Commentary

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Long-term research reveals potential role of hybrids in climate-change adaptation. A commentary on 'Expansion of the rare *Eucalyptus risdonii* under climate change through hybridisation with a closely related species despite hybrid inferiority'

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Eucalypts have radiated across Australia and beyond, with more than 700 species occurring in diverse environments, often with two or more species co-occurring or occupying adjacent ranges. Interspecific hybrids have been widely documented in the wild and/or from manipulated crossing (Griffin *et al.*, 1988). These hybrids, deployed clonally, are critical to eucalypt plantation forestry, often growing more vigorously than pure species in modified environments (Potts and Dungey, 2004) and have clearly played a pivotal role in speciation (e.g. McKinnon *et al.*, 2004; Robins *et al.*, 2020). However, in this issue of *Annals of Botany*, Pfeilsticker *et al.* (2021) add to an increasing body of research demonstrating that eucalypt hybrid offspring are often less fit than pure species, are strongly selected against in the wild, but may still present a significant pathway for adaptive geneflow. Understanding this apparent paradox is an important research objective.

Studying the occurrence of naturally occurring hybridization, the fate of the resulting progeny, and the impacts upon stand and population dynamics is technically challenging. Monitoring over decades, both *in situ* and in common-garden trials, is required to observe late-acting effects and partition genetic and environmental effects. Pfeilsticker *et al.* (2021) report on research conducted in these settings over a 30-year period in southern Tasmania. During this timeframe, climate change has impacted significantly on the study area, with increased temperature, and drought and fire frequency – a trend predicted to continue throughout southern Australia. Eucalypts are capable of only short-distance seed dispersal but are mostly pollinated by insects and birds that can transfer pollen over longer distances. Understanding the mechanisms that drive eucalypt speciation and adaptation through pollen flow and hybridization is therefore critical to eucalypt conservation and management.

Like other major forest tree genera such as *Populus* and *Quercus*, barriers to hybridization are relatively weak in eucalypts (Janes and Hamilton, 2017). Hybrids are occasionally found at low frequencies in natural stands or occupying an intergrading hybrid zone between geographically separate parent species. While numerous records of natural, interspecific hybridization have been recorded in sympatric eucalypt populations (Griffin *et al.*, 1988), only 15 % of combinations expected on geographical/taxonomic grounds had been recorded, and 37 % of these were known from a single herbarium record (Griffin *et al.*, 1988). While hybridization between species from different genera and subgenera does not occur, there are no broadly operating barriers below this level, though hybrid viability generally declines with genetic distance between parental species. The main pre-mating impediments to natural hybridization between compatible species are geographical separation and/or environmental partitioning, and differences in flowering time. There are few post-mating barriers to seed-set among closely related species, but a unilateral barrier to within-subgenus hybridization occurs due to the inability of pollen tubes from small-flowered species to elongate sufficiently in large-flowered species, a phenomenon giving rise to asymmetric gene flow (Field *et al.*, 2011). An additional physiological barrier between distantly related parents is more severe and results in pollen-tube abnormalities and arrest in the pistil. As discussed by Pfeilsticker *et al.* (2021), a major post-zygotic barrier is hybrid inferiority, expressed as outbreeding depression due to genomic incompatibilities, presumably due to breakdown of favourable epistasis (Larcombe *et al.*, 2015).

An important finding from Pfeilsticker *et al.* (2021) is that hybrids between *Eucalyptus risdonii* and *E. amygdalina* are generally not superior to their parent species in terms of vigour and survival. This is a common finding in other natural and manipulated eucalypt hybrids. Yet the message from the tree improvement literature is that hybrids are often more vigorous, displaying heterosis (Potts and Dungey, 2004). Globally, there are now more than 30 million hectares of eucalypt plantations, predominantly based on just a few *Symphyomyrtus* species. Interspecific hybrids have been critical to the success of plantation programmes overseas (Fig. 1), with the hybrid between *E. urophylla* and *E. grandis* perhaps the most widely planted of all eucalypts. However, it should be remembered that industrially deployed eucalypt hybrids are (1) individual genotypes selected at very high intensity from screening trials or plantations, and deployed clonally, and (2) planted in highly modified environments, often where the parents are less well adapted. Additionally, while their fitness in terms of growth is excellent, they may not be reproductively fit. Clearly, industrial eucalypt hybrids give an upwardly biased impression of hybrid fitness.

Most Australian eucalypt plantations are of pure species, predominantly *E. globulus* which possesses a large fruit and corresponding pollen-tube elongation capacity. Natural stands proximate to plantations are at risk of genetic pollution – i.e. pollen-swamping resulting in hybridization (Potts *et al.*, 2003). This risk is greatest for naturally small or anthropogenically fragmented stands situated near large plantations. While severe effects of genetic pollution have not been documented in eucalypts, ongoing monitoring will be required as Australia's plantation estate has expanded significantly in the last 25 years. Long-term pollen flow from plantations to native stands lead to hybridization and introgression of exogenous genes. As Pfeilsticker *et al.* (2021) discuss, although many F_1 hybrids lack vigour, those that survive may backcross to the parental species producing progeny that often regain significant fitness. Gradual depletion of the local native gene pool may result in loss of the native species' genetic identity.

However, the processes of hybridization and introgression associated with genetic pollution may provide adaptation to climate change for naturally occurring eucalypts. Although selection against hybrids is often

FIG. 1. Clonal plantation of *Eucalyptus camaldulensis* × *deglupta*, an intersectional *Symphyomyrtus* hybrid, grown for commercial wood production on a rice paddy bund in Thailand. Intersectional hybrids are rarely successful in nature, but individual, highly selected genotypes can be highly vigorous in modified environments.

strong, especially within the parental niches, F_1 hybrids typically have phenotypes intermediate to the parents. Hybrid survival is therefore more likely at the margins of the parental range, and on sites exposed to disturbance, potentially including the effects of climate change. As Pfeilsticker *et al.* (2021) found, gradual drying within the range of *E. risdonii* and *E. amygdalina* is driving differential selection, favouring phenotypes closer to the former species. Importantly, while selection against hybrids was strong in both the common-garden trial and the natural hybrid zone, the expression of hybrid inferiority was variable, with some individuals as fit as parental genotypes. Moreover, F_2 recovery of fitness was evident among the hardier *E. risdonii* phenotypes. This 'resurrection' of a species by hybridization and backcrossing provides a possible mode of pollen-based dispersal that can operate over longer distances than seed-based dispersal. Indeed, analysis of maternally inherited chloroplast haplotypes is providing increasing evidence that ancient hybridization shaped a number of eucalypt species extant today (McKinnon *et al.*, 2004).

Pfeilsticker *et al.* (2021) have demonstrated the importance of long-term monitoring of a wild hybrid zone to track the fate of offspring during a sustained period of hotter and drier climate. Their long-term monitoring provides robust evidence that though hybrid offspring of closely related eucalypts may be selected against, some individuals will survive and provide a means of pollen-mediated geneflow. In their case, hybrids possessing phenotypes closer to the hardier parent were favoured, providing insight into how eucalypts might adapt to climate change. Importantly, their institution has had the foresight to establish and maintain an associated common-garden trial, a resource that allows quantitative comparison of pedigreed progeny and partitioning of environmental and genetic effects. While the use of molecular markers will undoubtedly continue to help unlock the hidden past of hybridization effects, their work underlines the value of investment in classical, long-term, field- and trial-based research.

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