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Genetic and morphological evidence supports the hybrid status of *Adenanthos cunninghamii* (now *Adenanthos* × *cunninghamii*)

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ABSTRACT

Hybridisation is common among plants and is considered to be an important process in evolution. However, there is much debate as to the role of hybridisation in conservation, particularly whether species of hybrid origin should be protected. In general, conservation policy allows for the protection of hybrids and hybrid progeny if they are shown to be taxonomically distinct, stable and capable of self-perpetuation, and naturally produced. The rare species *Adenanthos cunninghamii* was suspected to be a hybrid between putative parents, *Adenanthos sericeus* and *Adenanthos cuneatus*, as it only occurs where these species co-occur and it displays intermediate and variable morphology. Genetic analysis of *A. cunninghamii* and the two putative parent species was consistent with this species being a hybrid between *A. sericeus* and *A. cuneatus*. Direct analysis of diagnostic loci and phenetic analysis indicated that *A. cunninghamii* was not genetically uniform and was genetically intermediate between the putative parents. *A. cunninghamii* is not a distinguishable taxon, morphologically or genetically, and does not produce offspring with morphology within the taxonomic description of the species, thus the species does not satisfy the criteria for protection of hybrids and listing as a rare species in Western Australia.

1. Introduction

Hybridisation is acknowledged as a significant force in plant evolution (Rieseberg and Carney, 1998; Ellstrand et al., 1999; Soltis and Gitzendanner, 1999; Allendorf et al., 2001; Whitney et al., 2010) and hybrids are known to occur in all major plant groups and analysis of floras has shown hybrids occur in 40% of families and 16% of genera (Whitney et al., 2010). Hybridisation may result in hybrid speciation (Arnold, 1992; Rieseberg and Wendel, 1993) or hybrids may occur as isolated individuals or hybrid swarms without necessarily leading to speciation due to continual resorting of alleles (Allendorf et al., 2001). Although many hybrids have reduced fertility compared to the parent species, hybrid individuals are rarely completely sterile and in many cases have increased fitness compared to either parent (Arnold et al., 2001). In contemporary landscapes, fragmentation and changes in community structure may increase opportunities for cross pollination of species (Field et al., 2008), and disturbance also provides increased opportunities for hybrid establishment (Ellstrand and Schierenbeck, 2000). Hybridisation is also known to contribute to invasiveness of species (Ellstrand and Schierenbeck, 2000; Gaskin, 2017).

Hybridisation has implications for recognition of species and management of plant populations, and it is important to distinguish situations of recent hybridisation and sporadic hybridisation events from those of stabilised hybrid taxa (Rieseberg and Wendel, 1993). There has been significant debate among conservation practitioners about whether conservation protection should be extended to hybrid individuals that are rare, or the hybrid offspring of a rare species (Soltis and Gitzendanner, 1999; Allendorf et al., 2001). One argument focuses on the recognition of species as discreet taxonomically stable entities and that only these species should be afforded conservation protection, and hence those entities that are genetically mixed should not be conserved (O'Brien and Mayr, 1991; see Soltis and Gitzendanner, 1999). The other argument is that hybridisation is an important evolutionary process and so hybrids should be conserved as dynamic components of biodiversity (Soltis and Gitzendanner, 1999; Allendorf et al., 2001), as well as providing potential habitat for preservation of other dependent species (Whitham et al., 1994; Hopper, 1995). Hybridisation is generally viewed as having negative connotations where it involves rare species, as it may lead to the extinction of a species through genetic swamping leading to genetic assimilation and the incorporation of the genetic material of a locally rare species into the gene pool of a more abundant or reproductively successful species (Rieseberg, 1991; Ellstrand et al., 1999; Soltis and Gitzendanner, 1999). Conservation policy generally allows for the protection of hybrids and hybrid progeny if they are shown to be taxonomically distinct, stable and capable of self-perpetuation, and naturally

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produced (Soltis and Gitzendanner, 1999; Allendorf et al., 2001). Application of these criteria facilitates the conservation of taxa that are stabilised derived hybrids but does not recognise recent hybrids that arise through ongoing gene flow as discrete entities.

Hybridisation is relatively common in the global biodiversity hotspot in south-west Western Australia, and its kwongkan heathlands, that have high levels of species richness and endemism and a large number of plant species that are listed as threatened, rare or poorly known (Hopper and Gioia, 2004). The high species richness and presence of many naturally rare species means that hybrids may be mistaken for a naturally rare taxon, and while these may be recognised as arising due to naturally processes, the scarcity of conservation resources means that it is important for conservation activity to be directed to those species that most warrant it. Identification of taxa considered to be hybrids allows appropriate assessment of their conservation status and requirement for conservation action.

Adenanthos cunninghamii (Albany Woolybush) is a rare plant found in the south-west of Western Australia that occurs as scattered individuals in kwongkan heathland in coastal areas around the Albany region, particularly at Torndirrup National Park and Two Peoples Bay. The plant grows in deep sand in association with heath or low scrub and is found scattered through populations of *Adenanthos sericeus* (Coastal Woolybush) and *Adenanthos cuneatus* (Coastal Jugflower) (Nelson, 1978; Robinson and Coates, 1995) where they overlap (Fig. 1). The species was originally described in 1845 (Meisner, 1845), and due to its restricted distribution was listed as 'Declared Rare Flora' under Australian and Western Australian legislation. More recently, it was suggested that *A. cunninghamii* may be a hybrid between *A. sericeus* and *A. cuneatus* as it is always found in conjunction with these two species, does not form homogenous stands, and leaf morphology appears intermediate between the two species (Robinson and Coates, 1995; Brown et al., 1998). Little is known about the propensity for *Adenanthos* to hybridise. However, it has been reported in the literature that *A. cuneatus* has formed hybrids with *Adenanthos dobsonii* and *Adenanthos forrestii* (Wrigley, 1989). The genus is a member of the Proteaceae family and is endemic to the southern parts of Australia with 30 of the 32 species occurring in south-west Western Australia.

Genetic analysis has been used as an effective means of identifying hybrids in kwongkan plants (e.g. Broadhurst et al., 2001; Lamont et al., 2003; Walker et al., 2009), and as *A. cunninghamii* was suspected to be comprised of hybrid individuals, genetic analysis was used to investigate the status of this species.

2. Materials and methods

2.1. Study species and sites

One putative parent, *A. cuneatus*, grows in deep sand and is commonly found in the heaths of the south coast, ranging from Albany to Israelite Bay (Fig. 1). The species is a shrub 1–2 m in height, with a prostrate, spreading habit. The leaves are flattened and lobed, with young leaves red in colour and mature leaves a pale green with silky hairs. Flowers are pink/red and inconspicuous, occurring throughout the year, particularly August–September. The plant has a number of stems rising from a lignotuber and is not killed by fire (Nelson, 1978; George, 1984; Wrigley, 1989). The second putative parent, *A. sericeus* is a bush or small tree growing to 5 m tall and occurs in the coastal heathlands and to the north (Fig. 1). The plant has dense, soft foliage, with terete and finely divided leaves, 3–4 cm in length. Flowers are inconspicuous and occur throughout the year, particularly between August and December. *A. sericeus* has no lignotuber and is killed by fire. The purported hybrid, *A. cunninghamii*, is an erect bushy shrub to 2 m in height. Flowers are small and red appearing from September to October. Leaves are soft, finely hairy, grey-green and are divided with flattened segments. *A. cunninghamii* grows in low scrub on sandy soils in association with *A. cuneatus* and *A. sericeus* (Fig. 1), as well as *Banksia attenuata*, *Banksia coccinea* and *Allocasuarina fraseriana*. The plants have no lignotuber and are killed by fire and the species is presumed

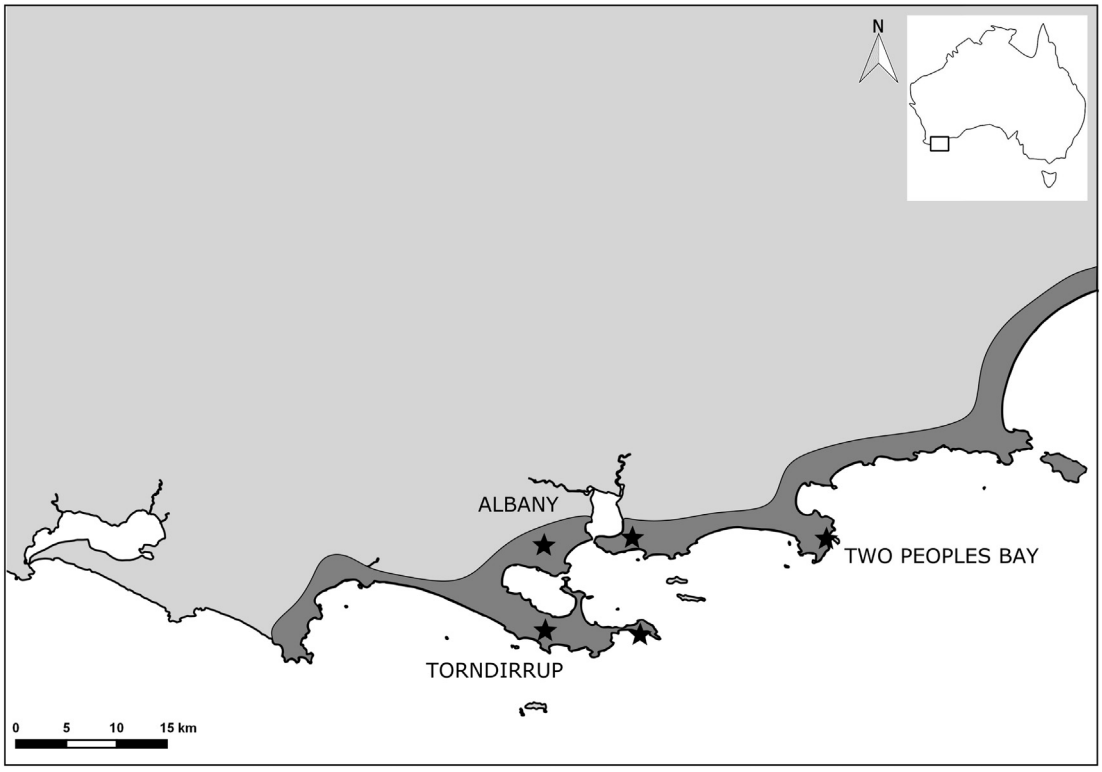

Fig. 1. Distribution of *Adenanthos sericeus* and *Adenanthos cuneatus*, and location of vouched collections of *Adenanthos cunninghamii*. *Adenanthos sericeus* occurs throughout the area of the map, *Adenanthos cuneatus* occurs in the dark shaded area and this represents the area of overlap in the distributions. Location of Western Australian Herbarium vouched specimens of *Adenanthos cunninghamii* identified as filled star symbols, other occurrences of *A. cunninghamii* have been reported in the overlap area but are not vouchered.

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