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Morphological evidence for introgressive hybridization in the genus *Psoralea* L. (Psoraleeae, Fabaceae)

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ABSTRACT

Introgression is interesting for plant evolutionary studies because it yields significant numbers of new genotypes, thus increasing genetic diversity, but also blurs species boundaries. Here we report a case of introgressive hybridization from a hybrid zone on the Swartberg Pass in the species rich Core Cape Subregion of South Africa. We analysed morphological data from 52 individuals between the hybridizing species *Psoralea* sp. 15 (*P.* "*forbesiae*" sp. nov. ined) and *P. sordida* C.H. Stirt and Muasya. The data were examined using the Andersonian hybrid index method and multivariate analyses. The results showed that *P.* "*forbesiae*" and *P. sordida* were distinct species linked through a range of intermediates and introgressants to both species and that the sampled populations comprised an introgressive hybrid swarm. Habitat disturbance via road-building has played an important role in the formation and maintenance of the swarm. While introgressive hybridization can increase genetic diversity in the short term in *Psoralea* it is unclear as to the future of the genetic integrity of the parent species and hybrid populations given the current differences in habitat specialisation (i.e. natural and disturbed habitats, respectively).
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1. Introduction

Hybridization produces new genetic combinations by introducing semi-compatible genes into another genotype, upon which interaction of environment and genetic variation can isolate a novel taxon from its parental types (Tavor-Sánchex and Oyama, 2004). It may cause spontaneous hybrids (intermediates) or involve back-crossing to either or both parents. Introgressive hybridization is the flow of genes from one species into the gene pool of another by the repeated backcrossing of an interspecific hybrid with one or both of its parent species (Rieseberg and Wendel, 1993; Arnold, 1997). The resulting hybrid offspring or introgressants then contain a complex mixture of parental genes, depending on the pathways of introgression. Interspecific gene transfer is an important evolutionary force because the genetic material introduced by introgression exceeds that which results directly from mutation (Anderson, 1949).

Ellstrand et al. (1996) have shown that certain phylogenetic groups are biologically predisposed for the formation and maintenance of hybrids. However, their review concentrated primarily on well-studied temperate floras and tropical Hawaii; the incidence of hybridization in most other biomes is still poorly known. This makes the study of hybridization both current and urgent if we are to understand the impacts of the breakdown of pre-zygotic and post-zygotic barriers between distinct evolutionary lineages (Vallejo-Marín and Hiscock, 2016).

The genus *Psoralea* has undergone rapid and recent radiation, with crown group age of ca. 4 million years, comprising ~75 species (Bello, 2016; Bello et al., 2017). Several cases of hybridization were observed in *Psoralea* (Bello pers. obs., Stirton pers. obs). Therefore, the current study will contribute towards understanding the role of recurrent hybridization among the processes that have driven the diversification of the species in the genus. Also, given that hybridization may drive rare taxa to extinction through genetic swamping — where the rare forms are replaced by hybrids (Todesco et al., 2016) — the current study is important to understand the role of hybridization in shaping the diversity and distribution of the studied taxa, as well as potential threats that hybrids may pose to species integrity.

Much of the evolutionary significance of hybridization depends on the fate of hybrids, which in turn depends on the fitness of hybrids relative to the parental species and the availability and persistence of suitable ecological niches (Anderson, 1949; Stebbins, 1959; Lewontin and Birch, 1966; Potts and Reid, 1988; Rieseberg and Wendel, 1993). If the genes of one species are introgressing into another, then the fitness of hybrids must be high enough to allow the hybrids to survive to maturity and backcross with parental individuals (Grant, 1981; Rieseberg, 1997).

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It has been observed that when natural selection stimulates the maintenance of hybrid zones, it is likely that the response of genes under selection will be unlike that of neutral genes (Cattell and Karl, 2004). This means that genes from species that are negatively selected in the alternate species are unlikely to introgress and may possibly be found in low frequency in the hybrid zone whereas genes under positive selection outside of the hybrid zone may spread into the alternate parental species (Arnold, 1997). Neutral genes can transgress hybrid barriers and integrate with the parental species (Arnold, 1997). However, the direction and magnitude of introgression, is determined by the rate of recurrence of backcrossing between the hybrids and the parental species, which may be more frequent than the initial production of F1 hybrids (Arnold, 1997; Cattell and Karl, 2004).

1.1. Hybridization and evolution of the Cape flora

The Cape flora, located in the southwestern tip of southern Africa, between latitudes 31° and 34°30′S (Fig. 1) is known for its outstanding levels of diversity (ca. 9000 species packed into ca. 90, 000 km^2) and endemism (68.8% of species) (Goldblatt and Manning, 2002; Manning and Goldblatt, 2012). These features have led to a special recognition of the Cape floristic region (now recognized as the Core Cape Subregion (CCR), sensu Manning and Goldblatt, 2012), as one of the world's six floral kingdoms (Takhtajan, 1986). The Cape flora has recently attracted a great deal of attention from botanical researchers (Linder, 2003; van der Niet and Johnson, 2009; Verboom et al., 2009). One of the major goals of researchers has been to better understand the processes driving the observed patterns of extreme species richness and endemism (e.g. Linder, 2005; Verboom et al., 2009). Most researchers support the idea that the unusual diversity of the Cape flora is the result of high rates of speciation ("an orgy of speciation", Linder, 2003; Verboom et al., 2009), rather than low rates of extinction (van der Niet and Johnson, 2009) or a combination of both processes (Linder, 2008). The major hypotheses that account for speciation in the CCR all include an aspect of ecological speciation (e.g. Linder et al., 2010) which in most cases are restricted to the role of divergent selection along ecological gradients without explaining the evolution of reproductive isolation or hybridization, making the CCR a suitable model system for testing its frequency (see Bello et al., 2015a). The role that hybridization may have played in increasing the frequency of speciation events remains largely unexplored in this flora.

Hybridization in the CCR is known in a few plant families and genera: Apocynaceae (*Microloma*, Bruyns and Linder, 1991); Ericaceae (*Erica*, Oliver, 1991); Geraniaceae (*Pelargonium* Bakker et al., 1998); Iridaceae (*Freesia*, Goldblatt, 1982; *Geissorhiza*, Goldblatt, 1985; *Romulea*, de Vos, 1972); Proteaceae (*Leucadendron*, Williams, 1972; Brits and van den Berg, 1991; *Protea* (Littlejohn et al., 2001) and Rosaceae (*Cliffortia*, where it is proposed as the fundamental cause of the diversity found within the genus, Whitehouse, 2002).

1.2. Hybridization in Fabaceae

Natural hybridization occurs in all subfamilies of the Fabaceae. Examples include: Caesalpinioideae (*Chamaecrista*, Conceição et al., 2008); Papilionoideae (*Baptisia*, Alston and Turner, 1963; Kosnik et al., 1996; Leebens-Mack and Milligan, 1998), *Glycine* (Jason et al., 2003), Loteae (*Lotus*, O'Donoghue et al., 1990); and the Mimosoideae (*Acacia*, Sedgely et al., 1992), *Prosopis* (Naranja et al., 1992), *Vachellia* (Ebinger and Seigler, 1987; Seigler and Ebinger, 1992, 2013; Binks et al., 2015). In southern Africa, legume hybrids have been reported in *Vachellia* (Ross, 1971); *Eriosema* (Stirton, 1981), *Aspalathus* (Ellstrand et al., 1996), *Otholobium* (Stirton pers. obs.) and in *Psoralea* (Bello et al., 2015b; Stirton pers. obs.).

Several models explaining the extreme pace of species diversification in the Cape neglect the potential contribution of hybridization. Of relevance to this study is that mature radiations are typical of the

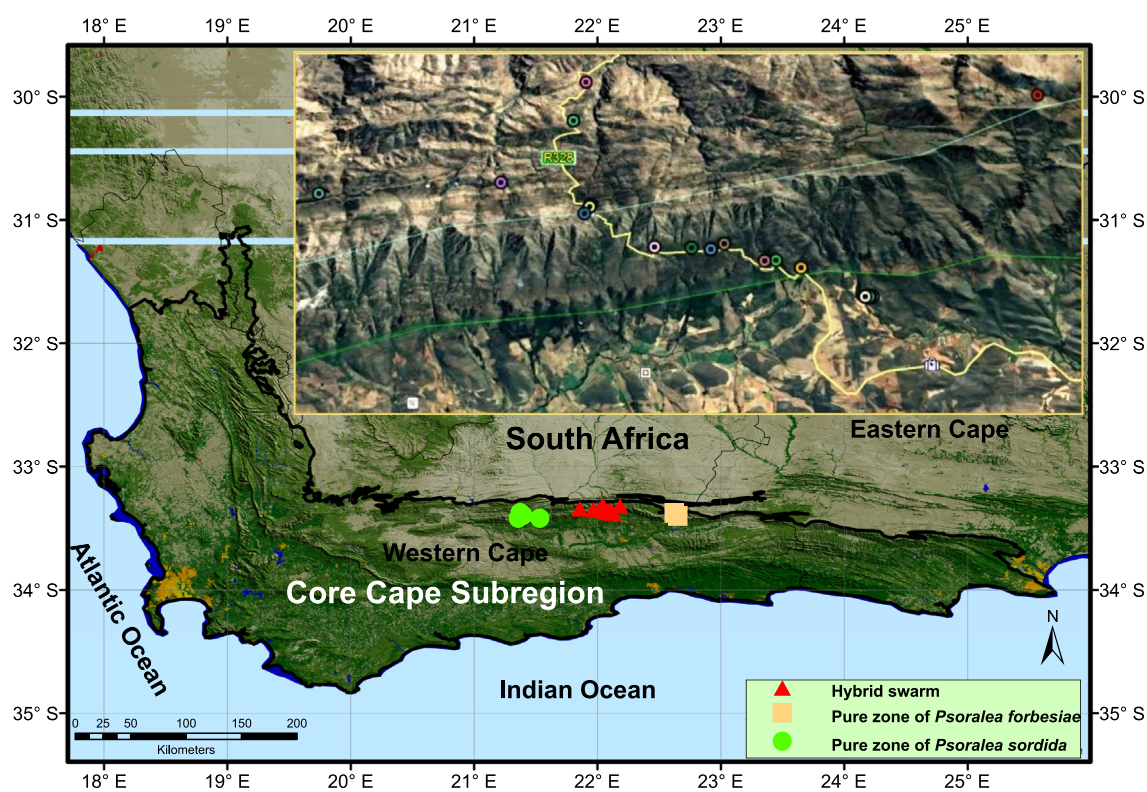

Fig. 1. Map of the Core Cape Subregion showing the Swartberg Pass where the samples were collected. The green circles show the pure zone (free from hybridization) where *Psoralea sordida* was collected while the brown squares show the pure location where *Psoralea* "*forbesiae*" was collected and the red triangles show the hybrid swarm where both the *P. sordida*, *P.* "*forbesiae*", the hybrids and the introgressants where collected. The enlarged portion in the top right corner of the map shows the pass (Dirt road: R328) as well as the sampling points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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