Going nowhere fast: a review of seed dispersal in eucalypts

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Abstract. Eucalypt species have several features that make them particularly well suited for climate change studies. A key assumption is that they have very limited powers of dispersal. If this is correct, it means that climate change analyses to the end of this century can concentrate mainly on assessing whether or not eucalypt species are likely to be able to survive at their existing sites. A recent major climate change study of more than 600 eucalypt species for the period 2014–2085 has used 5 km as a usual dispersal limit for the period to 2085, with the possibility of rare long-distance events. The review presented here considers how far natural stands of eucalypt species are likely to be able to migrate in the period to 2085. It is the first review to consider eucalypt seed dispersal as its major focus. It draws on evidence from millions of years ago to the present, and from eucalypt stands in Australia and around the world. Although rare long-distance events cannot be entirely ruled out, it is concluded that the great bulk of the evidence available indicates that the most likely potential dispersal rate is equivalent to about 1–2 m per year, i.e. ~70–140 m in the period to 2085. Over decades, this is likely to occur as a series of stepwise events, associated with disturbances such as bushfires. However, limitations such as inadequate remnant eucalypt stands and extensive agricultural developments may reduce actual migration rates below even this modest potential.

Additional keywords: *Angophora*, climate change, *Corymbia*, *Eucalyptus*, species distribution model.

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Introduction

Eucalypt species (including a total of ~800 species from the genera *Eucalyptus*, *Corymbia* and *Angophora*) have been identified as being particularly useful for climate change impact studies (Booth *et al.* 2015). Hundreds of eucalypt species have been evaluated at trial sites in numerous countries around the world, using unimproved seed collected from natural stands (see, for example, Poynton 1979; Jacobs 1981). So, unlike most plant and animal groups, much is known about the ability of eucalypt species to tolerate climatic conditions different from those of their natural distributions. Another key characteristic that makes eucalypts particularly useful for climate change studies is the assumption that they have very limited dispersal powers. If it can be assumed that over decades eucalypts disperse at rates equivalent to about 1–2 m per year, then climate change studies to the end of this century can concentrate on analysing locations within existing distributions. This greatly simplifies climate change studies, because complicating factors, such as dispersal distances and land use patterns, as well as edaphic suitability and competitive establishment at new sites, can be ignored. If their dispersal distances are very limited, the key question for eucalypt species for the next 70 years or so becomes: 'can they survive where they are presently located?'.

A recent major climate change study of eucalypts (González-Orozco *et al.* 2016) showed dramatic shifts in the 'the predicted species distribution of the suitable climate space' for 657 eucalypt species in the period from 2014 to 2085. This included many that involve changes of several hundred kilometres, with the greatest

being ~1400 km for *E. semota* C.J.Macpherson & Grayling. However, González-Orozco *et al.* (2016) stated in their methods section that 'most eucalypt species would not be expected to disperse beyond a single grid cell [5 × 5 km] during the time period in this study without a rare long-distance dispersal event'.

The purpose of the present review is to examine information about the seed dispersal capabilities of eucalypts, with a view to indicating how far most eucalypt stands are likely to disperse in the period to 2085. The difference between limited dispersal of ~100 m and dispersal up to several kilometres is important. Climatic and edaphic conditions are likely to be similar over very short distances, but the chances of experiencing different environmental conditions increases with greater distances.

Pollen movement (and hybridisation with other species) can contribute to migration of eucalypts. Dispersal studies suggest that eucalypt pollen regularly travels distances of over 1 km, although most is distributed within 200 m and seed crops are dominated by genetic material from nearby trees (Byrne *et al.* 2008; Broadhurst 2013). Pollen may well play a vital role in eucalypt gene flow over long periods (Potts and Wiltshire 1997), whereas seed dispersal is the critical means for movement of intact (i.e. non-hybridised) species over substantial distances in the next few decades. So, the focus here is on seed dispersal, particularly the distances likely to be achieved in the remainder of this century. Related aspects of the reproductive biology of eucalypts, such as flowering, pollination and seed maturation, are not considered here, but have been reviewed by House (1997). Factors affecting the establishment of eucalypt seedlings from

seed have been previously reviewed by Stoneman (1994), so are only briefly outlined here. For any eucalypt species, seed dispersal is the critical issue for short-term migration. If this is very limited, its natural abilities to colonise new locations will be greatly limited.

Relevant references for the present review were located first in the Web of Science™ and Google Scholar™ by searches using 'eucalypt' and 'seed dispersal' as key terms. However, many of these papers related to the dispersal of seed of non-eucalypt species in environments where eucalypts are also present, so 118 additional references were examined by searching papers that cited a key early eucalypt seed dispersal paper (Cremer 1977). The review is structured in the following way: basic mechanisms of seed dispersal and seedling establishment, alternative dispersal methods, dispersal over very long periods, dispersal within Australia and dispersal from plantings outside Australia. A final section before the discussion considers likely problems of establishment for the dispersal of eucalypt species under climate change in Australia.

Basic mechanisms of seed dispersal and seedling establishment

Eucalypt species use the following four regenerative strategies: obligate seeding, lignotuber sprouting, stem sprouting and combination sprouting (Nicolle 2006). However, their broad-scale dispersal depends on seed production. The basic strategy of eucalypt seed dispersal is to produce very large numbers of seeds, which are simply released and fall to the ground (see Vittoz and Engler 2007, for a review of different seed dispersal strategies). Some fast-growing eucalypts may produce seeds in as little as 3 years, but slow-growing species such as *E. regnans* F.Muell. may take 15–20 years (Gill 1981). Eucalypt seeds are relatively light in relation to most tree species (see, for example, Greene and Johnson 1994). Most range in weight from 0.16 g per 1000 seeds for *E. deglupta* Blume to 4.95 g per 1000 seeds for *E. globulus* Labill. (see the Royal Botanic Gardens Seed Information Database, data.kew.org/sid/, verified 14 July 2017). Variations in published weights for seeds of the same species are often due to whether chaff is included, and also whether seeds are air-dried or not. Eucalypt seeds lack any aerodynamic features, such as wings, to assist their spread. So, their dispersal is largely influenced by factors such as tree height, canopy width, seed weight and wind strength.

Early studies of seed dispersal in eucalypts showed that the bulk of the seeds fall within a distance roughly equal to the height of the tree (Grose 1957; Cunningham 1960; Cremer 1966). Cremer (1977) refined this simple assessment, by calculating dispersal distances in relation to wind velocity, height of release and terminal velocity. For example, from a height of 40 m with a 10 km h^{-1} (2.78 m s^{-1}) wind, the lightest seed tested (*E. deglupta*) was expected to disperse 52.9 m, whereas the heaviest tested (*E. globulus*) was expected to disperse 20.1 m.

The size of the seed crop varies in cycles between 2 and 4 years for many eucalypt species (Harwood 1990). Seed collection for research purposes usually involves sampling of mature dominant trees. This is performed by removing selected branches and placing them over plastic sheets. The heat of the sun causes the seed carrying capsules to open and seeds can be collected.

Heavy-seeding species, such as *E. camaldulensis* Dehnh. and *E. globulus*, may yield 5–10 kg of seed per tree in good seeding years (Harwood 1990). Under natural conditions, seed release in eucalypt forests and woodlands ranges from ~1 to 2.3 million seeds ha^{-1} (Loneragan 1979) to ~49 million seeds ha^{-1} (Burrows and Burrows 1992). There is generally a low level of seed release throughout the year, which is slower under wet conditions, but increases during periods of drought or following fires (Cunningham 1960).

Seed release following bushfires is important, because fires tend to clear away potentially competing vegetation. The role of seeds and seedling establishment in relation to fires has been considered by Gill (1997) as part of a review of eucalypts and fires. In eucalypt woodlands or forests, bushfires can involve ground fire (e.g. underground fire in peat), surface fire or crown fire. In surface fires, the tree canopy may be scorched, but does not burn. It is crown fires that are most likely to kill existing trees, providing opportunities for new individuals to establish, although some existing trees may resprout depending on the severity of the fire (Burrows 2013; Denham *et al*. 2016). Judd (1993) assessed seed survival of *E. regnans* under experimental conditions and Mercer *et al*. (1994) developed a time-dependent model of seed survival under fire conditions. Judd (1993) reported that film evidence showed that canopies can burn for as little as 10–30 s, and Ashton (1986) demonstrated that capsules of *E. obliqua* L'Hér. provide adequate protection to ensure that some seeds survive a crown fire.

Ants often eat large proportions of fallen eucalypt seeds (Yates *et al*. 1995). For example, Wellington and Noble (1985) estimated a period of only 5 days before half the fallen seeds of *E. incrassata* Labill. were eaten in long-unburnt semiarid stands in south-eastern Australia. Following bushfires, numbers of seed eating ants have been shown to increase in an *E. obliqua* L'Hér.–*Casuariana pusilla* Macklin woodland in south-eastern Australia (Andersen 1988). In an *E. delegatensis* R.T.Baker forest, O'Dowd and Gill (1984) showed that although ant numbers increase following fire, the numbers per available seeds declined as a result of the massive release of seeds. In the absence of fire, Andersen (1987) showed that ants limit seedling recruitment in an *E. baxteri* (Benth.) Maiden & Blakely ex J.M.Black–*C. pusilla* woodland in south-eastern Australia; however, predator satiation following massive seed release after fire produced high numbers of seedlings. Similarly, mass release of eucalypt seeds after fires also appeared to help satiate ants, and improve the chances of successful establishment at two old-field recolonisation sites in Western Australia (Harris and Standish 2008).

Stoneman (1994) and Bell and Williams (1997) reviewed the ecology and physiology of establishment of native eucalypt forests and woodlands from seed. Factors affecting germination and emergence, mortality and survival, and growth were considered. In summary, abiotic factors including water, temperature and, in some cases, light, were found to be major factors influencing germination and emergence (Boland *et al*. 1980; Gibson and Bachelard 1989; Battaglia 1993). Biotic factors included seed harvesting, which has already been mentioned. In addition, soil pathogens may cause mortality (Mwanza and Kellas 1987), and allelopathic effects may restrict emergence levels, but its importance depends on the species, the amount and

types of litter, soil properties and climate (May and Ash 1990). Direct effects included seedbed conditions and overstorey density. Emergence and survival of eucalypt seed is usually better on burnt than unburnt, and disturbed rather than undisturbed, seedbeds (Burrows *et al.* 1990). In experiments, eucalypt seed has performed best when planted at depths between ~0.5 and 5 cm (Free 1951; Cremer 1965). Not surprisingly, considering the small size of the eucalypt seed, mortality is often greater where competing vegetation is already present, although partial shelter in commercial forests can moderate climatic conditions and improve establishment (Keenan 1986). Despite these limitations, eucalypt seeds are so numerous that some survive to replace existing stands, even though eucalypt seed loses viability usually within a year (Grose 1960).

Research since 1997 has refined knowledge of the processes affecting seed germination and seedling survival. For example, López *et al.* (2000) showed that the larger seeds of *E. globulus* germinated better than smaller seeds across a range of temperatures. Close and Wilson (2002) showed that large *E. regnans* seeds germinated at a faster rate than small seeds, and chilling increased germination rates for high-altitude provenances. Schütz *et al.* (2002) showed that large-seeded species from the south-western Australia are able to penetrate the soil profile faster and deeper. A particularly interesting observation was in relation to seedling survival under environmental change. *Eucalyptus pauciflora* Sieber ex Spreng seedlings grown in the field under elevated CO_2 conditions ($2\times$ ambient) had 10 times more necrotic leaf area after an autumn freezing event than those grown under ambient conditions (Barker *et al.* 2005).

Alternative dispersal methods

Whereas the seeds of most eucalypt species fall within a distance approximately equivalent to the height of the tree, there are a few exceptions. If a species is found in riverine locations, the seeds may float downstream, and some may be delivered onto areas suitable for germination and establishment. For example, the spread of *E. camaldulensis* as an invasive weed along perennial, seasonal and intermittent watercourses in South Africa has often been reported (see, for example, Rejmánek and Richardson 2011). However, genomic research on 990 trees from 97 *E. camaldulensis* populations across the natural distribution in Australia has shown that genetic similarity was greatest between the nearest populations, regardless of whether or not they occurred on the same river system (Butcher *et al.* 2009).

A small number of bird species, including *Calyptorhynchus baudinii* Carnaby (long-billed black cockatoo), *Calyptorhynchus magnificus* Latham (red-tailed black cockatoo) and *Purpreicephalus spurius* Kuhl (red-capped parrot), derive a significant part of their diet from the unusually large seeds (~0.10 g each) of *Corymbia calophylla* (Lindl.) K.D.Hill & L.A.S.Johnson (House 1997). *Calyptorhynchus banksia naso* Gould (forest red-tailed black cockatoo), similarly, eat seeds from *C. calophylla* and, to a lesser extent, from *E. patens* Benth. and *E. staeri* (Maiden) Kessell & C.A.Gardner (Cooper *et al.* 2003). It is assumed that uneaten seeds are sometimes dispersed; however, no published data are available for how often this occurs or how far seeds are transported.

Australian stingless bees (*Tetragonula carbonaria* Smith) are attracted to and collect resin from the fruits of *Corymbia torelliana* (F.Muell.) K.D.Hill & L.A.S.Johnson (Leonhardt *et al.* 2014). In doing so, they pick up seeds, which may be removed by grooming on return to the nest. This can result in dispersal distances of up to 300 m (Wallace and Trueman 1995).

Seed dispersal by ants is not usually significant for eucalypts. Ants either eat eucalypt seeds *in situ* (Wellington 1989) or take them short distances, generally less than a few metres, back to their nests (Ashton 1979; Harris and Standish 2008). Many species of harvesting ants maintain seed stores below 15 cm of the soil surface (Andersen 1982). However, the seeds of most eucalypt species are so small that they cannot usually successfully germinate and establish if buried below ~5 cm (Cremer 1965).

Outlying populations

Advances in genetics and genecology are providing insights into variations within and among populations of eucalypts (Potts and Wiltshire 1997). If long-distance eucalypt-seed dispersal were taking place frequently, it might be expected that outlying stands would be common and that these stands would be genetically similar to parts at least of current main distributions. For example, a stand of *E. globulus* subsp. *bicostata* (Maiden, Blakely & Simmonds) J.B.Kirkp. that exists at Mount Bryan (South Australia) is located more than 600 km from the nearest other population of this subspecies. Vaillancourt *et al.* (2001) used random amplified polymorphic DNA (RAPD) molecular-marker analysis to assess the population, which appears to originate from a very old individual (possibly as old as 4000 years) that predates European settlement. Whether this stand is a result of natural long-distance seed dispersal, seed dispersal by the Aboriginal population or is a survivor of a much broader previous distribution of the subspecies is not clear. However, Vaillancourt *et al.* (2001) concluded that the simplest explanation was that the stand was once connected to the main Victorian populations and became isolated as conditions in the region became more arid.

Genetic differentiation has also been studied for 13 stands of *Eucalyptus diversicolor* F.Muell., which is found in a limited high-rainfall area in the extreme south-west of Western Australia (Coates and Sokolowski 1989). Two southern coastal outliers (William Bay and Many Peaks) showed insignificant genetic divergence from the main distribution, suggesting that separation may be recent. In contrast, outlying populations to the north-east and west showed greater differences from the main forest. This suggests that they have persisted as survivors of a more extensive distribution as conditions became drier from ~5000 years before present.

Other examples of isolated disjunct populations are found in the south-west of Western Australia. For instance, Byrne and Hopper (2008) used restriction fragment-length polymorphism (RFLP) markers to examine material from 11 locations of *E. caesia* subsp. *caesia* Brooker & Hopper and three locations of *E. caesia* subsp. *magna* Brooker & Hopper. The outlying populations showed high divergence, suggesting isolation over long periods. The outliers appear to represent surviving islands rather than being the result of recent dispersal.

One of the largest disjunctions for eucalypt species is shown by *Eucalyptus perriniana* F.Muell. ex Rodway. The main populations are located in south-eastern mainland Australia, whereas three small isolated populations are more than 500 km away in southern Tasmania. Genetic analyses showed that the Tasmanian populations were genetically distinct from the mainland populations, suggesting that they are surviving remnants rather than the result of recent long-distance dispersal (Rathbone *et al*. 2007).

Dispersal over very long periods

The current natural distribution of almost all eucalypt species is limited to the Australian continent, with a small number of species found to the north of Australia in Papua New Guinea, Indonesia and the Philippines (Boland *et al*. 1984). Intriguingly, the oldest *Eucalyptus* macrofossils have been found in Patagonia in Argentina, where the genus is no longer native (Gandolfo *et al*. 2011). These fossils have been dated to the early Eocene, ~51.9 million years ago. The earliest fossil eucalypt-type pollen from *Myrtaceidites tenuis*, which is considered to be a precursor of eucalypts, has been found not only in Australia, but also in eastern Antarctica (Macphail and Thornhill 2016). The point of origin of eucalypts is uncertain (Hill *et al*. 2016), but their dispersal to or from South America must have taken place when what has become Australia was still linked to South America by Antarctica (see Fig. 1). So, it is clear that eucalypts can disperse
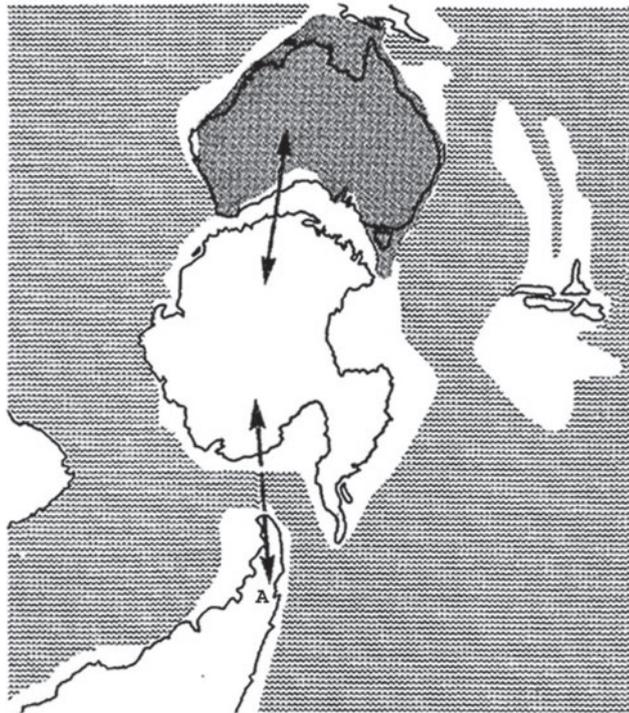

Fig. 1. Southern continents in early Eocene times (55 million years ago) following the breakup of Gondwanaland. White areas indicate approximate land areas at that time. Australia is highlighted by dark shading. Africa has separated to the left and what will become New Zealand to the right. South America has separated, whereas Australia is about to separate from Antarctica. 'A' has been added to indicate the location of the oldest eucalypt fossil finds in Patagonia. Figure from Boland *et al*. (1984), copyright CSIRO.

over vast distances given vast periods of time. But even the slowest rate of dispersal considered here (about 1 m per year), would be adequate given tens of millions of years.

There is a growing number of phylogeographic studies, which consider the historical and current distributions of eucalypt species in the light of genetics, and provide some insights into eucalypt dispersal over very long periods. In the Pleistocene epoch (from 2.588 million years ago to 11.7 thousand years ago), southern Australia experienced climatic oscillations with cyclic expansion and contraction of cool–dry (glacial) and warm–wet (interglacial) conditions (Markgraf *et al*. 1995). In contrast to much of Europe and North America, glaciation in southern Australia was not extensive, but was limited to the Central Plateau of Tasmania (Colhoun *et al*. 1996) and small parts of the Snowy Mountains in mainland Australia (Barrows *et al*. 2001).

Byrne (2008) reviewed phylogeographic studies during Pleistocene climatic cycles in southern Australia. In contrast to the major refugia found in the northern hemisphere, there appear to have been many localised refugia, with eucalypt species showing resilience rather than large-scale migration. For example, a phylogeographical study of *E. loxophleba* Benth. confirmed the importance of cyclic climatic expansions and contractions for eucalypts in the south-west of Western Australia (Byrne and Hines 2004). More recently, Nevill *et al*. (2010) used genetic analysis to show the long-term persistence of *E. regnans* in multiple refugia under harsh environmental conditions, which was followed by recolonisation of wider areas when more favourable conditions returned.

A study of *E. globulus* phylogeography in Tasmania and south-eastern mainland Australia showed genetic patterns corresponding to hypothesised glacial refugia (Freeman *et al*. 2001), which are consistent with limited seed based dispersal following deglaciation. Other studies in Tasmania have shown expansion of eucalypt species into previously glaciated inland plateau regions from eastern and south-eastern coastal refugia (McKinnon *et al*. 2001, 2004).

Seed dispersal from eucalypt sites in Australia

Dispersal distances of eucalypt seeds over periods of several decades are not surprisingly much more modest than is prehistoric spread over very long periods. For example, in 1932, *E. cladocalyx* F.Muell., a tree with some commercial uses but a limited natural distribution in South Australia, was introduced into King's Park, Perth, Western Australia, as part of a series of war-memorial avenues. It became invasive and spread into the native bushland of the park, which is dominated by *E. gomphocephala* DC. and *E. marginata* Donn ex Sm. Some 70 years later, Ruthrof *et al*. (2003) reported that it had spread 70 m from the original planting sites. Seedling establishment was affected by fire events, with high numbers of seedlings being found in burnt areas and low numbers in unburnt areas, and with *E. cladocalyx* showing quicker canopy recovery following fires than locally native species.

A novel approach has made use of the many kilometres of cleared buffer strips around commercial plantations to examine the dispersal of *E. globulus*. This is the major hardwood plantation species used in Australia, with over 500 000 ha of

plantations (ABARES 2015). Although comprising four major subspecies (recognised by some taxonomists as separate species), the commercial plantations are based on *E. globulus* subsp. *globulus*, which is native to Tasmania, as well as having very limited occurrences in southern coastal Victoria. Larcombe *et al*. (2013) inspected 290 km of plantation boundaries both within and outside the species' natural distribution. They recorded nearly 5000 wildlings (i.e. plants growing outside plantation boundaries), with 98% occurring within 10 m of the plantation edge.

Evidence of seed dispersal from eucalypt stands outside Australia

Eucalypts have been very widely tested and extensively planted around the world for commercial-forestry purposes. One of the great advantages of overseas dispersal studies is that movements of eucalypts from planted locations into natural vegetation can be distinguished very easily. Plantations are generally located in areas where commercially satisfactory growth can be achieved, so climatic and edaphic conditions just outside plantation edges do not usually limit survival of wildlings. An important part of assessments outside Australia is evaluating the risks that eucalypt species may pose as potential weeds. These studies also provide some evidence relevant to factors affecting their natural spread.

Features influencing invasive characteristics of Australian tree species have been reviewed by Booth (2014). Even though many eucalypt species have been introduced around the world, there are very few species that are major problems as weeds. Where they are a problem, such as *E. globulus* in California, it is often because they have been widely planted in the past, so dispersal, although limited, now occurs from many locations (Wolf and DiTomaso 2016). Rejmánek and Richardson (2011) suggested that eucalypts are only weakly invasive because of (1) their relatively limited seed dispersal, (2) their high seedling mortality and (3) lack of compatible ectomycorrhizal fungi. The following recent studies, not included in the Booth (2014) review, have also emphasised the importance of the feeble powers of dispersal of eucalypts and their high seedling mortality.

For example, Fernandes *et al*. (2016) assessed natural regeneration of *E. globulus* from plantations into natural areas in Portugal. They found that 92% of seedlings were recorded less than 15 m from the plantation edge, and the presence of native forest or grassland was very resistant to eucalypt seedling establishment. Águas *et al*. (2014) studied the natural establishment of *E. globulus* in burnt stands in Portugal and also found that the existence of 'close seed sources' was important. Similarly, Calviño-Cancela and Rubido-Bará (2013) examined seed dispersal, seedling recruitment and survival in areas around plantations of *E. globulus* in Spain. Most seed fell within the first 5 m from plantation edges (84.3%) and 98.6% within the first 15 m. Both emergence (3.3% and 0.9%) and survival up to 6 months (17.5% and 3.7%) were greater in nearby shrublands than in native forest.

Lorentz and Minogue (2015) assessed the potential invasiveness of *E. amplifolia* Naudin, *E. camaldulensis* and *E. grandis* W.Hill in Florida. They found that no seedlings established outside two plantation stands, so they conducted seed addition studies to assess emergence rates and found the probability of emergence of added seed for different treatment combinations to be very low ($P = 0.0$ to 0.0032). They concluded that invasiveness risk was low, and a buffer strip of native grasses would be more effective than the bare-soil buffer strips usually used around plantations.

A few studies have examined the spread of eucalypt stands over several decades, particularly those of *E. globulus* in California. For example, the expansion of 16 mostly *E. globulus* plantations on Angel Island in San Francisco Bay were examined as part of a plan for their removal (California State Parks System 1988). The sketch map shown in Fig. 2a (McBride *et al*. 1988) covers a period of 73 years from 1915 to 1988, which is a length of time similar to those being considered in many current climate change analyses. The figure shows how wildlings spread from the original plantation, with the greatest extension being ~98 m in an easterly direction. This corresponds to the prevailing winds in the San Francisco Bay area, which are predominantly from the west or west–north-west (see Fig. 2b). Eucalypt expansion was also favoured by moist swales, and on road cuts where competition from annual grasses had been eliminated (J. McBride, pers. comm.). The total area shown in Fig. 2a increased by 3.7 times, from 0.24 ha of the original plantation area in 1915 to 0.89 ha in 1988. The report mapped and tabulated areas of expansion for all the 16 stands, with the mean increase in the total area in 1988 being 3.6 times that of the original plantation area. Greatest dispersal distances for individual stands, estimated from the report's maps for this review, ranged from zero for roadside plantings (Site 14) to 133 m (Site 9). Similarly, Fork *et al*. (2015) analysed the spread of six eucalypt stands in the Elkholm Slough watershed (California). They found an average increase of 271% over 70 years (1931–2001), which was almost identical to that reported for the stands at Angel Island (i.e. 270%) over 73 years.

Problems of migratory eucalypt establishment in Australia

Although the present review has concentrated mainly on seed dispersal, it is appropriate to at least briefly consider the challenges of seedling establishment, because this is vital if individual eucalypt species are to respond to climate change by moving to new environments. The focus of interest here is on how difficult it is for eucalypts to migrate across landscapes, but much of the evidence comes from regeneration at or near existing sites.

For example, ~47 million hectares of the once extensive temperate eucalypt woodlands of southern Australia have been widely cleared for agriculture, with as little as 3% of the original areas of some types remaining in some areas (Department of the Environment and Water Resources 2007). The same problems that face restoration efforts limit the prospects of natural migration under climate change. These include clearing for agriculture, dryland salinity, excessive fertilisation, grazing, reduced fire regimes and exotic weeds (see review by Yates and Hobbs 1997).

Eucalypt woodlands have often been so effectively cleared that the remnants in many areas are inadequate to allow
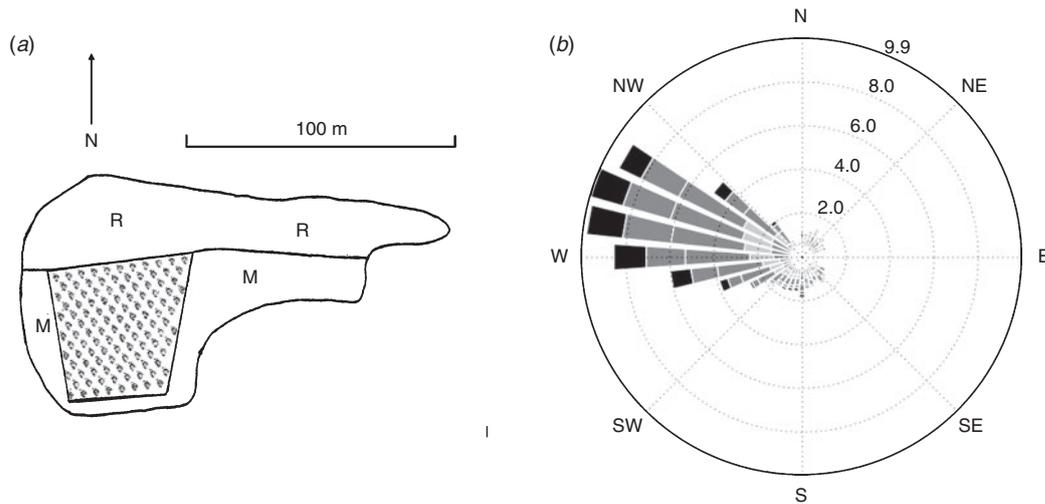
Fig. 2. (*a*) Sketch map of original eucalypt plantation and wildling establishment on Angel Island (San Francisco Bay) from 1915 (total area = 0.24 ha) to 1988 (total area = 0.89 ha). The figure has been rotated, so north is at the top of the page. 'M' indicates expansion from margins of stand, and 'R' indicates expansion into road cut or other heavily disturbed area. Map from McBride *et al*. (1988) in California State Parks System (1988). Reproduced with permission of California State Parks. (*b*) Wind direction distribution in percentage for whole year for San Francisco Airport, using data from 1 January 1970 to 9 August 2016. The wind direction is almost always from the west or west–north-west. Segments indicate wind speed, with the outer segment being winds greater than 32 km h^{-1}. Figure courtesy Iowa Environmental Mesonet, copyright Iowa State University.

recolonisation of abandoned farmland. For instance, Standish *et al*. (2007) examined three farmland areas in the wheatbelt of Western Australia that had been abandoned for as much as 45 years. They found that two old fields were dominated by non-native annual grasses. They found declining levels of native seeds in the soil seedbank at 0 m, 50 m and 100 m into the old fields. They attributed the failure of eucalypt species to reclaim these areas to lack of seed availability and recruitment failure. Only in one old-field situation were eucalypts showing some signs of successfully re-establishing. Their even height suggested that one recruitment event, perhaps a bushfire in 1963, had facilitated their establishment.

Eucalypt regeneration has also been surveyed at 519 sites in grassy dry forests and grassy woodlands of central Victoria (Dorrough and Moxham 2005) and was observed at 27% of sites. Factors that reduced regeneration included intensive past land use (cultivation), regular livestock grazing and high cover of exotic annual vegetation (i.e. grasses, graminoids and forbs). A long history of agriculture limited future recruitment, even when grazing was removed. Increasing distance to remnant trees was also a factor, presumably being related to inadequate seed dispersal.

While regeneration is difficult even at sites where remnant trees are present, similar factors are likely to limit the abilities of eucalypt species to track rapidly changing climates across landscapes. Agricultural and urban developments, even major roadways, present significant dispersal barriers. Prior to European settlement, spread of eucalypts across landscapes was easier, particularly given long periods of time, occurrence of natural fires and the use of fire by the Aboriginal population (Yates and Hobbs 1997). Bushfires, mainly set off by lightning strikes, are still experienced regularly (about 1 year in 4 in any area) in the semiarid tropical savannas of Western Australia and the Northern Territory (Williams *et al*. 2009), so a high proportion of the land area burns every year.

However, the mean height of eucalypts in the wet–dry climate of the north is generally much less than in the milder conditions of high-rainfall regions of southern Australia (Boland *et al*. 1984). Because tree height plays a major role in determining dispersal distances, migration rates under the most favourable conditions may not be dramatically different. Hypothetically, in level topography, a representative eucalypt stand in northern Australia might take 5 years to grow to a height of 5 m and then disperse seeds over 5 m, whereas a stand in southern Australia might take 20 years to grow to 20 m dispersing seeds over 20 m. Over 100 years, the distance of each step is different, but the total migration distance would be similar. In reality, of course, the occurrence of such step movements are likely to be highly variable.

Whereas Australia is relatively flat in comparison to other continents, topography provides both opportunities and challenges for eucalypt dispersal in hilly or mountainous terrain. Austin and van Niel (2011) examined the importance of topography in determining the distribution of *E. fastigata* H.Deane & Maiden and discussed its shifting to different slopes and/or aspects as a response to climate change. They suggested that 'species may need only to disperse across a valley to reach a suitable habitat, rather than to migrate hundreds of kilometres in latitude or hundreds of metres up an elevational gradient.', p. 17. The possibility of species retreating to higher, cooler locations is a response often mentioned in climate change studies, but Green and Venn (2012) found that seedling establishment of *E. pauciflora* was rare uphill of existing sites, because of the limitations of seed dispersal. Simple geometry means that eucalypt seed dispersal distances are likely to be less on uphill slopes than on level ground.

Changing environmental conditions are likely to impose stresses on existing tree populations and contribute to dieback events (Ross and Brack 2015), which will reduce seed production.

Even if they do not cause seedling or tree deaths, changing climatic conditions may interfere with reproductive processes. For example, *E. nitens* (H.Deane & Maiden) Maiden plantations grow successfully in South Africa under conditions that are warmer and drier than those within their natural distribution, but they do not flower and, hence, do not produce seeds (Booth *et al*. 2015). Similar problems have been observed with the majority of the more than 900 eucalypt species and subspecies being grown outside their natural distributions at the Currency Creek Arboretum in South Australia (Hay 2016).

Discussion

Studies described here have confirmed the general conclusions from pioneering eucalypt-dispersal studies of more than 50 years ago (Grose 1957; Cunningham 1960; Cremer 1966), which showed that eucalypts have very limited seed dispersal capabilities. It would be desirable to have more long-term studies of eucalypt dispersal, particularly from Australia. Nevertheless, the longer-term studies (see, for example, the studies from California and the Ruthrof *et al*. (2003) study from Australia) have suggested that eucalypt seed dispersal rates over periods of ~70 years are equivalent to about 1–2 m per year. Movements tend to take place in a stepwise fashion, taking advantage of disturbance events such as bushfires. Occasional long-distance dispersal events cannot be entirely ruled out, but the evidence presented here does not suggest that they are common events. Actual dispersal rates under climate change may well be below even the modest potential of 1–2 m per year, because obstacles such as inadequate remnants and extensive agricultural areas provide major impediments to natural migration.

There is no chance of natural migration of eucalypts by seed dispersal fully keeping pace with many of the distances indicated by even the moderate climate change scenario used by González-Orozco *et al*. (2016). Their fig. 1 was a reasonable way of summarising the large amount of data shown in their 657 supplementary maps. However, it would have been desirable to indicate in the caption that such great movements are not expected. If eucalypts are routinely capable of migrating only across landscapes in the order of ~71–142 m in 71 years, then no species should be capable of occupying any substantial part of the '2085 only' areas shown in the 25×25 km resolution supplementary maps of González-Orozco *et al*. (2016).

Eucalypt pollen dispersal was mentioned in the introduction, but the possibility of long-distance migration over many kilometres by means of reticulate evolution should be mentioned. This involves pollen spread, hybridisation with related species, backcrossing and re-assembly, leaving evidence in the signatures of the chromosomal DNA. Examples include evolution of eastern grey box eucalypt species (*Eucalyptus* supraspecies *Moluccanae*) in the Murray–Darling Basin (Flores-Rentería *et al*. 2017), and *E. globulus* with related *Symphyomyrtus* species in south-eastern Tasmania (McKinnon *et al*. 2004). The latter study referred to movements over very long periods from glacial refugia, so it appears unlikely that such evolutionary processes can have any significant effect over periods as brief as that from 2014 to 2085.

Any tree species that experiences climatic conditions outside those of its current natural distribution as a result of climate change can respond in one of the following three ways: adapt (tolerate), move or die (Aitken *et al*. 2008). As mentioned in the introduction, there is a wealth of information available from commercial trials about how eucalypt species and provenances respond to climatic conditions different from those found within their natural distributions. Evolutionary change can be considered to be a special case of adaptation. However, as many eucalypt species can live for hundreds of years (see table 1.1 in Williams and Brooker 1997), the likelihood of any evolutionary adaptation to climate change in most stands is not great over the period to 2085. The ability of eucalypts to move by dispersal to new locations has been shown here to be very effective over very long periods, but very limited over periods of a few decades. Regional and local refugia have been of critical importance in allowing eucalypt species to recolonise regions when conditions become more favourable. As suggested by Austin and van Niel (2011), refugia at the landscape scale are likely to be important for eucalypt species to withstand the climate changes expected to occur this century. Finer-scale species distribution modelling tools are required that take into account, not only broad-scale climatic conditions, but also the effects of factors such as slope, position on slope and aspect on microsite conditions.

Trials outside Australia have demonstrated that many eucalypt species have climatic adaptability beyond that indicated by conventional analyses of their natural distributions (Booth *et al*. 2015). The analyses of González-Orozco *et al*. (2016) endeavoured to assess some of this adaptability, and Prober *et al*. (2016) reviewed recent studies of the climatic adaptability of eucalypts. However, more research is needed to determine the degree to which eucalypt species can rely on this adaptability as well as the existence of suitable refugia to cope with climate change, and the extent to which they will have to depend on their limited dispersal capabilities.

Conflicts of interest

The author declares no conflicts of interest.

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