







Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples

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Abstract The effects of anthropogenic climate change on biodiversity are well known for some high-profile Australian marine systems, including coral bleaching and kelp forest devastation. Less well-published are the impacts of climate change being observed in terrestrial ecosystems, although ecological models have predicted substantial changes are likely. Detecting and attributing terrestrial changes to anthropogenic factors is difficult due to the ecological importance of extreme conditions, the noisy nature of short-term data collected with limited resources, and complexities introduced by biotic interactions. Here, we provide a suite of case studies that have considered possible impacts of anthropogenic climate change on Australian terrestrial systems. Our intention is to provide a diverse collection of stories illustrating how Australian flora and fauna are likely responding to direct and indirect effects of anthropogenic climate change. We aim to raise awareness rather than be comprehensive. We include case studies covering canopy dieback in forests, compositional shifts in vegetation, positive feedbacks between climate, vegetation and disturbance regimes, local extinctions in plants, size changes in birds, phenological shifts in reproduction and shifting biotic interactions that threaten communities and endangered species. Some of these changes are direct and clear cut, others are indirect and less clearly connected to climate change; however, all are important in providing insights into the future state of terrestrial ecosystems. We also highlight some of the management issues relevant to conserving terrestrial communities and ecosystems in the face of anthropogenic climate change.

Key words: biodiversity, biotic interactions, climate change, terrestrial.

INTRODUCTION

There is evidence from around the world that anthropogenic climate change is impacting biological systems at multiple scales – from genes to ecosystems.

Much of the early focus has been on the Northern Hemisphere where range shifts in both terrestrial and marine ecosystems have been documented, as well as phenological shifts involving the seasonal timing of growth and reproduction in birds, insects and flowering plants (Parmesan & Yohe 2003). In addition, there is now evidence for shifts in levels of genetic variation in populations and in spatial patterns of

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alleles and traits across populations, shifts in the structure of vegetation communities, and in measures of ecosystem functioning. Anthropogenic climate change has now impacted 82% of 94 core ecological processes recognized by biologists, from genetic diversity to ecosystem function (Scheffers *et al.* 2016).

In Australia, climate change effects on marine systems have been well documented. Notable examples include repeated severe bleaching events in the Great Barrier Reef (Hughes *et al.* 2017) and other reefs (Le Nohaïc *et al.* 2017), which has resulted in proposals for dramatic solutions given the biological and economic importance of this resource (Anthony *et al.* 2017). Other changes in marine systems receiving attention include distribution shifts of fish along the eastern seaboard (Pollock 2017), and the collapse of kelp forests (Verges *et al.* 2016). In addition, intertidal ecosystems including mangrove forests are being affected by increased variability of sea levels (Lovelock *et al.* 2017).

While natural terrestrial systems have perhaps received less attention, there are nevertheless emerging signs of the effects of climate change. In Australia's terrestrial systems, the signal-to-noise ratio of anthropogenic climate change is high because of background changes in climate-related factors such as droughts, bushfires, disease, extreme temperatures and rainfall volatility. Thus, scientists face difficulty separating anthropogenic climate change trends from cyclical events and their consequences. This means that signals of climate change may take decades before becoming detectable from background variability (Greenville *et al.* 2018). Examples of terrestrial shifts clearly linked to anthropogenic climate change include phenological shifts in the arrival time of common brown butterflies (Kearney *et al.* 2010), genetic changes in flies (Umina *et al.* 2005), leaf shape changes in vegetation (Guerin & Lowe 2013), push-pulse events in Gondwanan forests, river red-gum forests and the arid zone (Harris *et al.* 2018) and the first mammalian extinction in a low elevation sand cay in the Torres Strait (Waller *et al.* 2017). In an agricultural context, there are also well-documented examples linked to anthropogenic climate change, such as a shift in harvest time in vineyards (Jarvis *et al.* 2017).

Australian terrestrial research led the way in modelling predicted climate change and its effects. Early on, CLIMEX modelling was developed as a semi-mechanistic approach to understand how species interact with climate, to predict distribution shifts in a range of species (Sutherst & Maywald 1985). This was followed by local applications of these, and other species distribution models, to predict extinction risk (e.g. Williams *et al.* 2003a). Such models have highlighted the limits of our national reserve system in

maintaining biodiversity under climate change (Dunlop & Brown 2008). Detailed mechanistic models have also been developed to incorporate timing issues and evolutionary changes in predicting climate change impacts (e.g. Kearney *et al.* 2009; Bush *et al.* 2016). There is now a vast body of Australian literature on the predicted effects of climate change on species distributions, phenotypic traits and biodiversity more generally.

In this paper, our aim is to highlight the diverse ways in which climate change is – and is likely to – alter natural terrestrial biological systems. We undertake this exercise by focusing on eight examples (Appendix 1) that illustrate the types of effects being observed around Australia. The aim is not to provide a comprehensive survey of what is happening and what might happen in the future; such a report card was undertaken a few years ago (Bowman *et al.* 2013). Rather, we aim to provide examples that help raise awareness of individual cases, as well as an appreciation of the depth and breadth of the impacts of climate change. We hope to encourage managers to look at climate change in their own backyard from a variety of perspectives. We outline each example and then raise some general points at the end of the paper. Throughout and in keeping with other efforts (e.g. Williams *et al.* 2017), we emphasize future directions to inform planning in both management and research, especially given the urgency, complexity and importance of the situation.

CASE STUDY 1. DROUGHT-INDUCED CANOPY DIEBACK IN SOUTHWESTERN AUSTRALIA

Rising temperatures and altered rainfall patterns due to changing climate can cause large-scale forest dieback, with major consequences for the maintenance of biodiversity, ecosystem function and resilience of native forests and woodlands (Allen *et al.* 2010; Anderegg *et al.* 2013). Southwestern Australia, a Biodiversity Hotspot, has forest and woodland environments that have experienced significant decline directly attributed to a recently changing climate.

The long-term average rainfall in the southwestern region has already declined by 15–20% in the last 30 years (Bates *et al.* 2008) with a background temperature increase of ~1°C (The Australian Climate Observations Reference Network – Surface Air Temperature, www.bom.gov.au). In addition to this long-term trend of drying and warming, an acute drought (40–50% reduction in annual rainfall), and a series of heatwaves (53 days >35°C maximum daily temperature; Perth Airport, www.bom.gov.au) in the summer of 2010/11 resulted in a significant canopy

dieback across a range of forest and woodland types, including *Eucalyptus marginata*, *Corymbia calophylla* (Matusick *et al.* 2013), *Banksia attenuata*, *Banksia menziesii* (Bader *et al.* 2014; Challis *et al.* 2016) and *Eucalyptus gomphocephala* (Matusick *et al.* 2013). Dieback in the Northern Jarrah Forest (*E. marginata* and *C. calophylla*) (Fig. 1) was associated with sites with low water holding capacity, rocky outcrops (Brouwers *et al.* 2013a) and more xeric areas (Andrew *et al.* 2016). Furthermore, drought-affected trees with lower levels of tissue moisture were associated with an outbreak of the native *Eucalyptus* longhorned borer, *Phoracantha semipunctata* (Cerambycidae) (Seaton *et al.* 2015). Dieback also substantially increased fine fuel loads and standing dead wood, and fire spread rates were predicted to be 30% greater in dieback plots (Ruthrof *et al.* 2016). Following dieback events, the forest and woodlands systems are characterized by altered structure via a decrease in height and prolific resprouting (Pekin *et al.* 2009; Ruthrof *et al.* 2015; Matusick *et al.* 2016).

Decline in the woodland tree, *Eucalyptus wandoo*, has been documented over the past 30 years, and is believed to be associated with declining rainfall, particularly on the eastern (i.e. dry) margin of its distribution (Brouwers *et al.* 2013b; Poot & Veneklaas 2013). Phylogeographic analysis and spatial distribution modelling for this species indicate recent declines in drier areas may represent contraction from areas of previous expansion during more mesic conditions since the Last Glacial Maximum (Dalmaris *et al.* 2015).

Rainfall in southwestern Australia is predicted to decline further (Bates *et al.* 2008) and warming is predicted to occur with more frequent and intense droughts and heat waves (Field *et al.* 2014). The ability for populations to persist under a rapidly changing climate depends on their degree of sensitivity and/or resilience to limited water availability and high temperatures, which, in turn, is determined by physiological tolerance and adaptive genetic variation (Hoffmann & Sgrò 2011). Concern about management of climate change impacts in southwestern forests and woodlands has prompted investigation of signals of genetic adaptation to climate in eucalypts in this region. Widespread eucalypts in both western and eastern Australia show genetic connectivity and adaptive genetic variation associated with temperature and rainfall gradients (McLean *et al.* 2014; Steane *et al.* 2014, 2017a; Jordan *et al.* 2017). Theoretical and empirical studies have demonstrated genetic variation within populations can enhance the capacity to persist under climate change (Bush *et al.* 2016); however, it remains uncertain if long-lived trees with overlapping generations can undergo adaptive shifts to keep pace with rapidly changing climates.

Phenotypic plasticity in physiological processes is thought to be the primary mechanism for trees to be able to persist under climate change (Thomas 2011). Indeed, eucalypts have documented short-term (dynamic) and long-term (adaptive) plasticity in functional and physiological traits (McLean *et al.* 2014; Drake *et al.* 2015; Steane *et al.* 2017a). Dry origin species (e.g. *E. accedens*, *E. wandoo*) tend to maintain function during the hot, dry, Mediterranean summer, supported by enhanced physiological tolerance to drought through resistance to stem xylem cavitation (Poot & Veneklaas 2013). Adaptive genetic changes in response to increases in drought frequency and intensity are also possible. For example, *C. calophylla* in warmer regions exhibit greater drought tolerance (P50leaf) relative to counterparts in cool regions of southwestern Australia (Blackman *et al.* 2017). Such enhanced drought resistance may come at a performance cost in terms of photosynthesis and growth (Aspinwall *et al.* 2017) with carbon allocated to structural tissue (Mitchell *et al.* 2014).

The future

Adaptive management strategies, such as assisted gene migration (Aitken & Whitlock 2013) and climate-adjusted provenancing (Prober *et al.* 2015), may help mitigate the extent of forest dieback associated with climate change and maintain ecosystem function (Lunt *et al.* 2013). In southwestern forests and woodlands, assisted migration of widespread foundation species (such as *C. calophylla*) may provide much needed adaptive capacity to withstand ongoing drying and warming. Although climate adaptation management strategies can be implemented in forest management and woodlands restoration programmes (Prober *et al.* 2016) and a consideration of seed sourcing for climate adaptation has already been incorporated into the Western Australia Forest Management Plan 2014–2023, more research is required before specific recommendations can be made. Experimental plantings with a range of species and genetic diversity, including species outside of their natural range, established across temperature and rainfall gradients, are needed to complement field surveys and glasshouse experiments, as well as providing infrastructure to characterize genetic adaptation and physiological tolerance to climate change.

There is limited information regarding forest ecological responses to climate change, and possible intervention techniques, and knowledge gaps remain. Does adaptive capacity differ among rare and widespread species, and those with different life histories? How is forest composition changing and where? What are the flow-on effects for faunal habitat? Are there changes in forest function (e.g. nutrient



Fig. 1. Aerial photo of a portion of the Northern Jarrah (*Eucalyptus marginata*) Forest, Western Australia at (a) three, and 16 months following drought from the (b) air and (c) ground. Scale bar represents approximately 200 m ((a) and (b) reproduced from Ruthrof *et al.* (2015)).

cycling), and what are the interactions with disturbances (e.g. fire)? As evidence emerges from current investigations, managers will start to have information regarding vulnerable forest sites and species, and options for potential intervention techniques, such as assisted migration, translocations and ecological restoration.

CASE STUDY 2. PSYLLIDS AND EUCALYPT DIEBACK IN THE SYDNEY REGION

Recent climate change influences insect population dynamics and is predicted to increase frequency and severity of insect pest outbreaks (Barbosa *et al.* 2012; Björkman & Niemela 2015). Climate change effects on insect pests have been reported for Northern Hemisphere systems (Battisti *et al.* 2005); however, less is known about such responses in Australia, except for predicted range-expansions of native and alien insect pests (Sutherst *et al.* 2007). Several pioneering Australian studies have demonstrated direct insect population responses to climatic factors, e.g. rainfall and temperature dependency in plague thrips (Davidson & Andrewartha 1948) and plague

locust populations (Farrow 1979), as well as indirect plant-mediated effects such as water deficit-inflicted plant stress driving eucalypt–psyllid outbreaks (White 1969).

The climate-dependency of psyllid outbreaks and their impact on *Eucalyptus* dieback (Fig. 2) have recently received renewed attention. A remarkable example involves repeated outbreaks of what appears to be a new psyllid species across thousands of hectares of the critically endangered Cumberland Plain Woodlands (CPW) of Western Sydney (Hall *et al.* 2015). This psyllid forms a species complex with two other *Cardiaspina* species (Hall *et al.* 2016; Morrow *et al.* 2017), but is associated with a distinct parasitoid community (Hall *et al.* 2017) and has a unique host plant association, feeding specifically on grey box (*Eucalyptus moluccana*), a dominant species in the CPW. It has not yet been found on *E. moluccana* outside the CPW and may constitute a new narrow-range endemic that has become a significant ecological issue for the CPW and potentially beyond, as *E. moluccana* is a common woodland tree species in eastern Australia (Flores-Renteria *et al.* 2017).

Cardiaspina nymphs feed on mature *Eucalyptus* leaves, excreting their characteristic lace lerp covers

under which they develop. This feeding activity induces leaf nutrient mobilization, senescence, necrosis and abscission (Steinbauer *et al.* 2014). At high *Cardiaspina* densities, canopies become completely defoliated, and repeated defoliation can cause tree dieback with consequences for woodland biodiversity and function. A multitude of factors may have ignited the outbreaks in the CPW, such as woodland clearing, fragmentation and loss of biodiversity together with the impacts of changes to soil water, increased nutrient influx and pollution. Climatic factors such as temperature and precipitation are also important. CPW sites with higher mean winter temperatures were defoliated first and experienced more damage (Hall *et al.* 2015), and temperature differences across the CPW landscape may have disrupted psyllid-parasitoid synchrony (Hall *et al.* 2017). Furthermore, psyllid generation number per year varies across climates: in the CPW grey box *Cardiaspina* sp. has four distinct, non-overlapping generations per year, whereas *Cardiaspina* species that occur in warmer climates have more generations, and *Cardiaspina* species that occur in cooler climates have fewer generations. In 2013, summer heatwaves (maximum over 46°C) in combination with resource depletion due to defoliation resulted in the collapse of the outbreaking grey box *Cardiaspina* sp., and it became undetectable throughout the CPW (Hall *et al.* 2015).



Fig. 2. Grey box (*Eucalyptus moluccana*) in a Cumberland Plain Woodland (CPW) remnant in Western Sydney (NSW) defoliated by *Cardiaspina* sp.; trees have been defoliated repeatedly leading to extensive tree dieback and mortality (Hall *et al.* 2015).

However, by mid-2015, population numbers increased and large parts of the CPW were defoliated again until a heatwave in early 2017 (maximum over 46°C) led to extreme reduction in psyllid populations that have not been recorded since (M. Riegler, personal observation).

The dependency of psyllid population dynamics on rainfall patterns, temperature and resource availability was further confirmed by concurring outbreaks of other psyllid species on forest red gum, *Eucalyptus tereticornis*, at the *Eucalyptus* Free Air CO₂ Experiment (EucFACE) in the CPW (Gherlenda *et al.* 2016a). After summer rainfall, the *E. tereticornis* canopy showed a rapid increase in leaf area index (Duursma *et al.* 2016) and rapid population growth of *Glycaspis brimblecombei*, a psyllid species whose nymphs preferentially develop on flush leaves. The high abundance of *G. brimblecombei* did not cause defoliation and dropped after the flush of leaves ceased. At the same time, abundance of *Cardiaspina fiscella*, a mature foliage specialist, rapidly increased and caused repeated defoliation of the canopy over two consecutive years until summer heat and resource depletion stopped this outbreak (Duursma *et al.* 2016).

The future

Defoliating psyllid populations experience rapid boom-and-bust cycles that depend on the availability of suitable foliage driven by rainfall (Gherlenda *et al.* 2016a) and are limited by extreme summer heat that reduces both population growth (Hall *et al.* 2015) and top-down control by parasitoids (Hall *et al.* 2017). Therefore, changes to rainfall patterns and increased frequency of heat extremes are expected to increase psyllid outbreak events. Another key driver of anthropogenic climate change is elevated atmospheric CO₂ that stimulates photosynthesis, growth and nutrient allocation in plants. It can also influence herbivore development and performance through plant-mediated effects such as shifts in the carbon to nitrogen (C/N) ratio, and changes in plant defence, as demonstrated for *Eucalyptus*-feeding cup moths and leaf beetles (Murray *et al.* 2013; Gherlenda *et al.* 2015, 2016b).

In 2012, EucFACE was started as an ecosystem-scale CO₂ fumigation experiment in a CPW remnant containing mature *E. tereticornis* as well as a range of shrubs and grasses. Against expectation, within the first three years of EucFACE being operational, no increase of eucalypt productivity was observed, likely due to the phosphorus limitation of the site, characteristic of many Australian ecosystems. This may limit the capacity of plants to turn elevated CO₂ into increased productivity, and conversely, the capacity

of forest ecosystems to act as buffer against increasing atmospheric CO₂ concentrations (Ellsworth *et al.* 2017). Ongoing research at EucFACE is further addressing this. The psyllid outbreak at EucFACE was not caused by the CO₂ treatment but was a landscape-scale perturbation that had started 10 km west of the site. All three investigated psyllid species produced fewer lerp at elevated CO₂ indicative of smaller psyllid populations at elevated CO₂, while individual lerp of one of the three species, the flush feeder *G. brimblecombei*, were heavier at elevated CO₂, indicative of compensatory feeding behaviour in this species (Gherlenda *et al.* 2016a). A population decline was also observed for above ground arthropod populations at elevated CO₂ without affecting community composition (Gherlenda *et al.* 2016a; Facey *et al.* 2017).

Despite these insights, a better understanding is still required of how eucalypt–psyllid interactions respond to temperature, rainfall patterns and CO₂ in combination with other biotic factors such as populations of natural enemies including parasitoids and birds, as well as with changes in plant communities and land use. The potential of localized psyllid outbreaks to spread across the entire distribution of a tree species requires further investigation, including the question of whether wide provenancing of tree genotypes as a suggested adaptive approach will expose these genotypes to new herbivore communities creating new pest problems. Once this information becomes available, options for managers to monitor and control psyllid outbreaks can be developed.

CASE STUDY 3. VEGETATION CHANGES IN THE ALPINE LANDSCAPE

Alpine ecosystems globally are at acute risk from climate change and in Australia components are considered ‘endangered’ based on the IUCN Red list criteria (Pickering *et al.* 2004; Williams *et al.* 2014). Temperatures have increased on average by 0.2°C per decade and expected to increase by 4–5°C by 2100 (Harris *et al.* 2016). Snow depth and duration have declined since records began in the 1950s, the date of snow melt in the Australian Alps is getting earlier by 2.75 days per decade (Green 2010), and snow is expected to be restricted to the highest peaks by 2100 (Harris *et al.* 2016).

The Bogong High Plains in Victoria has some of the longest running monitoring plots in Australia, in particular Maisie’s plots established in 1944 and 1946 to investigate grazing impacts in Alpine grasslands and heathlands. These plots and others (see Williams *et al.* 2014) form a unique resource for tracking climate effects on Alpine vegetation, particularly when coupled with field experimental plots that

have manipulated temperature (Wahren *et al.* 2013) and fire (Camac *et al.* 2017). The combination of both long-term monitoring and field experiments provide critical insights into the factors affecting current and future changes in Australian Alpine vegetation and associated ecosystem dynamics.

The highest profile experimental site on the Bogong High Plains is OZTEX – associated with the International Tundra Experiment (ITEX). This experiment was established at four sites near Falls Creek in 2003 to examine the effects of temperature increases on vegetation, soils and invertebrates using open topped chambers (OTCs) (Jarrad *et al.* 2009; Wahren *et al.* 2013; Camac *et al.* 2015). These chambers passively warm plots during the growing season by 1.1°C and increase extreme ambient temperatures by as much as 2°C. The manipulated climatic changes are similar in direction and match those observed over the last 30 years in other monitoring sites, where spring temperatures have increased by 0.4–1.1°C and annual precipitation has decreased by 6–17%, with intense periods of dryness during El Niño years (Wahren *et al.* 2013).

These environmental changes have led to shifts in vegetation in both experimental and long-term monitoring plots. Between 2004 and 2010, the cover of grasses and other graminoids decreased by up to 25%. In contrast, forb and shrub cover increased by 9% and 20%, respectively (Wahren *et al.* 2013). While changes in cover did vary across species within these life forms, the sharp decline in grass cover was mostly attributed to severe drought, with increases in shrubs and forbs attributed to increases in temperature, bare ground and climate-induced changes in biotic interactions between these life forms (Jarrad *et al.* 2009; Wahren *et al.* 2013; Camac *et al.* 2015). Overall, mean canopy height and species diversity measures increased. Diversity changes largely reflect changes in relative abundance, as opposed to an influx of new species. By contrast, invertebrate invasions are occurring as a result of warmer conditions (Nash 2013). These findings match observations in other tundra and Alpine ecosystems worldwide, where vegetation composition and structural changes documented in ITEX plots have then occurred in unwarmed control plots over an extended period (Myers-Smith *et al.* 2011).

In addition to changes in vegetation composition, monitoring in both the OTC and control plots has shown that warming alters Alpine flowering phenology (Hoffmann *et al.* 2010). While the magnitude of these changes was less than year-to-year variation in phenology, the rate and degree to which species respond to warming varied. For example, earlier seed maturation of the forb *Craspedia jamesii* was detected in warmed plots in just one year. By contrast, most other species (e.g. the forb *Erigeron bellidioides*, the

shrub *Asterolasia trymalioides* and the graminoids *Carex breviculmis* and *Poa hiemata*) required 2–4 years of cumulative warming before differences in phenology were discerned (Hoffmann *et al.* 2010). Compensatory effects occurred in some species. For example, *Poa hiemata* in OTCs flowered earlier, but compensated this earlier flowering by increasing the duration of seed maturation.

These findings point to some Alpine species having the ability to alter phenology rapidly under climate change whereas others lack this ability; although the fitness consequences of these different responses are unclear, flowering time and seed maturation will likely influence pollination success and predation risk, respectively. Overseas research has linked shifts in flowering time to reduced flower abundance and exposure to frost damage (Wheeler *et al.* 2015).

Fire also plays an important role in Australia's sub-Alpine and Alpine 'treeless' ecosystems. Over 85% of the Australian Alpine bioregion has been burnt in the last two decades (Bowman *et al.* 2014), with fire frequency and severity expected to increase under changing climate (Hennessy *et al.* 2003; Bradstock 2009; Williams *et al.* 2014). The impacts of increased fire frequency and severity are already evident in both Alpine ash (*Eucalyptus delegatensis*) and Alpine snow gum (*Eucalyptus pauciflora*) where repeated wildfires have led to a small fraction of the Australian Alps being burnt up to 3x between 2002 and 2013 (Bowman *et al.* 2014; Fairman *et al.* 2017). In multiple burned sites, grasses and shrubs trees are rapidly displacing trees as the interval between fires is inadequate for seed production (of Alpine ash) or has diminished resprouting ability (for snow gum). This has led to drastic management interventions, such as aerial sowing programmes, to maintain Alpine ash ecosystems in burnt areas (Bassett *et al.* 2015).

In Australia's Alpine 'treeless' ecosystems, shrubs are the most flammable vegetation component (Williams *et al.* 2006; Fraser *et al.* 2016). Long-term monitoring has revealed substantial increases in shrub cover, often at the expense of less flammable grassland (McDougall 2003; Wahren *et al.* 2013). Post-fire field surveys and experimental warming have revealed synergistic effects of fire and warmer temperatures on recruitment, growth and survival of seedlings of dominant shrubs (Camac *et al.* 2017). Specifically, fire increases the establishment of seedlings by as much as 33-fold via the creation of bare ground, and experimental warming of 1°C postfire doubles seedling growth rates and increases seedling survival.

Warmer temperatures are not detrimental for Australian Alpine shrubs; Camac *et al.* (2017) found that experimental warming postfire did not reduce seedling recruitment or enhance grass competition. Australian Alpine shrubs are also highly resistant to

freezing caused by climate-induced earlier snowmelt (Venn & Green 2018), and thus may utilize longer growing seasons. Warmer temperatures may reduce fire intervals that deplete shrub seedbanks, but these likely only influence part of the landscape. Post-fire shrub recovery is also resilient to changes in fire severity (Camac *et al.* 2013).

The future

The combination of these findings indicates that climatic warming and increased fire activity will favour shrubs. Consequently, highly flammable fuels will expand and accumulate more rapidly. Ultimately, these changes will strengthen a feedback between shrubs and fire by increasing fire frequency and severity (Fig. 3). In turn, this creates more bare ground, and thus more shrub recruitment opportunities (Williams *et al.* 2014) – changes with consequences for fire risk management, carbon sequestration, water supply and biodiversity. Management actions will depend on priorities for this region. If grasslands and herbfields are to be maintained, physical removal of shrubs might be required, while removal of introduced hard hoofed animals might also help as these create bare ground patches favouring shrubs. Shrub removal on a local scale might protect infrastructure by creating a fire barrier.

CASE STUDY 4. BIOTIC INTERACTIONS IN THE AUSTRALIAN ALPINE BIOREGION

Key threats in Australian Alpine Bioregion linked to anthropogenic climate change include reduced snow cover, fire and sub-alpine vegetation encroachment. Biotic interactions within and among three key alpine taxa: The Mountain Pygmy-possum (*Burrhamys parvus*), the Mountain Plum Pine (*Podocarpus lawrencei*) and the Bogong Moth (*Agrostis infusaria*) are already responding to anthropogenic climate change.

The Mountain Pygmy-possum (MPP) is the only Australian mammal restricted to the Alpine and sub-Alpine regions (Mansergh 1984) with a distribution above the winter snowline (~1200 m a.s.l.) restricted to areas dominated by patches of granite boulder field habitat and shrubby heathland (Broome *et al.* 2012). The species is listed as Endangered (e.g. under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999*) and Critically Endangered (IUCN Red List). The main threats of snow loss, fire, drought and temperature changes (Appendix 1) and are expected to intensify (Smith & Broome 1992). Long-term monitoring of capture rates of MPP has indicated a decline since 1985 (Greenville *et al.* 2018).

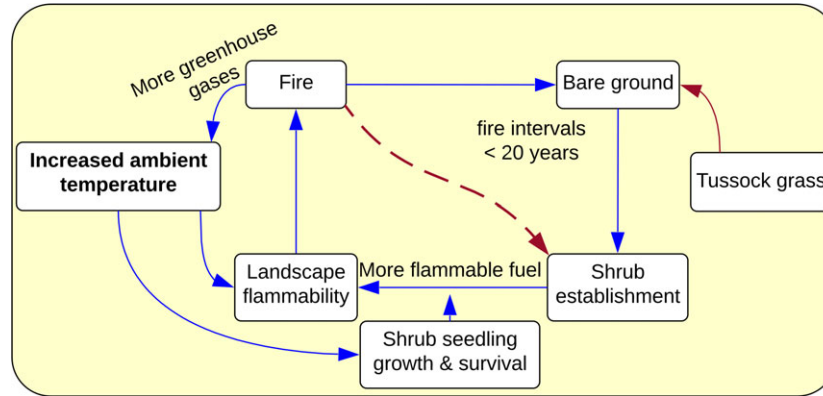


Fig. 3. Climatic warming – shrub – fire feedback based on evidence obtained from experiments and field surveys conducted in the Australian Alps. Blue = positive relationships, red = negative relationships, red/dashed = possible, but unlikely, effect of short fire intervals capable of breaking this feedback (Camac *et al.* 2017).

For successful breeding outcomes, MPP have a short gestation period and the young develop rapidly during summer to enable winter survival (Kerle 1984). The possums feed on arthropods, seeds and berries, depending on season, elevation, gender and reproductive status (Smith & Broome 1992). As the season warms, the abundance of Bogong Moths (a major arthropod food source) declines while available seeds and berries increase, forcing MPP to switch food sources (Fig. 4). Bogong Moths are more abundant at high elevations where they aestivate, whereas seeds and berries are most abundant at lower elevations (Smith & Broome 1992). Females eat more arthropods and fewer seeds and berries than males. Aestivating moths have high fat content (Common 1954), which makes them an important source of nutrition, especially for breeding females. Females switch to seeds and berries when moth numbers are low and in their post-reproduction phase (Smith & Broome 1992).

The preferred habitat of MPP is shrublands dominated by *P. lawrencei*, *Tasmannia xerophylla* and *Olearia phlogopappa* (Gullan & Norris 1984) around granite boulder fields. Habitats preferred by MPP are at higher elevations with long snow cover, small boulder crevices and multiple layers of rock (Broome *et al.* 2013; Shi *et al.* 2015). The occurrence of *P. lawrencei* is the best indicator of suitable possum habitat (Caughley 1986), critical for the possum during the coldest months when it hibernates in rock crevices (Körtner & Geiser 1998). Possums establish seed caches to sustain themselves when rousing from a winter torpor bout (Mansergh 1984). Resource distribution within suitable habitats explains the patterns and size of home range for females. During the breeding season, females prefer boulder fields at higher elevations with deeper small cavities (Broome 2001) favoured by the Bogong Moth for aestivation

(Common 1954). For male possums, home range is correlated with the season and reproductive status of females rather than habitat variables (Broome 2001).

Eggs and larvae of the Bogong Moth occur on foliage growing on self-mulching soils from the Darling Downs area in Queensland, through the western plains region of NSW and the Victorian north-western plains (Green 2010). The adult spring generation migrates to the Australian Alpine region in the same habitat area as MMP, to aestivate for up to four months. They return to breed at the end of summer or early autumn. Aestivation during late summer helps delay the breeding season and thus eggs do not hatch into a breeding ground lacking in resources and experiencing high temperatures (Warrant *et al.* 2016). If migrating moths arrive early, they are restricted to lower elevations without snow cover, moving upwards as the snow melts (Warrant *et al.* 2016). Snow cover may also be important for moth navigation (Warrant *et al.* 2016).

Podocarpus lawrencei, is the only Alpine conifer on mainland Australia (Gibson *et al.* 1995). It is widespread and usually associated with granite boulder fields typical of shrubby heathlands (McDougall *et al.* 2012). Furthermore, long fire-free intervals are required for the species to persist (Walsh & McDougall 2004; Williams *et al.* 2008b); the species is killed by fire, has transient seed storage and the seed is dispersed by bird regurgitate. The species grows slowly, taking decades to reach reproductive maturity (Williams *et al.* 2008a) and recolonize burned areas (Kirkpatrick & Dickinson 1984). Individuals can attain great longevity (>400 years old) in the absence of fire (Barker 1991) and it is the longest living plant species in the Australian Alps (Pickering *et al.* 2004). A chronological study has shown that it is sensitive to climate variables with higher air temperatures in spring increasing growth whereas persistent snow

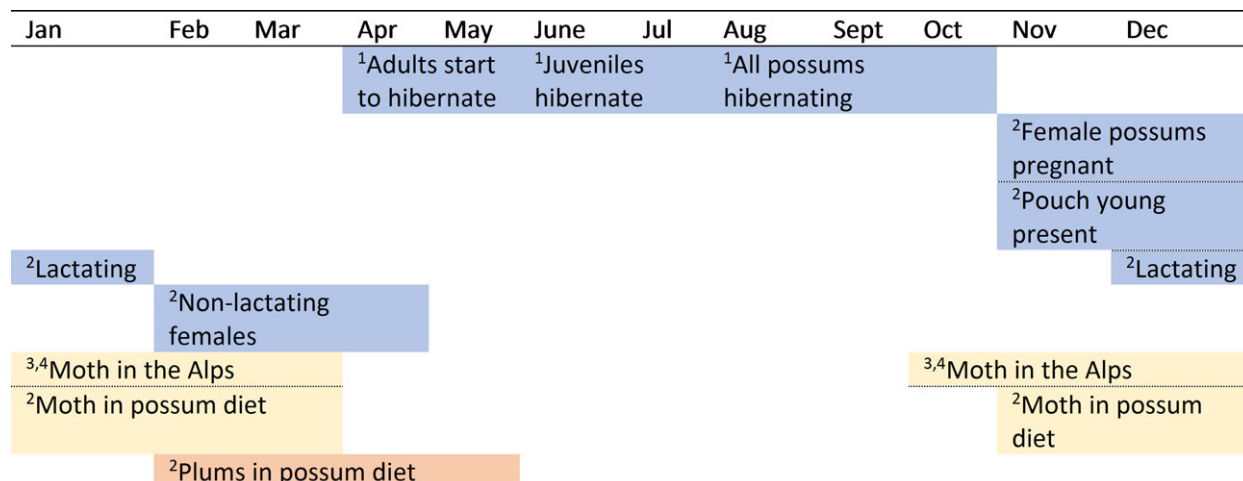


Fig. 4. Seasonal changes for three key alpine taxa the Mountain Pygmy-Possum (*Burrmys parvus*), the Mountain Plum Pine (*Podocarpus lawrencei*) and the Bogong Moth (*Agrostis infusata*), highlighting their temporal interactions. ¹Broome and Geiser (1995), ²Smith and Broome (1992), ³Common (1954), ⁴Broome (2001). Code: blue highlights relate to the possum; Yellow = moth; Orange = plum pine.

cover into spring delays growth due to a prostrate habit (McDougall *et al.* 2012).

The future

All three species rely on snow cover, which both modelling and data highlight will decline (Hennessy *et al.* 2008). Sánchez-Bayo and Green (2013) reported a snowpack depth decline at one site from 113 cm in 1954 to 85.7 cm in 2012. Whetton *et al.* (1996) estimated the total area with snow cover for >30 days per year could decline by 39–96% by 2070.

Since MPP numbers increase with altitude and MPP are restricted to mountain peaks (Pickering *et al.* 2004), they are expected to be susceptible to warming through loss of habitat associated with a retreating snowline. Under a 1°C increase in temperature and rainfall changes of +5% in summer and –5% in winter, it is predicted that MPP would not persist (Brereton *et al.* 1995). Physiologically, they are also vulnerable; air temperature affects the duration of torpor bouts and their metabolic rate; with lower temperatures (<2°C) increasing torpor bouts and lowering metabolic rates, an increase in air temperature causes torpor bouts to shorten and metabolic rates, and thus energy expenditure, to increase, impacting winter survival (Geiser & Broome 1993).

Decreasing snow cover could benefit the growth of *P. lawrencei* as noted above and provide more food for the MPP. However, due to the slow growth rate of *P. lawrencei*, the heath community may be vulnerable to colonization of sub-Alpine species more suited

to warmer temperatures and less snow cover. Likewise, the susceptibility of this species to fire will also likely have an impact. Unburnt vegetation surrounding boulder fields is important for MPP as post-fire refugia (Williams *et al.* 2008b).

Climatic impacts on Bogong Moth breeding grounds are poorly understood, although climate change could affect moth departure and arrival times. In years where snow melt occurred earlier, Bogong Moths arrived later (Green 2010). Late migration of moths to natal sites increases the risk of insufficient food for the return journey (Green 2006). Unfortunately, there is no monitoring of Bogong Moths in their breeding sites.

Habitat reduction is likely to interact with anthropogenic climate changes to further threaten MPP and *P. lawrencei*. Ski resort development reduced two populations of MPP believed to be of high quality due to their size and stability (Broome 2001) and resulted in the rapid loss of genetic variation in another population (Mitrovski *et al.* 2008). Key management interventions such as under-road tunnels can improve habitat connectivity for MPP (van der Ree *et al.* 2009), while deliberate introductions of new genetic material can help in population recovery (Weeks *et al.* 2017).

CASE STUDY 5. BIODIVERSITY IN THE WET TROPICS RAINFOREST

The Australian Wet Tropics World Heritage Area is one of the high biodiversity regions in Australia (45% of all Australian vertebrate species). Although not the largest tropical rainforest globally, or the most

diverse, it is the second most important World Heritage Area in the world due to its unique concentration of endemic, rare and ancient species (Bertzky *et al.* 2013). The vertebrate fauna of the Wet Tropics has exceptionally high levels of endemism and diversity, with the highest concentration in mountain rainforests (Williams *et al.* 2016). More than a quarter of the regions vertebrate (190 of 693) and plant (700 of 2800) species have restricted ranges and specialized habitat requirements with many classified as vulnerable and threatened (<http://www.wettropics.gov.au/endemic-species>). Most species are Gondwanan relicts including 33 vertebrate species classified among the top 10% of evolutionarily distinct taxa on the planet. Vertebrate biodiversity in the Wet Tropics is consistently greater in the uplands, likely driven by lower rates of species extinction where climatic stability is higher (Williams & Pearson 1997).

Climate change predicted in the region includes an increase in mean annual air temperature of 0.5–1.4°C by 2030, an increasingly drier and longer dry season, and an increase in extreme events such as flooding rains and cyclones (Suppiah *et al.* 2007). Changes in water availability and increased seasonality will be exacerbated by a reduction in cloud capture by the mountain rainforests canopy, caused by an increase in the average height of the orographic cloud layer (Pounds *et al.* 1999; McJannet *et al.* 2007). This reduction in water input via cloud stripping reduces water availability; hence productivity affects mountain-top species. More than 15 years ago, catastrophic impacts on the endemic vertebrate fauna were predicted for the coming century, with >50% of these species potentially becoming extinct (Williams *et al.* 2003b).

Ongoing long-term monitoring (Williams *et al.* 2010, 2016) has demonstrated that many vertebrate species have already declined in both distribution area and population size, both earlier and more severely than originally predicted. Over the last 20 years as detailed in these references, the local abundance and/or distribution area of several vertebrates has changed. Ringtail possum species have declined at the lower elevational limits of their ranges. Lemuroid Ringtail Possums (*Hemibelideus lemuroides*) and Herbert River Ringtail (*Pseudochirulus herbertensis*) have both disappeared from sites at 600 m since 2006 and 2008 respectively, although they remain common above 800 m. The southern population of Lemuroid Ringtail Possums increased at a site at 1000 m elevation on the Atherton Tablelands between the early 1990s and 2004, but has steadily declined since 2004. The northern population of Lemuroid Ringtails (Mt Lewis) severely declined after record heat waves in 2005 that coincided with extreme low rainfall and an absence of cloud cover (thus no cloud stripping). No individuals

were seen for several years although there are now signs of a slow recovery. The abundance of Daintree Ringtails (*Pseudochirulus cinereus*) on Mt Lewis has increased above 1000 m in recent years, although it is unknown if this is driven by warming temperatures or competitive release due to the decline in Lemuroid ringtails. Green Ringtail Possums (*Pseudochirops archeri*) are moving upwards; numbers have increased at the upper elevational limits and declined at their lower limits. These changes are in accordance with projected changes due to climate change.

Of 56 bird species with sufficient abundance data for statistical analysis, 28 species show upward shifts in elevation, often associated with declines in overall population size (Williams *et al.* 2016). There is a greater level of population decline in the rainforest-specialist species, especially rainforest obligates (Fig. 5), compared to broadly distributed birds that have, on average, increased population size.

These results are consistent with past modelled predictions of upwards shifts in population abundance (Williams *et al.* 2003b) and are in accordance with expectations under a warming climate and the physiological tolerances of these species to maximum temperatures.

The future

Future climate scenarios (Pachauri *et al.* 2014) were incorporated in predicting climate change impacts on biodiversity in the Wet Tropics (Williams *et al.* 2010, 2016). These predictions have been undertaken for

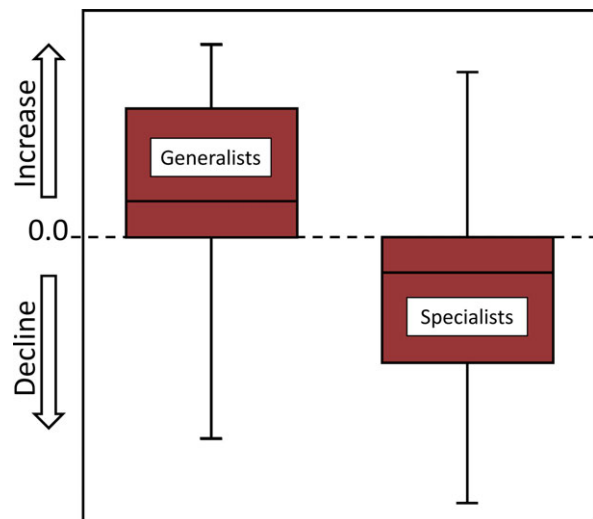


Fig. 5. Average change in total population size of bird species in the Wet Tropics region (Queensland) pre- and post- 2008 that are rainforest specialists and species that are generalists. On average, specialized species have declined while generalist species have increased.

202 rainforest vertebrate species with sufficient data. The climate change impacts on individual species, and biodiversity generally, were assessed against the latest IPCC emission scenarios for decadal time steps from 2015 to 2085. The results indicate significant pressure on endemic vertebrates and increasing rates of extinction, although this depends greatly on the emission scenario. With the ‘business-as-usual’ (RCP8.5) scenario, great losses in species are predicted by 2085 (Fig. 6): 59% of the 70 endemic vertebrates with >90% of habitat loss and thus critically endangered or extinct; 79% endangered or >70% population loss by 2085. This relates to 92% of all Wet Tropics endemic vertebrates becoming vulnerable, or worse, by 2085. As most low dispersal species include multiple genetic lineages (Moritz *et al.* 2009; Rosauer & Jetz 2015), the loss of genetic diversity is expected to be severe. By contrast, reasonable mitigation of greenhouse gases (e.g. RCP4.5 scenario) would substantially reduce this impact, potentially saving many species from extinction (9% of endemic species with > 90% habitat loss). However, even with lower emissions (RCP4.5), 37% of rainforest endemics are predicted to be in danger of extinction by 2085, with 63% vulnerable or worse (Fig. 6).

The rate at which Wet Tropics populations change is higher under the RCP8.5 scenario than the RCP4.5 scenario. Specifically, there is an

approximate 20-year lag in population change between the RCP4.5 and RCP8.5 emission scenario. This lag effect is less than the global average of approximately 30 years (Warren *et al.* 2013), again highlighting vulnerability of this fauna. Models also suggest that future populations will also become more fragmented as the landscape becomes hostile to dispersal and migration. There is a potential for biodiversity loss, especially of high conservation value species that the region was originally protected to preserve. There is a danger of cascading impacts resulting in the loss of the natural assets that underpin the regions conservation value and the loss of the vitally important contribution it makes to a regional economy reliant on natural capital for tourism and the provision of resources such as freshwater.

CASE STUDY 6. DIEBACK IN THE CRITICALLY ENDANGERED CUSHION PLANT, *AZORELLA MACQUARIENSIS* (APIACEAE) ON SUB-ANTARCTIC MACQUARIE ISLAND

First observed in 2008, sudden, widespread dieback in the endemic, keystone taxon and ecosystem engineer, *Azorella macquariensis*, is now evident on Macquarie Island. This dieback is of significant concern for the conservation of the species, and the structure

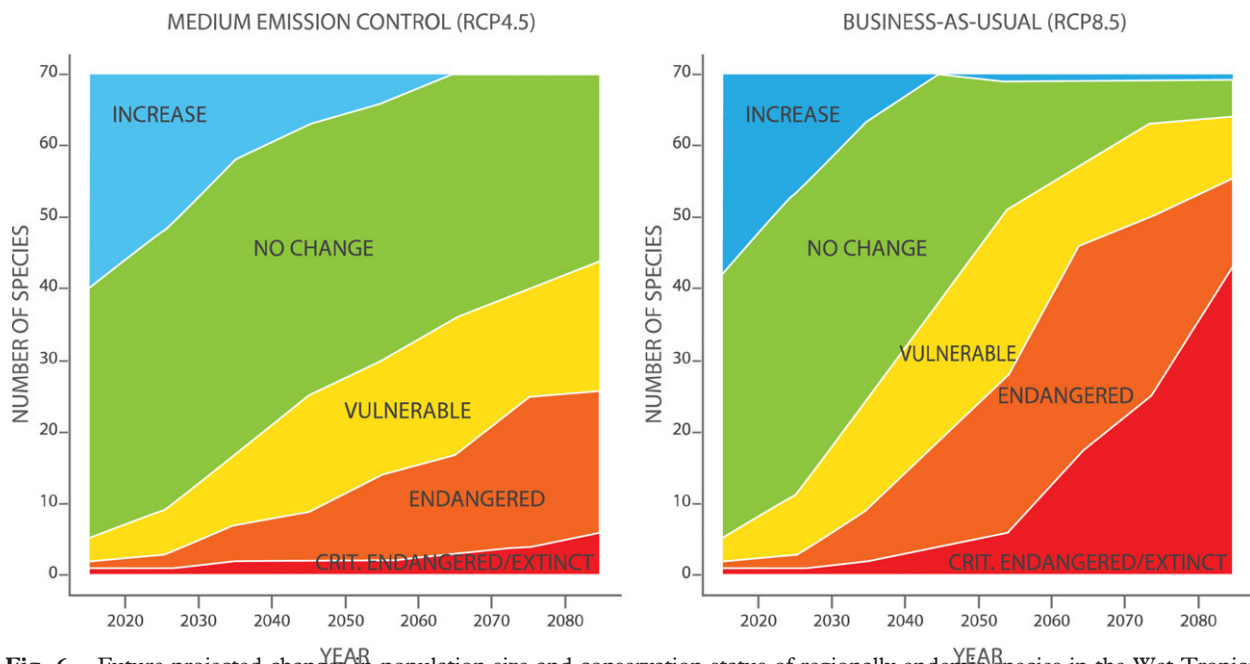


Fig. 6. Future projected changes in population size and conservation status of regionally endemic species in the Wet Tropics region (Queensland) following exposure to a (a) mitigation emission scenario (RCP4.5) and (b) business-as-usual emission scenario (RCP8.5). Data come from species distribution modelling with the mean from 18 global climate models for each scenario. The count of species within population change categories (relative to baseline 1990 with first prediction at 2015) as follows: Blue – Increase in population; Green – no change; Yellow – Vulnerable 50–70% population lost; Orange – Endangered 70–90% lost; Red – Critically endangered/Extinct 90–100% population lost. Changes in population size was based on regionally endemic species where the extent of modelled area contains species entire population ($N = 70$). (Williams *et al.* 2016).

and function of its fellfield and herbfield communities where it dominates plant biomass, generates self-organized terracing and other patterning (Selkirk *et al.* 1990; Selkirk-Bell & Selkirk 2013) and facilitates growth and survival of other species under the harsh fellfield conditions (le Roux *et al.* 2013).

The climate of the sub-Antarctic islands is heavily influenced by atmospheric and oceanic circulation patterns, with the region receiving constantly high winds from a westerly direction resulting from the decay of cyclonic depressions (Selkirk *et al.* 1990). Macquarie Island generally is cool, wet and windy (mean air temperature range, 3.8–6.6°C) (Pendlebury & Barnes-Keoghan 2007); importantly, for the last three decades there has been a poleward intensification of westerly winds (Kostov *et al.* 2017).

In the austral summer of 2008/09, many *A. macquariensis* plants did not emerge from their winter senescence, presenting as brown cushions rather than growing a green flush of spring leaves (Fig. 7) in contrast to other environmental damage (Fitzgerald & Kirkpatrick 2017). Sporadically, on some cushions a yellow band was observed over time to be moving across cushions, consistent with a plant pathogen infection (Fig. 7), followed by decline in condition and death of plant tissue. Bryophytes, a major component of the fellfield, were also often found dead (Whinam *et al.* 2014; Bergstrom *et al.* 2015).

The first survey of 115 locations across the island's alpine plateau in 2008–2009 found 88% contained affected cushions and 84% contained dead bryophytes (Bergstrom *et al.* 2015). Within-site dieback increased over time. Such death and damage to *A. macquariensis* has not previously been observed, with this endemic plant species transitioning from 'healthy and common' to 'critically endangered' by 2010 (Whinam *et al.* 2014).

Current understanding of the dieback is as follows (Fig. 8): (i) reduced summer water availability for 17 consecutive summers (Bergstrom *et al.* 2015) associated with previously identified southward shifts of weather systems despite an increase in annual precipitation; (ii) increases in mean wind speed, sunshine hours and evapotranspiration over four decades, with available water negative for the majority of the growing season for 17 successive years, leading to dieback in the austral summer of 2008.

Increased sunshine hours have resulted in reduced plant interception of mist or drizzle, while increases in wind speed enhanced water loss through evapotranspiration. With increased cyclonic activity, environmental conditions changed from generally moist, to fluctuating conditions of wet frontal systems followed by drying winds and sunshine. Fellfield plants dried out with various feedbacks of community water loss causing stress in *A. macquariensis* cushions, with

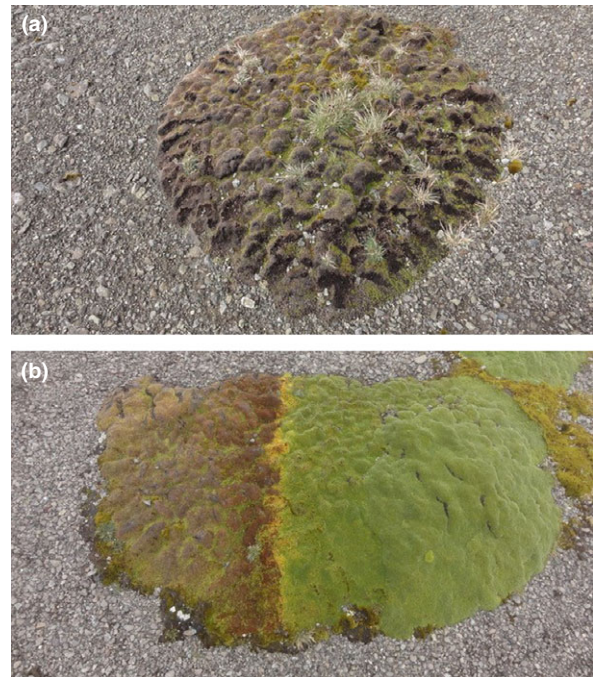


Fig. 7. Spread of dieback across an *Azorella macquariensis* cushion on Macquarie Island as an example of the most conspicuous form of pathogen-related dieback (above), and a dead cushion (below) covered by patches of moss and grass. ©Catherine Dickson

some succumbing to microbes that became pathogenic (Fig. 7).

Since 2011, death in *A. macquariensis* cushions has continued across the plateau, and many areas are now replaced with bare ground or grasses. During a recent exceptionally wet summer (2016–2017), plants did not exhibit water stress, and some recovery of cushion plants and mosses was observed; however, dieback associated with yellow bands was still recorded across the entire island plateau.

The future

The vulnerability of *A. macquariensis* to drought is confirmed, so further drying events will impact survival of this keystone species and the supported ecosystem. The key uncertainty in the system is the identity, origin and role of the single or multiple plant pathogens involved, as well as spatial–temporal dynamics of dieback and pathogen infection on the island (Fig. 7). The role of wetter winters potentially influencing fungal proliferation has yet to be confirmed.

A climate change (drying) stress-induced increase in susceptibility to fungal pathogens is expected, in line with other systems where pathogen–climate

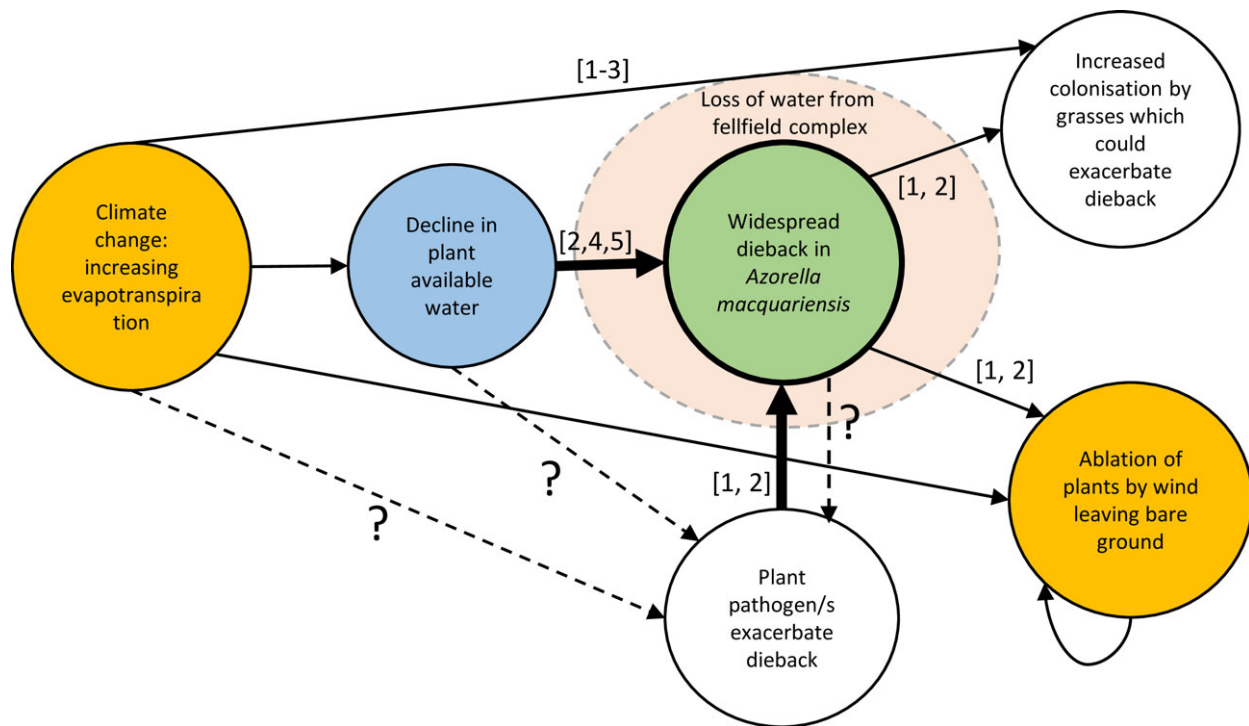


Fig. 8. Simplified causal pathway model of the direct and indirect drivers of dieback in *Azorella macquariensis* (cushion plant) from Macquarie Island and its consequences. The model illustrates (i) the direct effect of climate change on the cushion plant and (ii) the diffuse indirect impact via multiple interaction pathways hypothesized for the climate-cushion-plant pathogen interaction, with (iii) potential feedback between the pathogen and the cushion (particularly if multiple pathogens are involved). The two nodes on the right of the model are the two alternative outcomes observed following dieback. The loop represents the accelerated process of ablation that occurs once a cushion's canopy loses its surface integrity. Thick arrows represent direct, proximal negative impacts on the cushion plant, thin arrows represent distal and indirect impacts, and dashed arrows are those with no evidence. Numbers associated with nodes and interactions refer to literature discussing or providing evidence for the relationship or process: 1. (Whinam *et al.* 2014); 2. (Bergstrom *et al.* 2015); 3. (McGeoch *et al.* 2008); 4. (le Roux *et al.* 2005); 5. (Fitzgerald & Kirkpatrick 2017).

change interactions are happening (Hoberg & Brooks 2015); 'fairy rings' and repeat waves of dieback have been observed (Selkirk-Bell & Selkirk 2013). There are currently no data on how climate change and potentially plant pathogens, may impact the species, including flowering, seed set, germination and survival in immature plants. Recruitment in the species is poorly understood, and seeds have proved difficult to germinate *ex situ* (pers. comm. Royal Tasmanian Botanical Gardens 2017).

Regardless of what is driving this marked change on Macquarie Island, if the trend continues two potential futures exist for fellfield ecosystems. First, they are likely to become increasingly grass-dominated as sub-Antarctic grasses respond rapidly and positively to warming and drying conditions, with range expansion facilitated by cushion plant dieback (Fig. 7). Second, dieback happens rapidly and, particularly in highly exposed sites, the wind removes dead and dying plant tissue, along with humic material trapped within and under cushion plants, leaving bare ground (Fig. 7).

CASE STUDY 7. CLIMATE CHANGE AND THE MORPHOLOGY OF AUSTRALIAN BIRDS

Demonstrations of how climate change affects individual fitness of animals, and subsequent links with population demography, remain surprisingly rare. Most studies investigating these links have focused on phenological shifts (Ramula *et al.* 2015) and much less is known about morphological change, despite growing evidence for pervasive shifts in the body size and shape of organisms as a response to climate change (Millien *et al.* 2006; Gardner *et al.* 2011; Teplitsky & Millien 2014). Body size and shape are fundamental to performance and integrally linked with energetics and thermoregulation, which are affected by climate (Gillooly *et al.* 2001), so changing morphology will have implications for fitness and therefore population dynamics. Understanding the links between climate, fitness and demography improves our capacity to predict consequences for population persistence in the face of

ongoing climate change (Cahill *et al.* 2013). Moreover, understanding selection on body size is important because it may change the composition of a population via the selective disappearance of particular phenotypes which could therefore generate evolutionary change, assuming body size is heritable (Visser 2008).

There is considerable heterogeneity among studies reporting associations between body size and climate over the last 50–100 years, including studies of Australian bird species (Gardner *et al.* 2014a,b; Kruuk *et al.* 2015; Little *et al.* 2017). Although many studies report declining body size as a correlate of climate warming, a considerable proportion report increasing size or no change (Gardner *et al.* 2011; Teplitsky & Millien 2014). One likely reason for this variety of responses is that results may vary depending on the metric used to represent body size: structural body size versus body mass (Teplitsky and Millien). This is likely to confound our understanding of global trends in body size, contributing to observed heterogeneity. Nevertheless, of 24 Australian species studied to date, the majority of species that have changed in size over the last 50 years show a decrease in size (Gardner *et al.* 2014a).

Climate change can present considerable challenges for endotherms because they maintain high, relatively constant body temperatures across a range of conditions to ensure survival and optimize performance (Huey *et al.* 2012). Individuals exposed to changing climate must manage energy and water allocation to maintain homeostasis, with consequences for average body condition. Hence, there is potential for selection because body condition is strongly linked to fitness via survival and reproduction. Climatic effects on body condition are therefore fundamental to understanding how fitness is affected by climate change.

There is already good evidence for adverse effects of exposure to high temperatures. Severe heatwaves with temperatures above critical thresholds can have dramatic and immediate impacts on wild populations, leading to mass mortalities and major population crashes via fatal hyperthermia when avian body temperature exceeds about 45°C (Easterling *et al.* 2000; McKechnie & Wolf 2010), including the recent case of Carnaby's Cockatoo (Saunders *et al.* 2011). Such mortality will affect the range of phenotypes surviving in a population (McKechnie & Wolf 2010), and is likely to increase as the climate warms and temperatures surpass physiological thresholds (McKechnie *et al.* 2012).

There is also growing evidence for pervasive sublethal effects on phenotypes and fitness from exposure to temperatures in the 30–40°C range. Above about 30°C, birds actively dissipate heat by panting, which increases the potential for mass loss via

dehydration (McKechnie & Wolf 2010). The need to dissipate heat can also lead to trade-offs with foraging, resulting in reductions in foraging success, which can lead to loss of body condition (Cunningham *et al.* 2015; Edwards *et al.* 2015; Smit *et al.* 2016). Although short-term exposure to high temperatures might be harmless, prolonged exposure over days and weeks may have consequences for fitness (du Plessis *et al.* 2012). Indeed, increasing exposure to >35°C was associated with reductions in body condition in a honeyeater in semi-arid NSW (Gardner *et al.* 2016a). Heat-exposed birds in poor condition were less likely to be recaptured in the following spring and were presumed to have died (Gardner *et al.* 2016a). Smaller individuals appeared particularly vulnerable, likely contributing to an increase in average structural body size over several decades, highlighting links between body condition and structural size (Gardner *et al.* 2014a, 2016a).

Exposure to high temperatures can also affect reproduction, either directly or by changing the ways in which parents invest in offspring. There are consequences for nestling growth and development, and thus offspring body size (Cunningham *et al.* 2013; Wiley & Ridley 2016). Recent studies of Australian birds are starting to quantify the costs of heat exposure on breeding activity (Griffith *et al.* 2016; Langmore *et al.* 2016; Mariette & Buchanan 2016), although at least in one case (the superb fairy-wren) average chick mass has remained constant across years over 26 years (Kruuk *et al.* 2015). Thus, climate change does not always lead to detectable effects on fitness, at least at current stress levels.

Contrary to effects of high temperatures in summer, relaxation in selection pressures associated with warming winters can improve body condition as well as reduce winter mortality, with consequences for average body size. In two passerine species monitored over 39 years in southwestern Western Australia (Gardner *et al.* 2018), survival in the face of winter extremes was associated with body size, with evidence that size-dependent mortality was mediated by carry-over effects of climate in the previous season, likely driven by changes in body condition (Gardner *et al.* 2018).

Finally, morphological responses to climate are not limited to body size, mass and condition but can also include other traits linked to heat exchange. For birds, the bill is important in body temperature regulation; bill surface area, relative to body size, is strongly tied to heat exchange (Symonds & Tattersall 2010; van de Ven *et al.* 2016; Tattersall *et al.* 2017). Birds control blood flow to the bill, increasing it in hot conditions to achieve radiative heat loss across this non-permeable structure, thereby limiting water loss which is associated with evaporative cooling via panting (Tattersall *et al.* 2017). Heat exchange via

the bill can therefore be advantageous in arid zone species where high temperatures coincide with low water availability (Tattersall *et al.* 2017). Birds also reduce blood flow to the bill or simply cover it with body feathers to restrict heat loss in cool conditions (Ryeland *et al.* 2017). Bill size in Australian passerines is consistent with body temperature regulation and may underlie continental-wide patterns of bill size variation linked to both summer and winter conditions (Gardner *et al.* 2016b; Friedman *et al.* 2017). Gardner *et al.* (2016b) found that associations between bill size and weather were driven by humidity in summer, rather than temperature per se. Given strong associations between climate and bill size, increases in bill size are predicted under climate warming, as demonstrated for several Australian parrots (Campbell-Tennant *et al.* 2015).

The future

There is strong evidence for changes in morphological traits associated with climate change in Australian birds, but patterns are complex. The variety of responses may reflect the metric used to represent body size, the duration of the study period, the interaction between gradual warming and extreme climatic events and the extent of behavioural thermoregulation. An apparent lack of size response does not indicate a lack of sensitivity. Climate-driven changes in morphology are not restricted to body size, and nor are associations between morphology and climate simply associated with temperature. The pervasive effects on fitness of climate-driven changes in body condition may be at least as significant for population dynamics as the immediate consequences of extreme events. Research is needed to understand the relationship between body condition and structural body size, links between changing size and fitness and consequences for population dynamics.

CASE STUDY 8. PHENOLOGICAL CHANGES IN ORCHIDS

The seasonal timing of plant species growth or reproduction is often influenced by temperature (Körner & Basler 2010; Bartomeus *et al.* 2011) and therefore climate change (Polgar & Primack 2011; CaraDonna *et al.* 2014). Phenological changes have important functional ramifications, such as seasonal leaf emergence times in deciduous forests influencing carbon cycling (Polgar & Primack 2011). Spring phenology has advanced in 78% of plant species in Europe due to climate change (Menzel *et al.* 2006) at 2.5 days per decade (Körner & Basler 2010). Flowering times are critical to reproductive success, partly due to the

resulting availability of insect pollinators (Faast 2010). However, phenology has been investigated much less extensively in the Southern Hemisphere (Gallagher *et al.* 2009) and in Australian native species compared to crop and native species in the Northern Hemisphere (Beaumont *et al.* 2015).

Orchids are climate change indicators known to undergo phenological shifts in their short flowering periods; orchid phenology is particularly sensitive to seasonal temperature and day length, making analysis of phenological shifts feasible through assessment of herbarium specimens (MacGillivray *et al.* 2010; Robbirt *et al.* 2011). One process threatening wild orchid species is poor reproductive success (Faast & Facelli 2007), caused by factors which are likely exacerbated by climate change. MacGillivray *et al.* (2010) demonstrated that the Spring flowering time of the Donkey Orchid *Diuris orientis* (from South Australia) has advanced significantly since records began, with a notable change in the early 1970s coinciding with a climatic shift in the El Niño Southern Oscillation (ENSO), from an extended La Niña phase to an El Niño dominance (Wolter & Timlin 2011). However, for the sympatric *D. behrii*, no significant long-term phenological trend was found. Similarly, Gallagher *et al.* (2009) found two species of *Prasophyllum* orchid in the Australian Alps responded differently to climate change, with one species advancing time of flowering and the other receding.

Empirically detected phenological trends in orchids caused by climate change could have several consequences, such as decoupling of orchid–pollinator interactions, increased hybridization and disruption of whole community networks. Differences in phenological responses to climate change between orchids and bees or other pollinators may lead to reduced opportunities for pollination, for example if flowers emerge before bees in Spring, or vice versa (MacGillivray *et al.* 2010). Although Bartomeus *et al.* (2011) concluded that bee emergence was advancing at about the same rate as flowering, Australian bee specimens were not included and known Australian orchid phenology trends appear inconsistent in direction and magnitude. Decoupling events are likely for some species.

Many closely related orchids can hybridize (Whitehead & Peakall 2009), and convergence or divergence in flowering times may alter the frequency of hybridization events in sympatric species (MacGillivray *et al.* 2010). Hybridization may limit reproductive success due to decreased fertility, or influence gene pools through introgression and blurring of species boundaries (Cozzolino & Widmer 2005).

Complex facilitative and competitive phenological interactions among pollinators, flowering species and orchids that rely on deception to obtain pollination services, may be disrupted by climate change. Floral

mimicry is common among orchids. For example, *Diuris* flowers attract pollinators via mimicry of Australian native mirbelioid peas, which provide nectar rewards to bees (Beardsell *et al.* 1986; Indsto *et al.* 2006). The timing of orchid flowering in relation to the overall plant community varies, even in closely related species. For example, Faast (2010) reported that peak flowering of *Caladenia rigida* occurred before the main spring flowering period of neighbouring plants, whereas *C. tentaculata* flowered later, during times of high floral resources from neighbouring species. Decoupled interactions due to phenological shifts could inhibit reproductive success in some orchids, leading to increased likelihood of extinction.

The future

The impact of phenological changes in orchids under climate change is likely to be complex, and at this stage, more information is needed. One problem in assessing the impacts of climate change on orchids is a lack of verifiable records for many species, exacerbated by the small number of qualified taxonomists and short flowering periods. However, many amateur orchid enthusiasts photographically record orchid species along with co-located environmental information. Wild Orchid Watch (<https://www.wildorchidwatch.org/>) is a new citizen science programme that proposes to harness this sampling effort by providing citizen scientists with tools to gather and share information. The programme involves the creation of a mobile phone app, database and interactive website to provide a field guide for identification, and guided photography to obtain photographs of key diagnostic features. Identifications are provided by suitably skilled amateurs and professional taxonomists. The programme will become operational by June 2020 for widespread public use. We anticipate a wealth of new information on orchid species, enabling scientists to study the relationship between climate change and orchid phenology, which may then translate into management actions such as through the identification of vulnerable areas where rapid phenological changes are being observed.

CONCLUDING REMARKS

The above examples illustrate both the substantial changes already occurring in Australia's terrestrial ecosystems and point to the nature of changes to be expected in the future. The examples highlight that changes can be relatively subtle, like phenological shifts in flowering time, and phenotypic shifts in components of body size, or much more dramatic, such as severe local species declines in the Wet Tropics and sub-antarctic islands, community shifts in

Alpine areas, and direct damage to forests exposed to heat stress, drought and frequent fire. Regardless of whether changes are subtle or much more apparent, major repercussions are likely for the structure and composition of communities and ultimately for ecosystem processes.

Several case studies provide clear evidence of recent climate change associated with anthropogenic activities being the driving force behind the biological impacts. Where observed changes are starting to match predictions based on modelling or direct manipulations of environments, the evidence looks particularly strong. This seems to be the case for distribution changes being documented in the Wet Tropics, and the vegetation changes being detected in Alpine areas. Yet in other situations, direct links to anthropogenic climate change are subtler. Extreme events often drive changes in organisms, as in the case of damaging periods of high temperature stress in southwest Australian forests and in birds and mammals of the Wet Tropics, drought that affects Alpine grassland and Bogong Moth numbers and intense fire that kills Alpine ash forest and Alpine plants including *Podocarpus*. While it can be hard to attribute one extreme event to recent anthropogenic climate change, this is changing through developments in attribution science (e.g. King *et al.* 2016; Stott *et al.* 2017) but will often still require innovative ways of collecting long-term biological data such as citizen science programmes.

As highlighted in the case of cushion plants in the sub-antarctic islands and phenological changes in orchid species, the unpredictability of biological impacts of climate change lies in the extent to which related species respond quite differently to the same sets of conditions, which in turn influences their susceptibility to climate change. An understanding of the inherent differences in responses among related Australian species is incomplete, even for well-studied groups such as *Drosophila* (Overgaard *et al.* 2014) or eucalypts (Jordan *et al.* 2017; Steane *et al.* 2017b). Because anthropogenic climate change will influence Australia's terrestrial fauna and flora, the relative vulnerability and adaptive capacity of related species within clades and components of different biological communities need to be assessed. However, the case study on size-related changes in birds illustrates the complexities involved in identifying traits and genetic/plastic changes that might promote adaptive capacity.

In almost all the case studies, the value of long-term monitoring is reinforced. While short-term studies are valuable in highlighting the impacts of extreme events as in the case of southwest forests (Ruthrof *et al.* 2015; Matusick *et al.* 2016), the value of monitoring systems increases as more time is elapsed and longer cycles can be followed, which is unfortunately rare in the

Australian context (Lindenmayer *et al.* 2012; Williams *et al.* 2017b). The value of long-term monitoring can be enhanced by experimental and physiological approaches. By combining long-term monitoring with field-based experiments and physiological measures, a fundamental grasp of how things will change under future climate scenarios can be obtained. This type of information can then be used in mechanistic models, which are still lacking for many species and particularly in many plants. Monitoring also needs to be coupled to trigger points leading to management actions. How much decline from climate change can be tolerated before a population or community becomes threatened to the extent that interventions such as interfering with biotic interactions and translocating to other areas may need to be considered? Monitoring could be coupled to IUCN Red List criteria for assessing responses to threats, as in the case of alpine snow patch communities (Williams *et al.* 2015).

When predictions are made about future changes in terrestrial fauna and flora in Australia, these are mostly negative. In contrast, early evidence of biological responses to climate change in Northern Hemisphere countries often focussed on positive effects in species, as these expanded distributions into colder areas in Britain and Scandinavia, or moved up mountains as in Europe and North America, and shifted phenologically to take advantage of new seasonally available food sources, such as in the case of herbivores taking advantage of earlier spring growth and birds nesting earlier to use the earlier abundance of caterpillars (Parmesan & Yohe 2003; Visser 2008). Some potentially positive effects are noted in the case studies identified here, such as the expansion of shrubs in the Alpine environment, but we have been more concerned about documenting losers rather than winners, no doubt a legacy of the history of successful foreign invaders that have decimated many Australian ecosystems. Beyond identifying winners and losers, we need to understand how these effects at individual species levels manifest at broader scales (e.g. community structure, ecosystem function) and how they interact with other abiotic factors also expected to change under anthropogenic warming.

With modelling work pointing to massive changes in the composition of local communities, dramatic shifts in distributions that are often negative, and interacting factors that could produce a cascade of effects, where do we go from here? Are there unexpected levels of plasticity and other adaptive capacity that act to reduce impacts? Are there ecological processes that are poorly covered by local researchers, but that need to be addressed to capture the full range of biological effects likely to emerge? Uncertainty remains in making predictions in terrestrial ecosystems, particularly around the impact of extreme events, the potential for adaptive capacity,

and interactions among factors that have unforeseen consequences. As noted for both the southwestern forests, Alpine areas and Wet Tropics, interventions need to be considered, such as those involving assisted migration, enhanced gene flow, and perhaps engineering solutions. A debate around the need for interventions, some extreme, may be as important for terrestrial ecosystems as it is for the Great Barrier Reef and other marine systems, as is examination of approaches such as renewal ecology where mitigation of change is not possible (see Bowman *et al.* 2017). Relevant research to develop interventions should be a priority given the rapid rate of climate change and the long period required for communities to establish in new areas.

Minimizing the impacts of future climate change will require a multi-faceted policy and management strategy that uses information from targeted and systematic monitoring at the regional level to identify vulnerable species via comprehensive vulnerability assessment, particularly emphasizing endemic, specialized, ancient and rare species, and to identify high priority biodiversity refugia for protection and management. Habitat restoration is needed in places that will make the most significant contribution to both current and future connectivity, thereby maximizing the potential for species to move with their required climate. Local non-climate stressors, such as invasive species and habitat fragmentation, also need to be reduced. Research and adaptive management is needed to start testing potential adaptation strategies now, so we have the knowledge to act appropriately in the future.

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APPENDIX (1)

Case study	Region	Key threats	Nature of impact	Nature of data collected	Species/ecosystem impacted
1	Southwestern Australia	Drought and heatwave events	Canopy collapse, resprouting, beetle outbreak, altered fuel loads	Landscape-scale, stand and plot level forestry data	Forest co-dominant eucalypts
2	Western Sydney	Psyllid population outbreaks in eucalypt woodlands	Repeated and widespread defoliation of eucalypts leading to tree dieback and mortality	Data about psyllid populations and tree health across landscape and tree stand scales	Dominant eucalypt species in critically endangered woodland community
3	Victorian Alps	Fire incidence and intensity, drought, temperature, invasive species,	Increase in shrub cover and survival at the expense of grasslands, loss of some forbs	Experimental field manipulations, long-term monitoring plots	Alpine and sub-alpine grasslands and heathlands.
4	Australian alpine and sub-alpine region	Fire incidence and frequency, drought, temperature, habitat loss, reduced snow cover, sub-alpine vegetation encroachment.	Possum: decline in numbers, loss of food sources, loss of suitable habitat, reduced hibernation rates. Plum: decline in numbers. Moth: delay in migration timing, decline in numbers, loss of suitable habitat.	Field surveys, long-term monitoring plots, experimental laboratory manipulations.	Possum and plum: alpine bioregion. Moth: breeding grounds migration route and alpine bioregion.
5	Wet Tropics Bioregion	Increasing mean temperature, increasing temperature maximums, increasing severity of dry season, invasive species	Decline in distribution area and total population size especially of upland regionally endemic rainforest species	Long-term monitoring, current and future climate distribution models across thousands of species	Tropical rainforest particularly upland forest types
6	Macquarie Island	Temporal change in moisture availability, cloud cover, wind circulation and increasing temperatures; microbe pathogenicity	Dieback of edemic keystone plant species (<i>Azorella macquariensis</i>) with consequent changes in feldmark and cushion plant communities	Long-term monitoring plots, modelling, data on microbes/pathogens present, ecophysiology of <i>A. macquariensis</i>	Fellfield and herbfield
7	Australia wide	Temperature extremes; changes in availability of food, water; heatwaves	Affects on survival and reproduction, changes in body condition, body size and shape, behaviour	Long-term monitoring; examination of museum specimens; behavioural studies	All
8	Australia wide	Temperature increase	Advancing or receding of flowering times	Herbarium records	Orchids in genera <i>Diuris</i> and <i>Prasophyllum</i>

Process affected	Citations	Adaptation/mitigation strategies	Knowledge gaps
Population extinction, community composition, vegetation structure, regeneration, litter depth	Matusick <i>et al.</i> (2013), Brouwers <i>et al.</i> (2013a,b), Ruthrof <i>et al.</i> (2015), Andrew <i>et al.</i> (2016), Ruthrof <i>et al.</i> (2016), Matusick <i>et al.</i> (2016), Seaton <i>et al.</i> (2015), Blackman <i>et al.</i> (2017)	Assisted gene migration climate-adjusted provenancing, experimental plots with novel assemblages	Climate-adjusted provenancing, how forest composition is changing and where, flow-on effects for faunal habitat, changes in forest function (nutrient cycling)
Canopy-dependent processes, plant and animal species composition, eucalypt recruitment, nutrient and water cycles	Hall <i>et al.</i> (2015), Gherlenda <i>et al.</i> (2016b)	Maintaining diverse and healthy woodland communities, continuous monitoring of psyllid populations, early interventions to inhibit the spatial spread of localized psyllid outbreaks	Causes and spatial spread of psyllid outbreaks, interactions with other factors in causing tree dieback and mortality, effectiveness of intervention and restoration strategies
Vegetation composition, phenology, seed production, recruitment, growth, survival, species composition, snow cover duration and depth	Camac <i>et al.</i> (2017), Wahren <i>et al.</i> (2013b), Hoffmann <i>et al.</i> (2010), Green (2010), Nash (2013), Williams <i>et al.</i> (2014)	Interventions to reduce shrub encroachment, aggressive removal of invasive species,	Potential for adaptation, interactive impact of large herbivores (deer, horses), long-term effects of altered phenology and fire regimes
Vegetation composition, phenology, seed production, recruitment, growth, survival, species composition, snow cover duration and depth	Barker (1991), Broome <i>et al.</i> (2012), Common (1954), Geiser and Broome (1993), Green (2010), Hennessy <i>et al.</i> (2003), McDougall <i>et al.</i> (2012), Smith and Broome (1992), Warrant <i>et al.</i> (2016), Williams <i>et al.</i> (2014).	Possum: captive breeding and translocation programme. <u>Plum</u> : fire mitigation programme. <u>Moth</u> : protection of habitat in breeding grounds, habitat connectivity along migration route.	Possum: potential for adaptation. <u>Plum</u> : long-term effects of altered phenology and fire regimes. <u>Moth</u> : long-term effects of altered phenology, vulnerabilities at different life stages, migration success.
Species population declines, changes in species composition, changing rainfall regimes	Williams <i>et al.</i> 2003b, 2008b, 2010, 2016;	Mitigation is the most powerful influence on projected outcomes, protection of climate change refugia, protection and restoration of corridors affecting species redistribution patterns	Projections of climatic extreme regimes, interactive impacts of climate change and invasives, impacts on biotic interactions and ecosystem processes
Species composition and displacement, distribution, increased morbidity due to pathogens; frost intensity and duration,	Selkirk-Bell and Selkirk (2013), le Roux <i>et al.</i> (2013), Pendlebury and Barnes-Keoghan (2007), Fitzgerald and Kirkpatrick (2017), Bergstrom <i>et al.</i> (2015), Whinam <i>et al.</i> (2014)	Expansion of an experimental <i>A. macquariensis</i> seed orchard, maintain strict biosecurity protocols and detection	Potential for adaptation, fungal proliferation, assessment of pathogenicity of fungal species.
Metabolism, thermoregulation, energetics, fitness, offspring growth, survival, reproduction, population composition, behaviour	McKechnie and Wolf (2010), Gardner <i>et al.</i> (2011), Teplitsky and Millien (2014); Gardner <i>et al.</i> (2016a); Wiley and Ridley (2016); Campbell-Tennant <i>et al.</i> 2015	None identified	Links between climate, individual fitness and population dynamics; mechanisms underlying change, and their interactions over time; potential for adaptation; species sensitivities
Potential for decoupling of orchid-pollinator and community level interactions and altered frequency of hybridization events	Gallagher <i>et al.</i> (2009), MacGillivray <i>et al.</i> (2010)	Citizen science to gauge direction and magnitude of shifts and potential for reproductive failure	Trends across many species, impact on reproductive success