



Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Untangling a species complex of arid zone grasses (*Triodia*) reveals patterns congruent with co-occurring animals



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ARTICLE INFO

Article history:

Received 15 December 2015

Revised 10 May 2016

Accepted 10 May 2016

Available online 11 May 2016

Keywords:

Hybridization

Internal transcribed spacer

Molecular phylogenetics

Pilbara

Species complex

Triodia

ABSTRACT

The vast Australian arid zone formed over the last 15 million years, and gradual aridification as well as more extreme Pliocene and Pleistocene climate shifts have impacted the evolution of its biota. Understanding the evolutionary history of groups of organisms or regional biotas such as the Australian arid biota requires clear delimitation of the units of biodiversity (taxa). Here we integrate evidence from nuclear (ETS and ITS) and chloroplast (*rps16-trnK* spacer) regions and morphology to clarify taxonomic boundaries in a species complex of Australian hummock grasses (*Triodia*) to better understand the evolution of Australian arid zone plants and to evaluate congruence in distribution patterns with co-occurring organisms. We find evidence for multiple new taxa in the *T. basedowii* species complex, but also incongruence between data sets and indications of hybridization that complicate delimitation. We find that the *T. basedowii* complex has high lineage diversity and endemism in the biologically important Pilbara region of Western Australia, consistent with the region acting as a refugium. Taxa show strong geographic structure in the Pilbara, congruent with recent work on co-occurring animals and suggesting common evolutionary drivers across the biota. Our findings confirm recognition of the Pilbara as an important centre of biodiversity in the Australian arid zone, and provide a basis for future taxonomic revision of the *T. basedowii* complex and more detailed study of its evolutionary history and that of arid Australia.

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1. Introduction

Australia is dominated by an arid zone that extends over more than 60% of the continent. This arid zone formed over the past c. 15 Ma, with significant impacts from more recent Pleistocene (2.6 Ma to 10 ka; Walker et al., 2012) climate instability (reviewed in Byrne et al. (2008)). In Australia, Pleistocene glacial cycles were marked by cooler and drier conditions rather than the ice sheets that characterised the northern hemisphere (Williams, 1984). The formation of the arid zone, including the more intense Pleistocene aridification, is likely to have had a marked effect on the evolution of organisms that currently inhabit this region.

Abbreviations: MP, maximum parsimony; ML, maximum likelihood; BI, Bayesian inference; ITS, internal transcribed spacer; ETS, external transcribed spacer; rDNA, ribosomal DNA; MDS, multidimensional scaling; CAP, canonical analysis of principal components; WA, Western Australia.

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<http://dx.doi.org/10.1016/j.ympev.2016.05.014>

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An important part of the development of the Australian arid zone was the formation of sandy dune fields, which began to form c. 1 Ma (Fujioka et al., 2009), coinciding with a global shift to lower frequency, higher amplitude glacial cycles roughly 0.8–1.2 Ma (Clark et al., 1999; Mudelsee and Statteger, 1997; Pisias and Moore, 1981). These newly formed dune fields may have eliminated existing habitat for some organisms and created new habitat for others to expand into (e.g. geckos; Fujita et al., 2010; Pepper et al., 2011). It is not yet clear how plants were impacted by the formation of these dunes and associated aridification. The remarkable stability of the dune fields since their formation could be partly explained by persistent vegetation and/or soil particle binding (Hesse, 2011), but dust (Hesse et al., 2004) and pollen (Martin, 2006) records indicate some dune activity and more open vegetation during glacial maxima, suggesting some plants were unable to persist.

It has been hypothesised that mesic refugia in the Australian arid zone could have allowed local persistence of organisms through climate changes and served as a safe retreat for currently

widespread taxa during drier periods associated with glacial maxima (e.g. Beadle, 1981a; Byrne, 2008). The semi-arid Pilbara region of Western Australia (WA), with its complex topography and proximity to the coast, has been hypothesised to have functioned as one such arid zone refugium (Burbidge, 1959; Byrne et al., 2008). Consistent with the refugium hypothesis, recent work on geckos (Pepper et al., 2011) indicates that in topographically complex areas such as the Pilbara, extant genetic diversity is greater and coalescent times older than in surrounding sandy deserts. Also consistent with this hypothesis, the Pilbara has been recognized for its rich biodiversity and strong phylogeographic patterns that set it apart from surrounding regions (reviewed in Pepper et al. (2013b)), and as a centre of endemism (e.g. Halse et al., 2014).

The Pilbara biogeographic region (Department of the Environment, 2012) is divided into four subregions with distinctive substrates: sandy to clayey coastal plains (Roebourne), granite and greenstone plains and basaltic ranges (Chichester), sandy and clayey alluvial plains (Fortescue), and mountainous sedimentary and volcanic rock with banded ironstone formations and skeletal soils (Hamersley) (McKenzie et al., 2009) (see Fig. 1). Surveys of Pilbara biodiversity and more detailed studies have revealed strong geographic structure in frogs (Catullo et al., 2011), dragon lizards (Doughty et al., 2012), pebble-mimic lizards (Shoo et al., 2008) and geckos (Doughty et al., 2010; Pepper et al., 2013a, 2008), as well as in beetle (Guthrie et al., 2010) and spider (Durrant et al., 2010) species assemblages. The main phylogeographic patterns seen in the fauna are north–south differentiation between the Chichester and Hamersley subregions (separated by the Fortescue River valley) and between the Pilbara itself and the sandplains to the west (Pepper et al., 2013b). Detailed genetic studies of Pilbara plants are currently lacking but are critical for insight into the evolution of the region and the Australian arid zone, especially in comparison with recent work on animals.

Perennial hummock grasses of the genus *Triodia* R.Br. (Poaceae: Chloridoideae) are major and structurally dominant components of the vegetation across much of arid and semi-arid Australia including the Pilbara, covering more than 18% of the continent (Department of the Environment and Water Resources, 2007) where mean annual precipitation is typically <350 mm and soils are infertile (Beadle, 1981b; Griffin, 1990). *Triodia* species are commonly known as “spinifex,” and are notorious for their tough, needle-like rolled leaf blades. They are ecologically important and provide food and habitat for a range of animals including termites, which in turn support one of the most diverse lizard assemblages on Earth (Colli et al., 2006; Morton and James, 1988; Pianka, 1981). *Triodia* currently comprises 73 described species endemic to Australia (Armstrong, 2008; Barrett and Barrett, 2015, 2011; Barrett et al., 2005; Crisp et al., 2015; Hurry et al., 2012; Lazarides, 1997). Based on leaf anatomy and the production of resin, Burbidge (1953) recognized two morphological groups of spinifex: “hard” spinifexes with highly sclerified and pungent leaves, and typically without resin; and “soft” spinifexes with less sclerified and less pungent leaves, and typically with abundant resin. Soft spinifexes (with one possible exception) form a clade nested within a paraphyletic assemblage of hard species (Mant et al., 2000; Toon et al., 2015). A recent dated phylogeny of *Triodia* (Toon et al., 2015) suggests that its ancestors probably arrived in Australia c. 24–14 Ma and radiated extensively during Miocene aridification. *Triodia* is thus a key genus for understanding the evolution of Australian arid zone plants. *Triodia* still poses significant taxonomic challenges, however, especially in poorly explored areas and for broadly applied names that likely encompass multiple species. This taxonomic impediment affects our understanding of evolutionary history in the group and restricts our ability to make broader comparisons, which have the potential to reveal

evolutionary drivers affecting entire biomes (Arbogast and Kenagy, 2008; Bermingham and Moritz, 1998; Carstens et al., 2005).

One group of *Triodia* species that exemplifies this taxonomic challenge is the *Triodia basedowii* E.Pritz. species complex. *Triodia basedowii* and related species *T. lanigera* Domin, *T. plurinervata* N. T. Burb., *T. concinna* N.T. Burb., *T. rigidissima* (Pilg.) Lazarides and *T. desertorum* (C.E. Hubb.) Lazarides form a clade (see Toon et al., 2015) distinguished from other hard spinifexes by their many-nerved glumes. Within the clade, *T. rigidissima* and *T. desertorum* are morphologically distinct in having long awns on their lemmas (vs. no awns) and were originally placed in a separate genus (*Plectrachne*) that is now synonymous with *Triodia* (Lazarides, 1997). Previous morphological treatments (Lazarides, 1997; Lazarides et al., 2005) placed *T. plurinervata* and *T. concinna* in a separate informal species group from *T. basedowii* and *T. lanigera*, the former two taxa having shortly lobed (vs. deeply lobed) lemmas. The *T. basedowii* species complex comprises *T. basedowii* and *T. lanigera* along with four informally named taxa (Western Australian Herbarium, 1998): *T. sp.* Shovelanna Hill (S. van Leeuwen 3835), *T. sp.* Little Sandy Desert (S. van Leeuwen 4935), *T. sp.* Peedamulla (A.A. Mitchell PRP1636) and *T. sp.* Warrawagine (A.L. Payne PRP 1859). *T. lanigera* is commonly differentiated from *T. basedowii* based on the relative length and shape of its lemma lobes (typically having a proportionately longer midlobe). *T. sp.* Shovelanna Hill is distinct from *T. basedowii* in its smaller habit with shorter leaves and in its often unbranched inflorescence. *T. sp.* Warrawagine is morphologically similar to *T. sp.* Shovelanna Hill, but has a branched inflorescence with a greater number of spikelets. *T. sp.* Peedamulla differs from *T. lanigera* in its glabrous (vs. woolly) leaf sheaths and orifices, and in its shorter glumes and less hairy lemma midlobes. *T. sp.* Little Sandy Desert differs from *T. basedowii* in its glabrous (vs. woolly) leaf orifices and in the shape of its spikelets and textures of its lemmas (more induration in the lobes). Members of the complex occur throughout much of central and western Australia, including the Pilbara region.

Due to overlapping morphological variation and variability within currently recognized species, taxa in the *T. basedowii* complex are challenging to differentiate from each other. Wide morphological variation across specimens recognized as *T. basedowii* led Lazarides et al. (2005) to suggest that taxonomic resolution within *T. basedowii* would require assessment of genetic variation. Given the challenging nature of this species complex and the limited resolution from morphological evidence, additional sources of evidence are needed to delimit taxa (“integrative taxonomy”; Dayrat, 2005; Padial et al., 2010; Schlick-Steiner et al., 2010). Accurately resolving units of biodiversity (taxonomy) in this complex will allow broader comparisons of distribution patterns across the biota.

This study seeks to clarify taxonomic boundaries in the *T. basedowii* complex using integrated morphological and molecular evidence, and to compare geographic patterns of taxon distribution and genetic partitioning in this plant group with those found in previous studies of co-occurring animals. We assess whether our results are consistent with the hypothesis of the Pilbara as a refugium and what they suggest about the impacts of geologically recent climate changes on Australian arid zone plants.

2. Methods

2.1. Taxon sampling and a priori identification

Putative taxa were identified *a priori* primarily based on morphological differences observed during a survey of herbarium material from across the distribution of the complex and on field

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