes. In the experiments, observed optimal seed germination probability for all species occurred with average day temperatures of \( \bar{X}_{\text{day}} \approx 22^\circ\text{C} \), except for P. acerosa, which had the highest germination probability at average day temperature of \( \bar{X}_{\text{day}} \approx 15^\circ\text{C} \) (Figure 3). Observed optimal night temperatures, however, varied between all the species. Explained variance by binomial individual seed germination models was relatively low and varied among species, ranging between 17% (P. acerosa and P. levis) and 44% (P. linearis; Table 3). When modelled at a population scale, as the number of seeds germinated per cell, explained variance was higher, ranging between 63% (P. pauciflora) and 86% (P. pinifolia; Table 3).

Models predicted declining germination probabilities for all of the six species in response to warmer day or night temperatures, and three (P. levis, P. nutans and to a lesser extent P. pauciflora) species were also sensitive to cooler day or night temperatures. Cooler \( \bar{X}_{\text{day}} \) and \( \bar{X}_{\text{night}} \) temperatures were most favourable for P. acerosa, which linearly declined with warmer temperatures (Figure 3a). The responses of P. nutans and P. pauciflora, respectively, were driven by convex negative associations with \( \bar{X}_{\text{night}} \) and \( \bar{X}_{\text{day}} \) temperatures (Figure 3d,e). P. linearis, P. levis and P. pinifolia had convex negative germination probabilities responses to warmer \( \bar{X}_{\text{day}} \) temperatures, generally displaying linear negative associations with warmer \( \bar{X}_{\text{night}} \) (Figure 3b,c,f). Declines in germination probabilities driven by cooler or warmer temperatures are reflected in both temporal and spatial predicted outcomes. For example, declines with warmer temperatures resulted in peak \( P_{\text{term}} \) during winter months and reductions in spatial germination probabilities under warmer conditions, while germination sensitivities driven by cooler temperatures resulted in the opposite outcomes (Figure 4, Figure 5).

3.1 | Temporal models

Germination models predicted likely temporal shifts and reductions in germination probabilities in summer months under the three RCPs for five species, and slight increases in germination for P. nutans across the year (Figure 4). Relative temporal and spatial shifts were associated with negative linear responses for P. acerosa, with peak germination probability during February (summer) decreasing with higher RCP climate scenarios, and no significant change during the winter months (Figure 4a). Warmer climate scenarios also resulted in temporal shifts for P. pauciflora, P. linearis and P. levis, with reduced germination probabilities under warmer temperatures causing a contraction of peak germination into the cooler months, while germination probability for P. levis increasing notably in cooler months with warmer temperatures. P. pinifolia maintained an historic germination preference for cooler months; however, a slight reduction in germination probability with warming temperatures was still observed. Predicted sensitivity of P. nutans to cooler temperatures relates to the lower germination probabilities in winter months and a slight increase under warmer climate change scenarios (Figure 4d).

3.2 | Spatial models

Across bioregions, spatial shifts in germination probabilities largely aligned with species-specific temperature sensitivity (Figure 5, Appendix 3, Table 3). For P. acerosa, P. pauciflora and P. linearis, the effects of warming temperatures were reflected in consecutively predicted declines in germination probabilities under climate change scenarios (Figure 5, Appendix 3, Table 3). In these instances, areas supporting the highest 40% germination probabilities decreased between 90% (RCP 8.5) and 56% (RCP 2.6) for P. acerosa, 33% (RCP 2.6) to 60% (RCP 8.5) for P. linearis, 60% (RCP 2.6) to 98% (RCP 8.5) for P. pauciflora and 33% (RCP 2.6) to 71% (RCP 8.5) for P. pinifolia (Appendix 3). In contrast, the spatial extent of high germination probabilities of P. nutans considerably increased with warmer RCP scenarios with the highest 40% increasing by 50% under RCP 2.6 and by 240% under RCP 8.5 (Figure 5d), while those of P. levis did not significantly change (Figure 5b, Table 3). When protected areas were considered, possible areas of high germination probabilities of P. nutans and P. pauciflora were further restricted, while P. acerosa, which is already largely restricted to protected areas, while the ranges of the three common species were fragmented and restricted to varying extents (Appendix 3, Table 3).

4 | DISCUSSION

Germination in the six studied Persoonia species was found to display unique temperature sensitivity and optima, with distinct predicted responses to climate change. Under examined RCP scenarios, germination probabilities for five species were predicted to decline, raising concerns over the long-term viability of many populations and
Figure 3  Persoonia germination probabilities in response to average diurnal temperatures represented in three-dimensional plots and two-dimensional response curves ($\bar{X}_{\text{day}}$ (red), $\bar{X}_{\text{night}}$ (blue), DT$\delta$ (green) with 95% confidence intervals (dashed) based on averaged generalized additive models.
TABLE 3

Explained variance ($R^2$) of germination models and predicted spatial extents of Persoonia germination probability within biogeographic subregions (“Range”) (Geoscience Australia & Department of the Environment and Energy, 2018) and within protected areas (PA) (CAPAD, Commonwealth of Australia, 2017a, 2017b) under historical (1970–2000) and future (2080) RCP 2.6, RCP 6.0 and RCP 8.5 emission scenarios (Hijmans et al., 2005).

| Species         | Historic (km²) | RCP 2.6 (km²) | RCP 6.0 (km²) | RCP 8.5 (km²) |
|-----------------|----------------|---------------|---------------|---------------|
|                 | $P_{\text{arm}}$ | $\text{Range}$ | $\text{PA}$  | $\text{Range}$ | $\text{PA}$  | $\text{Range}$ | $\text{PA}$  | $\text{Range}$ | $\text{PA}$  |
| P. acerosa      | 0.036–0.041     | 7.2           | 0.0           | 0.0           | 708.5         | 159.8         | 1,116.0       | 421.2         | 672.5         |
| Total (km²)     | 0.041–0.045     | 391.7         | 2.9           | 0.0           | 5,439.6       | 3,863.5       | 4,919.0       | 3,713.8       | 4,318.6       |
| Range: 9,430    | 0.045–0.050     | 1,386.0       | 250.6         | 0.0           | 3,247.2       | 2,395.4       | 3,221.3       | 2,204.6       | 3,739.7       |
| Protected area: 6,413 | R² = 0.17/0.64 | 0.050–0.055   | 6,345.4       | 4,992.5       | 109.4         | 41.8          | 247.7         | 121.0         | 774.0         |
| P. levis        | 0.143–0.153     | 59.8          | 59.0          | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           |
| Total (km²)     | 0.153–0.163     | 515.5         | 445.7         | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           |
| Range: 43,808   | 0.163–0.172     | 4,135.0       | 3,144.2       | 0.0           | 245.5         | 203.0         | 2,743.9       | 191.5         | 8,802.0       |
| Protected area: 25,504 | R² = 0.23/0.71 | 0.172–0.182   | 18,942.5      | 9,528.5       | 14,840.6      | 4,714.6       | 28,877.0      | 7,361.3       | 30,558.2      |
| P. linearis     | 0.194–0.238     | 0.0           | 0.0           | 0.0           | 2,501.3       | 143.3         | 9,911.5       | 1,428.5       |
| Total (km²)     | 0.238–0.283     | 0.0           | 0.0           | 0.0           | 8,308.8       | 1,328.4       | 29,532.2      | 2,814.5       | 54,442.1      |
| Range: 93,113.4 | 0.283–0.327     | 4,477.0       | 185.0         | 0.0           | 62,772.5      | 4,087.4       | 75,311.3      | 9,206.6       | 61,187.0      |
| Protected area: 39,006.5 | R² = 0.44/0.80 | 0.327–0.372   | 66,509.3      | 5,048.6       | 65,337.8      | 14,436.0      | 48,540.2      | 13,203.4      | 48,857.8      |
| P. nutans       | 0.120–0.131     | 1,062.7       | 20.2          | 0.0           | 121.7         | 5.8           | 0.0           | 0.0           |
| Total (km²)     | 0.131–0.142     | 1,264.3       | 30.2          | 0.0           | 913.0         | 20.9          | 333.4         | 11.5          |
| Range: 2,747.9  | 0.142–0.153     | 449.3         | 1.4           | 0.0           | 1,351.4       | 24.5          | 1,545.1       | 36.0          |
| Protected area: 51.1 | R² = 0.18/0.74 | 0.153–0.163   | 0.7           | 400.3         | 0.7           | 786.2         | 4.3           |
| P. pauciflora   | 0.321–0.327     | 1,806.5       | 0.0           | 0.0           | 1,922.4       | 50.4          | 1,223.3       | 64.8          |
| Total (km²)     | 0.320–0.330     | 133,707.6     | 0.0           | 0.0           | 1,922.4       | 50.4          | 1,223.3       | 64.8          |
| Range: 43,808   | 0.302–0.311     | 0.36          | 0.0           | 0.0           | 2,059.9       | 74.9          | 959.8         | 46.8          |
| Protected area: 226.1 | R² = 0.30/0.63 | 0.311–0.321   | 2,767.0       | 22.3          | 1,089.4       | 59.0          | 1,203.8       | 124.6         |
| P. floribunda   | 0.284–0.293     | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           |
| Total (km²)     | 0.293–0.302     | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           |
| Range: 5,858    | 0.302–0.311     | 3.6           | 0.0           | 0.0           | 715.0         | 1.4           | 1,922.4       | 50.4          |
| Protected area: 226.1 | R² = 0.30/0.63 | 0.311–0.321   | 2,767.0       | 22.3          | 1,089.4       | 59.0          | 1,203.8       | 124.6         |
| P. pinifolia    | 0.215–0.241     | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           | 0.0           |
| Total (km²)     | 0.241–0.267     | 1,322.6       | 367.9         | 0.0           | 2,522.9       | 385.2          | 5,991.8       | 1,561.0       |
| Range: 18,932.6 | 0.267–0.294     | 5,464.4       | 1,412.6       | 0.0           | 8,273.5       | 3,207.6       | 6,423.8       | 3,462.5       |
| Protected area: 9,195.3 | R² = 0.31/0.86 | 0.294–0.320   | 11,224.1      | 7,167.6       | 5,433.8       | 3,836.9       | 5,006.2       | 3,825.4       |

4.1 Implications for long-term viability

Due to human activity are the most vulnerable to climate change and often the first to disappear (Abbott, Doak, & Peterson, 2017; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Dinnböck et al., 2011; McLaughlin, Hellmann, Boggs, & Ehrlich, 2002; Parmesan, 2006). More the 90% of P. nutans occurrences are currently restricted to an area of <2 km² (DEC, 2006; Robertson et al., 1996) with no juveniles or seedlings found in this population. In addition, no recent regeneration was observed in P. acerosa nor in P. pauciflora populations which are now entirely restricted to within a few km² (OEH, 2012). Evident regeneration failure suggests a potential extinction debt, a time-delayed but inevitable extinction, occurring when unsuitable environments
Annual temperature plots of Persoonia germination probabilities and 95% confidence intervals (dashed) for each species as a response to monthly $\bar{X}_{\text{day}}$ and $\bar{X}_{\text{night}}$ under historical (1970–2000), RCP 2.6, RCP 6.0 and RCP 8.5 scenarios in the bioregions relevant to current distributions for each species.
arrest recruitment but maintain extant individuals (Tilman, May, Lehman, & Nowak, 1994), often identified in fragmented populations of species (Nield et al., 2014). Within the potential ranges of *P. acerosa* and *P. pauciflora*, germination probabilities were predicted to decrease under climate change, further enhancing recruitment deficits. In contrast, germination probability of *P. nutans* was predicted to increase within its potential range with warmer temperatures. This may initially increase much needed recruitment and help to address the extinction deficit in the currently ageing *P. nutans* populations. However, higher rates of germination could also destabilize populations in the long term. For instance, warmer temperatures may illicit higher germination, but are also expected to decrease seedling survivorship (Walck et al., 2011). Fire frequency is also expected to increase with a warmer and dryer climate, and with long (7–12 years) sexual maturation periods, *Persoonia* species, particularly obligate seeders like *P. nutans*, rely on ungerminated, residual soil seed banks to persist through recurring fire events within the period of sexual maturation. A possible cause of regenerative failure in *P. nutans* as well as *P. acerosa* and *P. pauciflora*, however, may be due to lack of recent fires in many areas. While some populations of *P. acerosa* experienced recent fires and still show no signs of recruitment, most populations of these three species occur proximal to housing and infrastructure where natural fire regimes are suppressed. The role of fire in the germination of *Persoonia* species is therefore complex and requires more research.

4.2 | Compounding threats

Continuing habitat and population destruction is a major threat to the persistence of all three rare and threatened species (DEE, 2008; DEC, 2006; Robertson et al., 1996), decreasing their adaptive capacity by depleting the existing gene pools directly through destruction of individuals as well as by impacting genetic mixing of remnant populations by limiting dispersal between patches (Higgins & Richardson, 1999; Lowe, Boshier, Ward, Bacles, & Navarro, 2005). Furthermore, *Persoonia* fruit is known to be ingested by animals, and although the importance of zoochory for germination has not been established, animal ingestion is considered important for dispersal (Mullins et al., 2002; Nield, 2014; Rose, 1973). Habitat destruction will therefore not only result in a direct decrease in colonizable habitat and impact fire and rainfall regimes in remnant ecological systems, it will also disrupt dispersal mechanisms and the possible effects of zoochory on germination indirectly by impacting animal populations (Gill & Williams, 1996;
4.4 | Predicted outcomes

Temperature is recognized as a major driver by which climatic change impacts population persistence (Aitken et al., 2008; Gilman et al., 2010; Jagdish et al., 2016). Under projected climate change, soil temperatures are expected to increase as a direct result of increased radiative force, but also as a result of increased frequency and intensity of fire events resulting in more exposed soil (Auld & Ooi, 2008; Ooi, 2012; Ooi, Whelan, & Auld, 2006). With no accurate estimates for soil temperatures, our predictions may in fact represent a conservative model that does not account for the higher temperatures of soil and the compounded effect of increased fire events under climate change scenarios. Warmer temperatures will affect other aspects critical for population persistence, such as seasonality of germination and seedling survival, seed bank longevity, as well as pathogen activity (Adler & HilleRisLambers, 2008; Aitken et al., 2008; Fay & Schultz, 2009; Lloret, Penuelas, & Estiarte, 2004; Ryan, 1991; Wagner & Mitschunas, 2008; Walck et al., 2011). The outcome of many of these shifts prefigures the risk of extinction, particularly for already endangered species (McLaughlin et al., 2002; Springthorpe & Penfield, 2015; Walck et al., 2011). Suitable conditions for population persistence will shift both geographically and temporally for many species, while colonization and access to resources may be restricted by habitat fragmentation, limiting colonization potential in habitat refugia (Jump & Peñuelas, 2005; Le Galliard, Massot, & Clobert, 2012; Schurr, 2005).

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DATA AVAILABILITY STATEMENT

Plant location data available at https://www.ala.org.au/.

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BIOSKETCHES

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Author contributions: K.C. reviewed literature, acquired secondary funding, conducted experimental design, field and laboratory experiments, collated and documented data, wrote the manuscript, and assisted with data analysis. G.B. conducted data analysis and assisted in writing the manuscript. C.A.O. acquiring the initial funding, gave guidance throughout the research and assisted in writing the manuscript. All collections made under NSW collecting licence (SL 100569).

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Results of seed moisture content derived from a seed coat ratio testing, showing desiccation in a Persoonia species are desiccation tolerant.

| Species       | Seed moisture content (%) | p-value | Statistical value | Sample size | Desiccation tolerant |
|---------------|---------------------------|---------|-------------------|-------------|----------------------|
| P. linearis   | 5.95                      | <.001   | 5.00E−04          | 12          | Yes                  |
| P. levis      | 9.03                      | <.001   | 8.00E−04          | 12          | Yes                  |
| P. glaucescens| 10.07                     | <.001   | 4.00E−04          | 12          | Yes                  |
| P. lanceolata | 6.87                      | <.001   | 4.00E−04          | 12          | Yes                  |
| P. pinifola   | 8.1                       | <.001   | 6.00E−04          | 12          | Yes                  |

Generalized additive model selection for each of the Persoonia species, modelling the response between germinating probability (first table), number of seeds per compartments (second table) and $X_{day}$, $X_{night}$ and DT9.

| Species       | Intercept | Xday | DT | Xnight | $R^2$ | df  | logLik | AICc | Delta | Weight |
|---------------|-----------|------|----|--------|------|-----|-------|------|-------|--------|
| P. acerosa    | -5.4      | +    | +  | +      | 0.2  | 4   | -63.2 | 135.7| 0     | 0.4    |
|               | -5.4      | +    | +  | +      | 0.2  | 4   | -63.2 | 135.7| 0     | 0.4    |
|               | -5        | +    | +  | +      | 0.1  | 4   | -64.6 | 137.6| 1.9   | 0.1    |
|               | -4.3      | +    | +  | +      | 0.1  | 2   | -66.6 | 138.8| 3     | 0.1    |
|               | -4.3      | +    | +  | +      | 0.1  | 4   | -65.9 | 140.2| 4.5   | 0.0    |
|               | -4.8      | +    | +  | +      | 0.1  | 2   | -69   | 143.7| 8     | 0.0    |
|               | -4        | +    |    |        | 0.0  | 0   | -71.3 | 148  | 12.3  | 0.0    |
|               | -3.6      |      |    |        | 0.0  | 0   | -74.6 | 151  | 15.4  | 0.0    |
| P. levis      | -2.1      | +    |    |        | 0.1  | 2   | -218.4| 442  | 0.3   | 0.3    |
|               | -2.1      | +    | +  | +      | 0.1  | 3   | -217.7| 443  | 0.6   | 0.2    |
|               | -2.1      | +    | +  | +      | 0.1  | 3   | -217.7| 443  | 0.6   | 0.2    |
|               | -2.1      | +    | +  | +      | 0.1  | 3   | -217.7| 443  | 0.6   | 0.2    |
|               | -2.1      | +    |    |        | 0.0  | 3   | -223.3| 452.6| 10.1  | 0.0    |
|               | -2.1      | +    |    |        | 0.0  | 2   | -225.0| 454.1| 11.5  | 0.0    |
|               | -2.0      |      |    |        | 0.0  | 0   | -228.0| 457.9| 15.3  | 0.0    |
|               | -2.0      | +    |    |        | 0.0  | 2   | -227.8| 459.7| 17.1  | 0.0    |
| P. linearis   | -2.5      | +    |    |        | 0.3  | 2   | -223.6| 453  | 0.0   | 0.3    |
|               | -2.4      | +    | +  | +      | 0.3  | 4   | -222.5| 454  | 0.8   | 0.2    |
|               | -2.4      | +    | +  | +      | 0.3  | 4   | -222.5| 454  | 0.8   | 0.2    |
|               | -2.5      | +    | +  | +      | 0.3  | 3   | -223.2| 454  | 1.3   | 0.2    |
|               | -2.2      | +    | +  | +      | 0.3  | 4   | -233.1| 475.7| 22.5  | 0.0    |
|               | -1.9      | +    |    |        | 0.1  | 2   | -266.5| 538.8| 85.6  | 0.0    |
|               | -1.8      | +    |    |        | 0.1  | 2   | -269.0| 543  | 90.7  | 0.0    |
|               | -1.6      |      |    |        | 0.0  | 0   | -285.5| 572  | 119.7 | 0.0    |
| P. nutans     | -2.2      | +    | +  | +      | 0.1  | 4   | -216.4| 442  | 0.0   | 0.3    |
|               | -2.2      | +    | +  | +      | 0.1  | 4   | -216.4| 442  | 0.0   | 0.3    |
|               | -2.2      | +    |    |        | 0.1  | 2   | -218.7| 443  | 1.2   | 0.2    |
|               | -2.2      | +    | +  | +      | 0.1  | 3   | -218.2| 444.3| 2.2   | 0.1    |
|               | -2.1      | +    |    |        | 0.0  | 2   | -222.1| 450  | 7.9   | 0.0    |
|               | -2.1      | +    | +  | +      | 0.0  | 3   | -222.0| 451  | 9.8   | 0.0    |
|               | -2.0      |      |    |        | 0.0  | 0   | -228.0| 457  | 15.8  | 0.0    |
|               | -2.0      | +    |    |        | 0.0  | 2   | -227.8| 459  | 17.6  | 0.0    |

(Continues)
### APPENDIX 2 (Continued)

| Species         | Intercept | Xday | DT  | Xnight | $R^2$ | df  | logLik | AICc | Delta | Weight |
|-----------------|-----------|------|-----|--------|------|-----|-------|------|-------|--------|
| *P. pauciflora* | -1.8      | +    | +   | +      | 0.2  | 5.0 | -148.2 | 307.0 | 0.0   | 0.5    |
|                 | -1.9      | +    | +   | 0.1    | 4.0  | -149.7 | 308.8 | 1.9   | 0.2    |
|                 | -1.8      | +    | +   | +      | 0.1  | 4.0  | -150.0 | 309.2 | 2.2   | 0.2    |
|                 | -1.7      | +    | 0.1  | 2.0    | -153.0 | 311.8 | 4.9   | 0.0    |
|                 | -1.8      | +    | 0.1  | 2.0    | -157.1 | 320.1 | 13.1  | 0.0    |
|                 | -1.6      | +    | 0.1  | 2.0    | -160.8 | 327.4 | 20.5  | 0.0    |
|                 | -1.5      | 0.0  | 0.0  | -166.4 | 334.7 | 27.8 | 0.0    |
| *P. pinifolia*  | -2.3      | +    | +   | 0.2    | 4.0  | -212.5 | 434.1 | 0.0   | 0.4    |
|                 | -2.3      | +    | +   | +      | 0.2  | 3.0  | -214.4 | 436.7 | 2.6   | 0.1    |
|                 | -2.2      | +    | 0.1  | 3.0    | -215.6 | 439.1 | 5.0   | 0.0    |
|                 | -2.2      | +    | 0.1  | 2.0    | -219.8 | 445.6 | 11.4  | 0.0    |
|                 | -2.1      | +    | 0.1  | 2.0    | -227.3 | 459.3 | 25.1  | 0.0    |
|                 | -2.0      | +    | 0.0  | 2.0    | -235.2 | 476.2 | 42.1  | 0.0    |
|                 | -1.9      | 0.0  | 0.0  | -241.7 | 485.4 | 51.3 | 0.0    |
| *P. acerosa*    | -2.0      | +    | +   | 0.7    | 4.0  | -17.5 | 47.4  | 0.0   | 0.3    |
|                 | -2.0      | +    | +   | +      | 0.7  | 4.0  | -17.5 | 47.4  | 0.0   | 0.3    |
|                 | -0.9      | +    | 0.6  | 2.0    | -20.7 | 48.2  | 0.8   | 0.2    |
|                 | -1.6      | +    | 0.6  | 4.0    | -18.8 | 48.7  | 1.3   | 0.2    |
|                 | -0.9      | +    | 0.6  | 4.0    | -20.1 | 51.2  | 3.8   | 0.0    |
|                 | -1.4      | +    | 0.4  | 2.0    | -23.1 | 53.0  | 5.6   | 0.0    |
|                 | -0.6      | +    | 0.3  | 2.0    | -25.3 | 57.2  | 9.8   | 0.0    |
|                 | -0.3      | 0.0  | 0.0  | -28.5  | 59.2  | 11.8 | 0.0    |
| *P. levis*      | 1.1       | +    | 0.6  | 2.0    | -38.6 | 84.2  | 0.0   | 0.4    |
|                 | 1.1       | +    | 0.6  | 3.0    | -37.9 | 86.0  | 1.8   | 0.2    |
|                 | 1.1       | 0.6  | 3.0  | -37.9  | 86.0  | 1.8   | 0.2    |
|                 | 1.1       | +    | 0.6  | 3.0    | -37.9 | 86.0  | 1.8   | 0.2    |
|                 | 1.2       | +    | 0.3  | 3.0    | -43.0 | 93.4  | 9.2   | 0.0    |
|                 | 1.2       | +    | 0.2  | 2.0    | -44.5 | 93.6  | 9.4   | 0.0    |
|                 | 1.3       | 0.0  | 0.0  | -47.1  | 96.4  | 12.1  | 0.0    |
|                 | 1.3       | +    | 0.0  | 2.0    | -46.9 | 98.6  | 14.3  | 0.0    |
| *P. linearis*   | 0.8       | +    | 1.0  | 2.0    | -36.9 | 81.1  | 0.0   | 0.6    |
|                 | 0.8       | +    | 1.0  | 3.0    | -36.6 | 83.6  | 2.5   | 0.2    |
|                 | 0.8       | +    | 1.0  | 4.0    | -36.3 | 83.9  | 2.8   | 0.1    |
|                 | 0.8       | +    | 1.0  | 4.0    | -36.3 | 83.9  | 2.8   | 0.1    |
|                 | 1.0       | +    | 1.0  | 4.0    | -45.2 | 103.6 | 22.4  | 0.0    |
|                 | 1.3       | +    | 0.8  | 2.0    | -72.3 | 151.7 | 70.6  | 0.0    |
|                 | 1.4       | +    | 0.7  | 2.0    | -74.5 | 156.2 | 75.1  | 0.0    |
|                 | 1.6       | 0.0  | 0.0  | -88.9  | 180.0 | 98.9  | 0.0    |
| Species       | Intercept | Xday | DT   | Xnight | $R^2$ | df  | logLik | AICc | Delta | Weight |
|---------------|-----------|------|------|--------|-------|-----|--------|------|-------|--------|
| *P. nutans*   | 1.1       | +    | 0.6  | 2.0    | −39.7 | 86.7| 0.0    | 0.4  |       |        |
|               | 1.1       | +    | +    | 0.6    | 4.0   | −37.7| 87.9   | 1.3  | 2.1   | 0.2    |
|               | 1.1       | +    | +    | +      | 0.6   | 3.0 | −39.3  | 88.8 | 2.1   | 0.1    |
|               | 1.2       | +    |       |        | 0.4   | 2.0 | −42.8  | 92.7 | 6.0   | 0.0    |
|               | 1.2       | +    | +    |        | 0.4   | 3.0 | −42.8  | 95.7 | 9.0   | 0.0    |
|               | 1.3       | +    |       |        | 0.0   | 0.0 | −48.0  | 98.2 | 11.6  | 0.0    |
| *P. pauciflora* | 0.1      | +    | +    | +      | 0.5   | 5.0 | −58.8  | 129.4| 0.0   | 0.4    |
|               | 0.1       | +    | +    |        | 0.5   | 4.0 | −59.8  | 130.4| 1.0   | 0.2    |
|               | 0.1       | +    |       | +      | 0.5   | 4.0 | −60.2  | 130.9| 1.4   | 0.2    |
|               | 0.2       | +    | +    |        | 0.5   | 4.0 | −60.5  | 131.3| 1.9   | 0.1    |
|               | 0.2       | +    |       |        | 0.4   | 2.0 | −62.8  | 132.0| 2.5   | 0.1    |
|               | 0.2       | +    |       | +      | 0.3   | 2.0 | −65.9  | 138.2| 8.8   | 0.0    |
|               | 0.3       | +    |       |        | 0.2   | 2.0 | −69.3  | 144.9| 15.4  | 0.0    |
|               | 0.4       | +    |       |        | 0.0   | 1.0 | −74.0  | 150.0| 20.6  | 0.0    |
| *P. pinifolia* | 1.0       | +    | +    |        | 0.9   | 4.0 | −39.8  | 91.7 | 0.0   | 0.4    |
|               | 1.0       | +    | +    | +      | 0.9   | 4.0 | −39.8  | 91.7 | 0.0   | 0.4    |
|               | 1.0       | +    |       | +      | 0.9   | 3.0 | −41.2  | 92.6 | 0.9   | 0.2    |
|               | 1.0       | +    | +    |        | 0.9   | 3.0 | −42.6  | 95.3 | 3.6   | 0.1    |
|               | 1.1       | +    |       |        | 0.8   | 2.0 | −45.8  | 98.8 | 7.0   | 0.0    |
|               | 1.1       | +    |       | +      | 0.7   | 2.0 | −52.1  | 110.2| 18.4  | 0.0    |
|               | 1.3       | +    |       |        | 0.4   | 2.0 | −59.3  | 125.7| 34.0  | 0.0    |
|               | 1.3       | +    |       |        | 0.0   | 0.0 | −65.0  | 132.3| 40.6  | 0.0    |
APPENDIX 3

Germination probability within protected areas of the species ranges under historic (1970–2000) conditions of monthly $\overline{X}_{\text{day}}$, $\overline{X}_{\text{night}}$ and $\Delta T\delta$ (Bureau of Meteorology, 2018) and three climate change projections of temperatures under future (year 2080) Representative Concentration Pathways (RCPs) (Vuuren et al., 2011).