

Population variation in germination traits and its implications for responses to climate change in a fire-prone plant species complex

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Abstract Many plants in fire-prone environments have limited dispersal ability and thus rely on in situ mechanisms such as evolutionary responses to persist through climate change. The regenerative phases of the plant life cycle, such as seed dispersal, germination and seedling establishment, are likely to be critical to defining species' environmental niches and, in fire-prone environments, are cued to fire events. Adaptive potential in traits that regulate these processes is key to in situ persistence, yet variability in fire adaptive traits at the population level remains largely unexplored. To investigate adaptive potential, we quantified population-level variability in the thermal germination niche of a widespread fire-prone species complex, the *Banksia spinulosa* group. In one of the first studies of rising temperatures on germination in serotinous plants, we sampled seeds from 12 source populations spanning seven degrees of latitude and more

than 1000 m of elevation and tested germinability over a range of incubation temperatures in common laboratory conditions. Thermal germination niches varied appreciably among source populations, suggesting local adaptation or other mechanisms of differentiation. Some of this variation was explained by current taxonomic boundaries, but germination responses also varied within recognised taxa and within populations. A small but significant portion of the interpopulation variation was related to thermal conditions at the source populations. As well, intrapopulation variation was greater within source populations of taxa from warm climates than those from cooler climates. The expected effect of warming is to narrow the window for germination to the cooler months of the year. The development of fire management strategies that reduce risks of post-fire mortality of seeds and seedlings, and exploit adaptive potential to promote in situ persistence as the climate changes, should therefore be a priority for climate adaptation research.

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Introduction

Species may persist through climatic change either by displaying phenotypically plastic responses that buffer negative change, migrating to track shifts in

suitable climates, or by adapting in situ to new conditions (Hoffmann and Sgrò 2011). The latter may occur through phenotypic plasticity (Nicotra et al. 2010) or selection of variants in local populations, perhaps aided by migration of genotypes from other populations across the landscape. Such adaptive responses require genetic variability in ecologically relevant traits (Sgrò et al. 2010; Nicotra et al. 2010).

Early studies of adaptive diversity suggest interactions between genotype performance and the environment. In *Eucalyptus camaldulensis*, for example, Gibson et al. (1995) found that genotypes from arid environments allocated more resources to root development than those from humid environments, conferring a fitness advantage in dry conditions and, in part, defining the environmental niche of the species. Often, these genotype-environment relationships may have strong spatial expression, suggesting local adaptation in response to selection pressure and limited gene flow among populations.

In plants, the most relevant traits to population persistence are likely to be those influencing dispersal, germination and establishment because selection pressures are likely to be highest in these regenerative phases of the life cycle (Harper 1977). The environmental conditions in which these regenerative processes operate define the ‘regeneration niche’ of a species (Grubb 1977). If prevailing environmental conditions move beyond those defining the regeneration niche, recruitment cannot replace established individuals that senesce or die of other causes, resulting in eventual local extinction unless the population rapidly adapts to recruit under the new conditions (Hudson et al. 2015).

Many plants have limited dispersal ability compared to other organisms (Kinlan and Gaines 2003) and may be unlikely to track suitable habitats at the pace that they are projected to shift as the climate changes. For some species, the area of climatically suitable habitat is projected to contract and disappear in the coming decades (Thomas et al. 2004). Whether a species is unable to track shifts in habitat or whether habitat disappears, persistence of populations in situ is the only means of avoiding extinction. Adaptive potential is therefore crucial to persistence under environmental change (Sgrò et al. 2010).

In fire-prone environments, the conditions that define plant regeneration niches are closely associated with fire events (Keith 1996). Considerable advances

have been made in understanding the range of mechanisms and plant traits that influence recruitment in the post-fire environment (Auld and O’Connell 1991; Thomas et al. 2010; Ooi et al. 2012). However, few studies have examined the adaptive potential of these mechanisms and traits by investigating genetic or phenotypic variability at the population level. While significant intraspecific variation in germination response has been documented in a number of studies, patterns in relation to climatic gradients are generally inconsistent (Cochrane et al. 2014b). Hudson et al. (2015) found contradictory evidence on intraspecific variability in conditions required to break physical seed dormancy among the very few studies that addressed the issue. Intraspecific variability is even less understood in other aspects of fire-related plant regeneration niches.

To improve understanding of the adaptive potential of fire-prone plant species in a changing climate, we investigated germination responses to ambient temperatures, which are projected to increase in different parts of the world by up to 6 °C under a range of greenhouse gas concentration scenarios (IPCC 2013).

As an analytical framework for our study, we propose a simple bell-shaped model of a thermal germination niche (Cochrane et al. 2014a) whereby, in species with non-dormant seeds, germination response can be measured by the time taken for germination (radicle emergence) after seed wetting. Thus, germination is expected to occur most rapidly at the species’ thermal optimum, with germination times increasing as temperatures increase or decrease until thermal limits are reached, beyond which germination cannot occur. We used this model to examine variation in the thermal germination niche between and within populations of the *Banksia spinulosa* group, a species complex distributed widely across a climatically and edaphically heterogeneous fire-prone region in south-eastern Australia.

We undertook laboratory experiments to quantify (1) levels of variation in thermal germination niches between source populations and subspecific morphotaxa; (2) relationships between interpopulation variation and environmental conditions at the source population; (3) relationships between thermal germination niches and projected temperature changes at the locations of source populations; and (4) levels of variation in germination time within populations. We consider the implications of the results for adaptive

responses to climate change in fire-prone plants. We believe this is one of the first studies of germination responses to rising temperatures in fire-prone serotinous plants.

Methods

We collected seed from 12 populations (Table 1) across the distribution of the *Banksia spinulosa* group sensu lato in southeastern Australia. Sampling of populations was stratified along latitudinal (29.9–37.5°S) and altitudinal (4–1130 m) gradients. The taxa currently recognised within this group include *Banksia spinulosa* Sm. var. *spinulosa* (four populations sampled), *Banksia spinulosa* Sm. var. *collina* R.Br. (A.S. George) (four populations sampled), *Banksia cunninghamii* Sieber ex Rchb. (three populations sampled) and *Banksia neo-anglica* (A.S. George) Stimpson and J.J. Bruhl (one population sampled). All four taxa form a distinct clade (Cardillo and Pratt 2013) and had previously been regarded as races or forms within *B. spinulosa* (Jacobs and Pickard 1981).

In southeastern Australia, *Banksia* seed germinations occur outside the summer months, depending on the timing of the weakly seasonal rainfall. After warm season fires, seed release occurs *en masse* with most germinations typically delayed until autumn. A small fraction of seeds can be released spontaneously at

various times of the year and spring fires may result in germinations during late spring or early summer.

We collected infructescences (fruiting cones) from three maternal plants per population in March 1981, selecting the youngest mature cones available (all <2 years old). In the laboratory, we exposed the cones to heat in a muffle furnace for 60 s to stimulate the woody follicles to open, allowing manual extraction of seeds the next day. Prior testing had shown fully formed, firm seeds to be 100 % viable and germinable when watered. *Banksias* appear to have temperature requirements that are satisfied by constant, rather than alternating temperatures, despite diurnal variations in the field (Cochrane et al. 2014a). We therefore exposed three replicate samples of 15 fully formed, firm seeds from each maternal plant within each population to five constant incubation temperature treatments: 10; 15; 20; 25 and 30 °C. We placed seeds in sterile petri dishes on filter paper, irrigated them with distilled water and monitored individual seeds each day until emergence of a radicle. The experiment was terminated after 50 days, when new germinations had slowed to a trace rate and all 15 seeds had germinated in the majority of replicates.

To examine germination responses, we calculated the median germination time (G50): the time taken for radicle emergence in half of the seeds that germinated within 50 days for each replicate. We fitted a series of

Table 1 Source populations of *Banksia spinulosa* sensu lato from which seeds were sampled for the germination experiment

Taxon	Population	Location	Elevation (m)	Latitude (°S)	Longitude (°E)
<i>Banksia spinulosa</i> var <i>collina</i>	HW	Halfway Creek	85	29.9081	153.0673
<i>Banksia spinulosa</i> var <i>collina</i>	AR	Arakoon	24	30.8802	153.0722
<i>Banksia spinulosa</i> var <i>collina</i>	LA	Laurieton	26	31.6323	152.7551
<i>Banksia spinulosa</i> var <i>collina</i>	KA	Karuah	38	32.6336	152.0097
<i>Banksia spinulosa</i> var <i>spinulosa</i>	MO	Mt Ousley	436	34.3899	150.8799
<i>Banksia spinulosa</i> var <i>spinulosa</i>	SI	Sussex Inlet	44	35.0859	150.5040
<i>Banksia spinulosa</i> var <i>spinulosa</i>	EL	East Lynne	74	35.5402	150.2993
<i>Banksia spinulosa</i> var <i>spinulosa</i>	SM	South Merimbula	4	36.9052	149.9013
<i>Banksia neo-anglica</i>	TO	Torrington	1130	29.2989	151.6870
<i>Banksia cunninghamii</i>	KW	Kanangra Walls	1084	33.9906	150.1033
<i>Banksia cunninghamii</i>	FF	Fitzroy Falls	658	34.647	150.4818
<i>Banksia cunninghamii</i>	WI	Wingan Inlet	140	37.5897	149.4808

Latitude and longitude are given in decimal degrees on the Geodetic Datum of Australia 1994

generalised linear models with Poisson error distributions and log link functions to G50 after examination of residuals indicated reasonable linearity, normality and homogeneity of variance. The base model was a quadratic function of incubation temperature, simulating bell-shaped thermal germination niches. We quantified variation in response between populations by fitting a generalised linear mixed model that included the quadratic terms for incubation temperature and a random population term. We compared the Akaike Information Content (AIC) of this mixed model with the base model and calculated R^2 to quantify the variation in germination response accounted for by the incubation treatment and source population.

To investigate how features of the seed source population affect germination responses, we fitted models including the base quadratic terms for incubation temperature and additional terms representing the taxonomic relationships and bioclimatic characteristics of the source populations. Taxonomic relationships were represented by a fixed factor with one level for each of the four recognised taxa. We investigated whether ambient temperature conditions at the source populations influence germination response by fitting mean, maximum and minimum annual temperature values for the 30-year period centred on 1990 for each location. Similarly, we tested the effect of temperature variability at the source populations by fitting mean diurnal temperature range and temperature seasonality based on the coefficient of variation of weekly means relative to the annual mean. We first tested these predictors individually and then tested whether combinations of the best predictors produced a more informative model in terms of AIC and R^2 values. All bioclimatic variables were estimated from a spline surface fitted to weather station data in ANUCLIM 6.1 (<http://fennergchool.anu.edu.au/files/anuclim61.pdf>).

Finally, we quantified projected changes in temperature for variables that were identified in the models as good predictors of germination response. We used outputs from four global circulation models under the A1FI greenhouse gas emission scenario (IPCC 2007). These four models (CSIRO-Mk3; GDFL-CM2; MPMP-ECHAM5 and UKMO-HADCM3) had previously been shown to produce regionally skilled projections of temperature for southeastern Australia (Suppiah et al. 2007).

Results

There was a strong quadratic response of germination time to incubation temperature, which accounted for 31 % of the variation in the base model with no covariates (Base GLM, Table 2), supporting the bell-shaped thermal niche model (Fig. 1). There was significant variation in this response between populations, with a random effect term accounting for 34 % of the remaining variation in the data after variation accounted for by the base model was excluded (Population GLMM, Table 2).

Addition of a ‘taxon’ factor to the base model produced a substantially more informative prediction of germination response than the base model, accounting for a total of 50 % of variation in the data (Taxon GLM, Table 2). Mean germination times (Fig. 2) did not differ between the two varieties of *B. spinulosa* ($t = 1.13$, $P = 0.26$); however, *B. neo-anglica* had somewhat shorter germination times ($t = 3.11$, $P = 0.002$) and *B. cunninghamii* had markedly longer germination times ($t = 8.81$, $P \ll 0.0001$).

Mean annual temperature (T_{mean} GLM) and mean minimum temperature (T_{min} GLM) did not improve the fit of the base model; however, mean maximum temperature accounted for 10 % of remaining variation after the base model (T_{max} GLM, Table 2). Diurnal temperature range at the source population (T_{diurnal} GLM) accounted for 16 % of remaining variation in the data over the base model, but temperature seasonality (T_{seas} GLM) did not improve the fit of the base model. Germination times were inversely related both to maximum temperatures and diurnal temperature range at the source population (Table 2; Fig. 1).

The most informative model included a taxon factor and Diurnal temperature at the source population (Taxon + T_{diurnal} GLM, Table 2). This model accounted for 56 % of total variation in the data and 36 % of remaining variation after fitting the base model.

Intrapopulation variability in germination responses differed between populations and was positively related to the mean maximum temperature at the source population (Fig. 3).

Temperatures are projected to increase at similar rates across all populations during the twenty-first century but the projected rates differed between the four GCMs. We therefore present projections for each GCM averaged across all populations. The CSIRO-

Table 2 Models of germination response to incubation temperature

Model	Rationale	Incubation temperature	Additional predictor(s)	AIC	R ²
Base GLM	Underlying germination response to temperature	Linear and quadratic terms	–	1287.6	0.314
Population GLMM	Test whether germination response varies between populations	Linear and quadratic terms	Random population factor (12 levels)	1142.4	0.548
Taxon GLM	Test whether & how germination response vary between taxa	Linear and quadratic terms	Fixed taxon factor (4 levels)	1173.2	0.497
Tmean GLM	Compare temperature means and extremes at source as potential selection pressure on germination response	Linear and quadratic terms	Linear variable mean annual temperature at source population	1270.5	0.343
Tmax GLM	Compare temperature means and extremes at source as potential selection pressure on germination response	Linear and quadratic terms	Linear variable mean maximum temperature at source population	1243.8	0.384
Tmin GLM	Compare temperature means and extremes at source as potential selection pressure on germination response	Linear and quadratic terms	Linear variable mean minimum temperature at source population	1289.2	0.314
Tdiurnal GLM	Compare indices of temperature variability at source as potential selection pressure on germination response	Linear and quadratic terms	Linear variable mean temperature range at source population	1218.7	0.422
Tseasonal GLM	Compare indices of temperature variability at source as potential selection pressure on germination response	Linear and quadratic terms	Linear variable mean temperature range at source population	1286.7	0.318
Tmax + Tdiurnal GLM	Explore best predictive model for germination response	Linear and quadratic terms	As for respective variables above	1187.8	0.472
Taxon + Tdiurnal GLM	Explore best predictive model for germination response	Linear and quadratic terms	As for respective variables above	1133.2	0.562

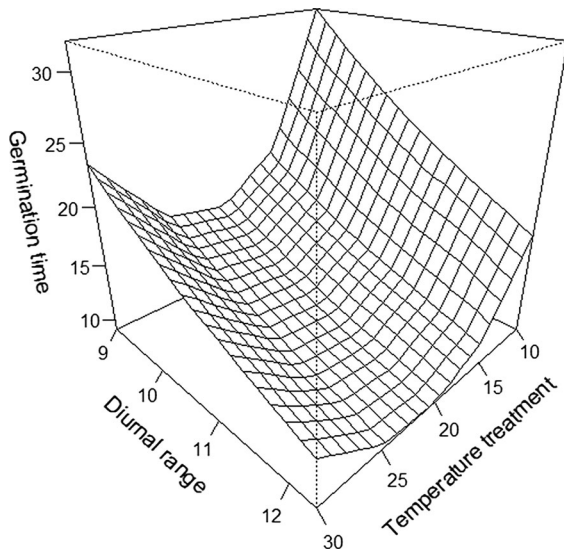


Fig. 1 Modelled variation in median germination time with incubation temperature and diurnal temperature range at source population. Model is $G50 = 4.66 - 1.49T + 2.91T^2 - 0.18DR$, where $G50$ is the time (days) taken for half the germinable seed sample to germinate, T is the incubation temperature and DR is the mean diurnal temperature range at the location of the source population

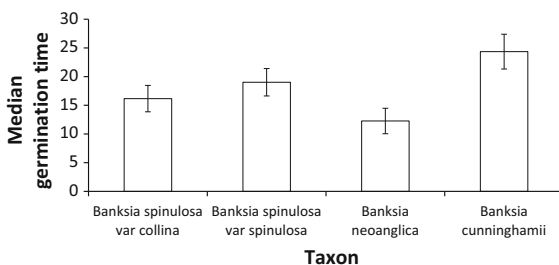


Fig. 2 Taxonomic variation in median germination time ($G50$) in days

Mk3 model projected an increase in the mean diurnal temperature range of 0.5–1.1 °C by year 2100, whereas the other three models projected no appreciable change. Over the same period, projected increases in mean maximum temperatures varied from 3.7 °C (UKMO-HADCM5) to 5.8 °C (CSIRO-Mk3) (Fig. 4).

Discussion

Our results suggest substantial variation in thermal germination niches between populations. Phylogeny

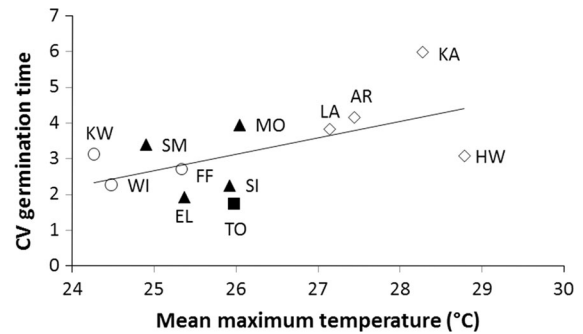


Fig. 3 Relationship between intrapopulation variation in germination time and mean maximum temperature (T_{max}) for 12 study populations of *Banksia spinulosa* sensu lato. Data are pooled for all five incubation temperatures (coefficient of variation CV for $n = 45$ seeds). Linear regression $CV_{Germination\ time} = 0.46T_{max} - 8.75$, $R^2 = 0.32$, $n = 12$. See Table 1 for population codes. Symbols represent different taxa: open circles—*B. cunninghamii*; filled squares—*B. neoanglica*; filled triangles—*B. spinulosa* var. *spinulosa*; open diamonds—*B. spinulosa* var. *collina*

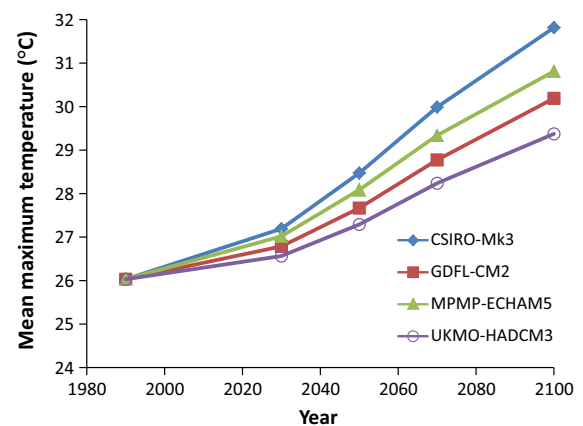


Fig. 4 Projected increase in mean maximum temperatures pooled across twelve *Banksia spinulosa* sensu lato. Study populations for AIFI greenhouse gas emission scenario based on four regionally skilled global circulation models (GCMs)

accounted for much of this variation, with *B. cunninghamii*, the sister group to the other three taxa (Cardillo and Pratt 2013), having the most distinct thermal germination niche. Based on molecular dating, Cardillo and Pratt (2013) estimate that *B. cunninghamii* diverged from the other taxa about 2.5 million years ago. It is also noteworthy that *B. cunninghamii* is the only obligate seeder in the group, and hence entirely dependent on regeneration from seed after fire. Among the facultative seeders, the available data suggest that *B. neoanglica* and *B. spinulosa* var. *collina* had different thermal

germination niches and diverged more recently from each other than they did from *B. cunninghamii*, but estimates of both the niche and the phylogeny for *B. neo-anglica* were based on small sample sizes and warrant further resolution.

We detected a weak relationship between thermal germination niche and thermal conditions at the source population. Specifically, for a given incubation temperature, seeds from sites with larger diurnal temperature ranges and higher maximum temperatures had more rapid germination times than seeds from sites with converse conditions. Although these signals were weak (accounting for 16 and 10 % of variation in niches within taxa, respectively), they contrast with *Banksia* species from southwestern Australia, in which intraspecific variation in germination niche was unrelated to climate (Cochrane et al. 2014a). The covariables were derived from modelled spline surfaces interpolated from weather station data, and are likely to offer a rather coarse and indirect representation of temperatures experienced by seed on post-fire soil surfaces in the field. Future development of finer resolution temperature data reflecting local topographic variations in field temperatures (Ashcroft and Gollan 2013) should enable more definitive analyses of field conditions experienced by maternal plants.

Although our data suggest that intrapopulation variability in germination time may increase with maximum temperature at source populations across all taxa, this was almost entirely due to greater variability within populations of *B. spinulosa* var. *collina* relative to other taxa. Our estimates of intrapopulation variability were also limited by the fact that the 45 replicate seeds were sampled from only three maternal plants per population. Further work is needed to determine whether the climate influences intrapopulation variability in germination niches.

There appears to be considerable capacity for seeds from all sampled populations to germinate under a wide range of thermal conditions. At least 50 % of seeds from all populations germinated within 50 days at the highest temperature tested (30 °C). Cochrane et al. (2014a) found similar responses at 30 °C among southwestern Australian banksias, but germination responses of those species appear to be diminishing more rapidly at high temperature than in eastern taxa. Indeed, optimal germination temperatures (at which germination is most rapid) were higher and varied

across a wider range among populations of the *Banksia spinulosa* group (24–29 °C) compared to the four more phylogenetically divergent taxa from the south coast of Western Australia (15–17°), studied by Cochrane et al. (2014a). Although their estimates were based on mean germination times, rather than G50, the magnitude of difference is substantial and possibly reflects stronger selection for germination to occur in cooler months in southwestern Australia to coincide with strongly seasonal winter rains. In comparison, seasonal patterns of rainfall are relatively weak in the southeast and selection for germination in winter may be weaker.

A number of possible mechanisms could explain the expression of variation in thermal germination niches under common laboratory conditions. These include genetic divergence (local adaptation) in germination traits among populations, genetically based differences in phenotypic plasticity between populations, epigenetic processes operating during the development of ovules or seeds, or differences in resourcing (e.g. rainfall) during seed development at the source populations (Nicotra et al. 2010). Resolution of these mechanisms requires further experimentation.

On the face of it, the relatively broad niches observed in this experiment suggest that germination in these taxa is relatively robust to temperature changes, at least to the more modest increases projected across the populations. The shapes of responses suggest that the upper thermal limit for most populations is considerably greater than 30 °C. Mean maximum (air) temperatures at all source populations are currently below this level. However, soil surface temperatures experienced by seeds are substantially greater than air temperatures. Ooi et al. (2012), for example, found that maximum soil surface temperatures were, on average, 1.8 times greater than maximum air temperatures in a semi-arid sand dune landscape. If a similar relationship applies for post-fire soil surfaces in our study area, then the mean maximum soil surface temperature at our warmest site could exceed 50 °C.

While further investigations are needed to determine how close ambient post-fire soil surface temperatures are to thermal limits of germination for different populations, the expected effect of warming is a narrowing of the germination window to the cooler months of the year. For fires occurring between late

spring and late summer, this could mean a more prolonged exposure of seeds to pathogens and predators until temperatures become suitable for germination. In situ population persistence will also hinge on the sensitivity of processes such as inflorescence production, seed set and seedling establishment to future climates, particularly future rainfall and its interaction with changing fire regimes (Enright et al. 2015).

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References

- Ashcroft MB, Gollan JR (2013) Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: understanding factors that promote microrefugia. *Agric For Meteorol* 176:77–89
- Auld TD, O’Connell MA (1991) Predicting patterns of post-fire germination in 35 Eastern Australian Fabaceae. *Aust J Ecol* 16:53–70
- Cardillo M, Pratt R (2013) Evolution of a hotspot genus: geographic variation in speciation and extinction rates in *Banksia* (Proteaceae). *BMC Evol Biol* 13:155
- Cochrane A, Hoyle GL, Yates CJ, Wood J, Nicotra AB (2014a) Predicting the impact of increasing temperatures on seed germination among populations of Western Australian *Banksia* (Proteaceae). *Seed Sci Res* 24:195–205
- Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2014b) Will among-population variation in seed traits improve the chance of species persistence under climate change? *Glob Ecol Biogeogr* 24:12–24
- Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front Ecol Environ* 13:265–272
- Gibson A, Bachelard EP, Hubick KT (1995) Relationship between climate and provenance variation in *Eucalyptus camaldulensis* Dehnh. *Aust J Plant Physiol* 22:453–460
- Grubb P (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145
- Harper JL (1977) *Population biology of plants*. Academic press, London
- Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature* 470:479–485
- Hudson AR, Ayre DJ, Ooi MKJ (2015) Physical dormancy in a changing climate. *Seed Sci Res* 25:66–81. doi:10.1017/S0960258514000403
- IPCC (2007) *Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change*. IPCC, Geneva
- IPCC (2013) *Annex I: atlas of global and regional climate projections* (van Oldenborgh GJ, Collins M, Arblaster J, Christensen JH, Marotzke J, Power SB, Rummukainen M, Zhou T, eds). In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) *Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge
- Jacobs SWL, Pickard J (1981) *Plants of New South Wales: a census of the cycads, conifers and angiosperms*. Royal Botanic Gardens, Sydney
- Keith DA (1996) Fire-driven mechanisms of extinction in vascular plants: a review of empirical and theoretical evidence in Australian vegetation. *Proc Linn Soc NSW* 116:37–78
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. *Trends Plant Sci* 15:684–692
- Ooi MKJ, Auld TD, Denham AJ (2012) Projected soil temperature increase and seed dormancy response along an altitudinal gradient: implications for seed bank persistence under climate change. *Plant Soil* 353:289–303
- Sgrò CM, Lowe AJ, Hoffmann AA (2010) Building evolutionary resilience for conserving biodiversity under climate change. *Evol Appl* 4:326–337
- Stimpson ML, Weston PH, Telford IRH, Bruhl JJ (2012) First instalment in resolution of the *Banksia spinulosa* complex (Proteaceae): *B. neoanglica*, a new species supported by phenetic analysis, ecology and geography. *PhytoKeys* 14:57–80
- Suppiah R, Hennessy KJ, Whetton PH, McInnes K, Macadam I, Bathols J, Ricketts J, Page CM (2007) Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. *Aust Meteorol Mag* 56:131–152
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ et al (2004) Extinction risk from climate change. *Nature* 427:145–148
- Thomas PB, Morris EC, Auld TD, Haigh AM (2010) The interaction of temperature, water availability and fire cues regulates seed germination in a fire-prone landscape. *Oecologia* 162:293–302