Phylogeographic analyses for *Kalloora* (*Podocarpus drouynianus*) conservation management in the Southwest Australian Floristic Region

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The following approvals were obtained prior to commencing the relevant work described in this thesis: Flora collection licenses - Regulation 4 (CE006517) and Regulation 61 (FT61000955). Human Research Ethics – (RA/4/20/6165).

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Abstract

In southwestern Australia, plants have persisted through significant climate shifts in ancient landscapes and the evolutionary responses are apparent in their genetic signature. *Kalloora* (*Podocarpus drouynianus*), a southern conifer with Gondwanan ancestry, belongs to a genus typically found in wet, montane environments. It is unique among its relatives in having developed mechanisms, including post-fire flowering, to survive in drought- and fire-prone mesic forests characterising the southwest corner of Australia. *Kalloora* features in the practical, spiritual, and social realms of Pibbulmun-Wadandi lifeways, who recognise aspects of these survival mechanisms in the biocultural maintenance of this plant species. This study arose from concerns raised by Pibbulmun-Wadandi custodians, who value, use, and manage *kalloora* in relation to their understanding of a general shift in distribution and fruiting variability under current land management approaches. To address these concerns, this study embedded a phylogeographic analysis of *kalloora* chloroplast and nuclear genetic markers in a community-based framework informed by a Pibbulmun-Wadandi Elder. With consideration of its Gondwanan-ancestry, known seed dispersal by emus, and Pibbulmun-Wadandi connections, this study aimed to determine 1) if *kalloora* persisted through historical climatic and geological shifts by contracting to refugial areas, 2) how extensive gene flow is across its geographic range, and 3) if a community-based framework can increase shared understandings among research collaborators. The genetic assessment of *kalloora* indicated high genetic variation across its full distribution, a genetic patterning consistent with large population sizes and long-term persistence in the landscape. With the exception of a distinct haplotype assemblage of some outlier populations, phylogeographic structure was not evident across the species' distribution. These patterns are not congruent with persisting within refugia, typical in other *Podocarpus* species in the Southern Hemisphere, and instead suggests long term, localised persistence similar to other species with prolonged presence in this region. Extensive gene flow was indicated by the widespread distribution of shared haplotypes across its main range which suggests reliance on long-distance seed dispersal for effective genetic distribution. In addition, the study demonstrates community-based frameworks do increase shared learnings, contributing to unique insights and interpretations throughout the research process; specifically related to the connectivity of plants, animals, and people. The connectivity of disperser habitat is considered a significant factor to maintain the demographic and evolutionary processes of *kalloora*. We discuss how landscape connectivity, embedded with cultural practices and knowledge systems informed by Pibbulmun-Wadandi management strategies and supported by understandings in conservation biology, was identified as a potential conservation approach to support the resilience and persistence of *kalloora* into the future.

Table of Contents

List of Figures

List of Tables

Foreword

I don't think anyone forgets their first emu plum. I know I haven't as it wasn't by accident or happen-chance. It was by dust, dirt, and flying pebbles trailing a four-wheel drive Jeep barreling down a gravel driveway that I learned of emu plums. It was on a typical day late in the Bunuru season, late March, in southwestern Australia. The winds were calm, nearly nonexistent, warmth still filled the air, the sun drawing out 'second summer' before the inevitable winter rains around the corner. The serenity of that early afternoon was affronted by young cultural leader, Iszaac, peeling down his driveway and into the house alerting us the "plums are fruiting!" At that moment it was all hands-on deck, grabbing any bag or container we could find, to load into Jenny the Jeep and head back out to the patch of plums. I was shocked and confused but the urgency was intoxicating. We drove like a numbat out of wildfire hell, slowing as we neared the place with plums. The gravel road was reddish yellow, contrasted on its edges by the green forest nearly enveloping the blue sky above; a succession of bracken fern, zamia, tea tree, Bull banksia, Jarrah, and… emu plum. This was a plant I hadn't noticed before; however, having seen it then, it was quite literally everywhere. An understory shrub so common it had eluded me until now. The underbrush was mostly clear, and leaves littered the forest floor. The emu plum plants were abundant with ample room in between the hundred or so individuals scattered amongst the understory of the Jarrah Forest. *Here they are*. Zac jumped from the car, grabbed some bags, and we followed suit. *Leave fruit on the plant, for the others. Scatter the gathering so we don't strip the fruit from each plant*, he told us. Zac is Pibbulmun-Wadandi. He's from the southwestern corner of Australia, Pibbulmun country - the 'land of plenty.' A light burn traveled through this part of the forest roughly a year prior. These purple fruits, what look like melted plums imagined from a world of Dr. Seuss, were the result of that burn. The fruits hang like ornaments draped from the shrub-like green conifers. I stood in awe in this patch of plums – enthralled by a conifer covered in purple fruit. Intrigue, and hunger, crept in. How had I not seen this plant before having traversed these forests over the last few years with the Pibbulmun-Wadandi community?

I met Zac and his family years before when I first landed in Australia for a field school in applied archaeology as part of my undergraduate degree. Within an hour of meeting, we were on a dingy in Undalup (Geographe Bay) and I was pulling crab nets for the first time in my life; how exactly this fit into an archaeology field school would become clear to me over time (mostly). I returned home to Montana to finish university with a Bachelor of Arts in Anthropology only to realise, like many fresh graduates, my education would now begin another path. What started as an introduction to community archaeology, eventuated into a series of ongoing heritage and land management projects with communities across Australia and North America. Working alongside Elders, and community and cultural facilitators like Zac, taught me, among many things, archaeology is about people and landscapes – that heritage is alive. I was taught that cultural material encased by years of sediment was embedded with the stories of Ancestors, held in custodianship by community. I was taught that these stories are also held beyond the lithics and beyond those features hardened by time. Stories of place and heritage include the forest and landscapes we walk through each day and the plants and creatures that comprise these places. I was taught the imperative of protecting places and that on-ground action catalysed by community builds foundational momentum. In this way, I was shown that land management is embedded in the journey with Elders, youth, and community, and it is carried in the relationships we have with one another. It is the energy and laughter of youth on-country, Elders whispering in your ear the right way to pick spruce tips, and that seemingly random stops along the edges of highways to look at a single flowering orchid are actually windows into complex ecological understandings. It is in these lessons and over these years, that this Masters research began. Long before picking my first emu plum.

I couldn't shake that day. It was enthralling to follow Zac into the forest to harvest plums. Why the urgency? How does it fruit like that? And how did Zac know? Returning to that patch of plums also wasn't by accident. This return was based on Zac knowing that burn occurred in that area, at that particular time, and having the strong sense and awareness fruit would be there a year or so later. This sense of country is awe inspiring. This country, these places and people, are truly intertwined. Enrolling at the University of Western Australia for this study happened years after this day in the fruiting patch of emu plums. It began another journey of learning and voyaging other worlds of knowing. Talking about this research with community and research scientists I was made keenly aware of a thread of understanding that weaves its way through people and plants. There is a connection and love for plants among many and especially so a certain keen interest and intrigue about the emu plum from those living in plum country. This intrigue had me intrigued and this continues in this way to this day. This connection to plants embeds itself in everyday conversation, observations on walks, enlightening quips, interesting snippets, thought-provoking one-liners, if only fleeting, are what led to this genetic study of emu plums. It was in similar conversations with Zac's family that concern for this plant emerged. Concern of overgrown vegetation or land stripped bare, threat of too hot or too frequent fires, drying aquifers, impeded creeks, and parceled land; the altering of a landscape all too familiar in southwestern Australia. This was a region that experienced early and rapid colonisation - a land too plentiful to harness hungry hearts. I'd come to learn emu plums are a hardy plant embedded with the inherent sensitivity of long evolution, with its characteristics that favour certain burning regimes, the emu seeking its large purple fruit as an off-season food source, and at its crux, the hurt felt by the caretakers of Pibbulmun country, in which emus, plums, and culture is intrinsically weaved. This corner of the world is increasingly renowned for its fermented grapes, its forested trails, and boundless surf - a land of contemporary plenty. Though, as I've learned and continue to learn, it is through a stewardship lens, alongside and under the guidance of Elders, in which lies the imperative of interacting with and managing these special places. These experiences and lessons are built into the research design of this study and guide my journey with emu plums, Country, and people. Under the direction of custodians, I still scratch the ground for looking for lithics, but I look up now too, humbled to take in the dynamic cultural landscapes around me.

Chapter 1: Introduction

In southwestern Australia, there exist a multitude of plant species imbued with cultural importance (e.g., Hansen & Horsfall, 2019; Lullfitz *et al.,* 2022; Lullfitz *et al.,* 2023). The layered contemporary land management perspectives in this region warrant an integration of conservation efforts founded on the millennia of transgenerational cultural connection. The field of conservation biology, in particular phylogeography, offers a pathway to link understandings of cultural systems of management as a critical component of ecosystem resilience, by exploring a species' evolutionary context (Bobo-Pinilla *et al.,* 2022, Byrne, 2007, Cristobal-Perez *et al.,* 2021), to include people-plant relationships (Kondo *et al.,* 2012; Lullfitz *et al.,* 2020a). Community-based frameworks provide a platform for the integration of knowledge systems, embedding cultural understandings within the research process (Guilfoyle *et al.,* 2009; Hernandez, 2022; Lullfitz *et al.,* 2017). Importantly, this is knowledge shared with regard to adaptive, culturally led conservation rather than extraction of ethnographic information related to cultural stories, pathways, events, and ways of life which remain protected under cultural custodial management (W. Webb pers comms 2018).

This study presents the results of a phylogeographic analysis of *kalloora* (*Podocarpus drouynianus* F. Muell.), a significant cultural plant to the Pibbulmun-Wadandi people of southwestern Australia, conducted within a community-based framework. The study developed from a community identified research topic related to concerns for the health of this plant across its distribution. Embedded within the research design is guidance from Pibbulmun-Wadandi custodians. This research is framed by three main points: 1) identifying the persistence strategies of *kalloora*, 2) realising the extensiveness of its gene flow, and 3) whether community-based frameworks can increase shared learnings. This thesis situates *kalloora* within its cultural and biogeographical setting before providing an analysis of its genetic variation. It then discusses how phylogeographic interpretations can inform aspects of landscape-scale conservation biology, applied in a community-based management framework.

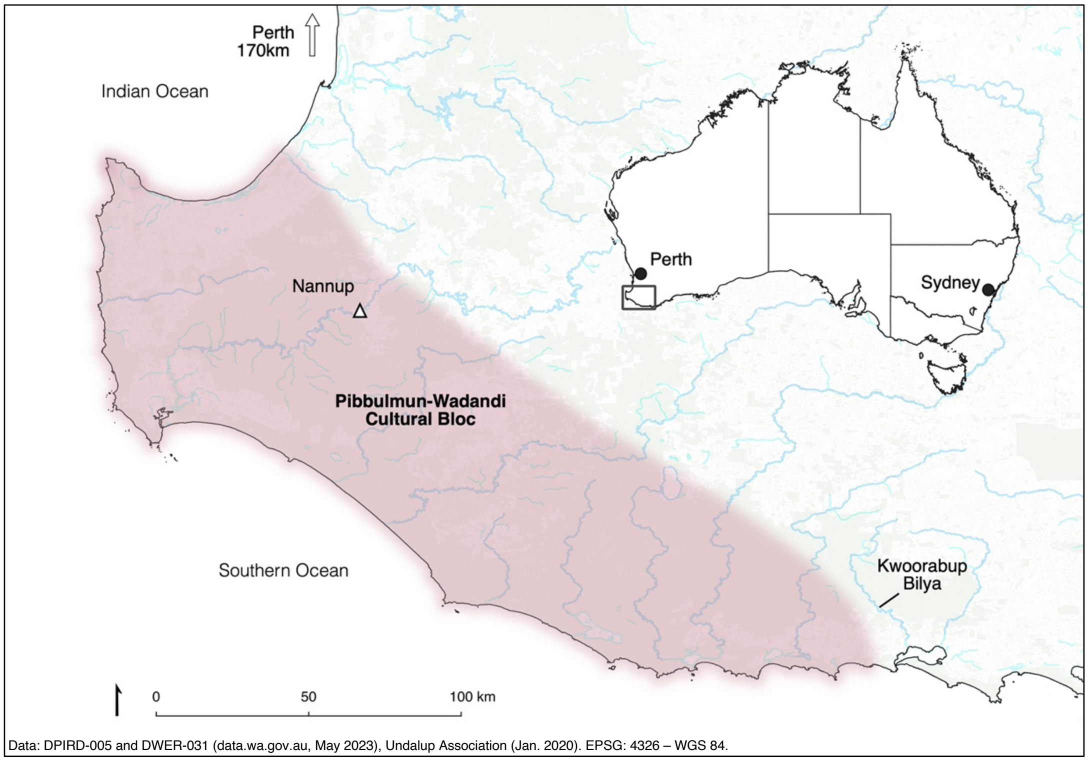
Community-based Frameworks in Pibbulmun-Wadandi Country

The southwestern region of Australia is defined by a cultural bloc that includes a collection of subgroups whose cultural boundaries are determined by ecotones within the landscape. Pibbulmun-Wadandi country, a subgroup of the broader Pibbulmun (Bibbulmun, Pibelmun) cultural bloc, is centred on the extreme southwestern corner of Australia (Figure 1). The area of Nannup defines its eastern edge, the Kwoorabup Bilya (Denmark River) delineates the southeastern most extent, and the Indian and Southern Oceans provide western and southern boundaries (Bates, 1985; Guilfoyle *et al.,* 2015). The presence of people in this region has spanned the course of millennia whereby the Pibbulmun-Wadandi people have continually occupied and interacted with the ecologies of the region for at least 48,000 years BP, indicating a sustained human ecological presence in this region (Dortch, 2001; Guilfoyle *et al.,* 2015; Lullfitz *et al.,* 2017; Turney *et al.,* 2001). As such, the Pibbulmun-Wadandi people were witness to the large-scale climatic shifts and sea level rise and fall of the late Pleistocene (~50-12kya) which contributed to the southwest corner of Australia developing into the unique biogeographical region we see today (Byrne *et al.,* 2008; Dortch, 2001). During this time, intricate, dynamic, and adaptive knowledge of local environments developed (Guilfoyle *et al.,* 2015; Lullfitz *et al.,* 2017; Muir *et al.,* 2010; Ottewell & Byrne, 2022). Incorporating local observational knowledge of ecological phenomena into practical resource use activities, including beliefs in where people relate to ecosystems (Berkes *et al.,* 2000), shapes custodial obligations and is increasingly recognised as integral in assessing the health of biomes in evolutionary and contemporary contexts (Barnhardt & Kawagley, 2005; Berkes *et al.,* 2000; Hoagland, 2017; Kimmerer, 2011; Lertzman, 2010; Lullfitz *et al.,* 2017; Moller *et al.,* 2004).

"We tell our stories, of our connection to Country, how the Country works, and how it all goes hand in hand." Wayne 'Wonitji' Webb, 2019

Transgenerational observations orally passed down were critical in the necessary adaptation and survival of people in this variable climate, and this knowledge and methodology of knowledge transmission is kept in tradition, practice, and identity maintained by the Pibbulmun-Wadandi community (Guilfoyle *et al.,* 2015; Hernandez, 2022; Lullfitz *et al.,* 2022; W. Webb pers comms 2019). Custodial obligations of passing on and maintaining knowledge in Pibbulmun-Wadandi culture is organised along familial lines, with specific recognition of those who maintain continual connection to the land in which one is born (Davies *et al.,* 2020; Guilfoyle *et al.,* 2015). The Pibbulmun-Wadandi Elder supervising this research has been identified by the wider community and researchers as someone with authority to share and maintain custodianship of Pibbulmun-Wadandi knowledge systems (Dortch *et al.,* 2014; Goode, 2003; Guilfoyle *et al.,* 2015). This study is structured within a community-based framework and operates under the tenets of collaborative and co-developed research (Guilfoyle & Hogg, 2015; Guilfoyle *et al.,* 2009; Hernandez, 2022; Lullfitz *et al.,* 2017; Mitchell *et al.,* 2013; Smith *et al.,* 2021). As such, the research topic was derived from community priorities and information shared by a Pibbulmun-Wadandi Elder informed stages of the study (e.g., identifying the research topic, forming research questions and hypotheses, determining a sampling strategy, in-field observations, and analysing and interpreting results). This methodology is determined by Pibbulmun-Wadandi custodians to ensure cultural safety and appropriate supervision (Collier-Robinson *et al.,* 2019; Hughes & Barlo, 2021; Smith *et al.,* 2003) and embed aspects of Pibbulmun-Wadandi heritage and identity into the research process and associated outcomes (Country *et al.,* 2019; Guilfoyle *et al.,* 2015).

Community-based frameworks exist across a variety of fields (Kwon *et al.,* 2018; Scheurich *et al.,* 2017; Smith *et al.,* 2003; Trolle *et al.,* 2012), including the biological sciences (Cisternas *et al.,* 2019; Collier-Robinson *et al.,* 2019). Here, a community-based framework is conceived as a flexible and transparent process embedded with customary protocols and driven by community initiatives with a focus in social, cultural, and environmental outcomes (Guilfoyle *et al.,* 2009; Mahajan *et al.,* 2019; Trolle *et al.,* 2012). The 'community' of the community-based framework applied to this study is comprised of Pibbulmun-Wadandi Elders, cultural facilitators, and members of the Wadandi Cultural Conservation Corps. Although the study is informed by the Pibbulmun-Wadandi Elder identified previously, considering the whole of community within the framework is essential as it applies a culturally appropriate model of operation (Guilfoyle *et al.,* 2015). The nature of the trust-based, collaborative relationship that initiated this study requires a commitment to uphold customary protocols and priorities. Traditional and western science-based knowledge sets are recognised on equal grounds as a commitment to decolonise research, planning, and management, and to recognise complementary evidence for sustainable biodiversity management (Ahuriri-Driscoll *et al.,* 2007; Guilfoyle & Hogg, 2015; Hernandez, 2022; Pyke *et al.,* 2018; Tengö *et al.,* 2012).



Data: DPIRD-005 and DWER-031 (data.wa.gov.au, May 2023), Undalup Association (Jan. 2020). EPSG: 4326 – WGS 84.

Figure 1. The Pibbulmun-Wadandi cultural bloc is situated in the southwestern corner of Australia and the area of Nannup and the Kwoorabup Bilya (Denmark River) are identified as places that define its boundary. Major cities of Perth and Sydney are located for reference.

Culturally embedded maintenance of resources, encompassing practical, spiritual, and social realms, are vital to the interaction with and manipulation of species and environments for long-term sustainability (Amundsen-Meyer, 2013; Bond *et al.,* 2019; Coughlan & Nelson, 2018; Vaughan, 2018). The imperative here is in recognising that complex knowledge systems, sustained interactions, and extended histories exist. Further, by deriving research and conservation priorities and land management practices through community-based frameworks (Bond *et al.,* 2019; Guilfoyle *et al.,* 2009; Hernandez, 2022; Reid *et al.*, 2020), ensures socially relevant and practically focused outcomes (Collier-Robinson *et al*., 2018; Vaughan, 2018; Wehi & Lord, 2017; Winter *et al.,* 2023). Critically, this study is not beholden to the extraction of cultural knowledge to inform its research. Rather, it is aligned with situating Knowledge Holders as supervisors and incorporating input and perspectives derived from place-based transgenerational observations with an understanding the research may support broader landscape management aspirations (Hernandez, 2022; Reid *et al.,* 2020; Wehi *et al.,* 2019). In this study, this is done so via interpretations from phylogeographic analysis of a cultural plant.

Phylogeography, Landscape Antiquity, and Podocarpus

Phylogeography is an integrative field that uses genetic information to infer a species' evolutionary history and the biogeographical factors contributing to a species' distribution (Beheregaray, 2008; Byrne, 2008; Sampson & Byrne, 2022). Through a deeper understanding of the evolutionary and ecological processes shaping a species extent and genetic diversity, phylogeography provides a clear picture of the processes responsible for the maintenance of communities (Ottewell & Byrne, 2022; Quiroga *et al.,* 2019). In doing so, studies within phylogeography aim to infer the strategies and mechanisms utilised and developed by species that enable survival through widespread and long-term environmental changes. Dispersal and gene flow, and population fluctuation by contraction and expansion from suitable habitat leave signatures on the genetic composition of species responding to biogeographic activity (Byrne, 2008).

The landscape-scale patterning of genetic diversity is partially influenced by gene flow whereby dispersal mechanisms determine the rate and distribution extent of pollen and seed movement through the landscape. Understanding potential influences on the mechanisms of gene flow is foundational to understanding a species level of resilience to environmental changes (Llorens *et al.,* 2017; Ottewell & Byrne, 2022; van Strien *et al.,* 2014). In response to geologic activity and climate oscillations, plant taxa also utilise persistence strategies for survival. These strategies include contracting to and expanding from refugia, and developing highly specific habitat requirements, and are apparent in the genetic record in parallel with evidence of dispersal mechanisms. The intensity at which populations expand and contract from areas of suitable habitat largely defines whether a species is seeking refugia or has developed specific habitat requirements. Refugia, characterised by recent 'leading edge expansion' (*sensu* Hewitt, 2001), is reflected as relatively high genetic diversity in core areas with lower genetic diversity along or around the edge of these areas (Byrne *et al.,* 2008). Species utilising refugia typically show a considerable measure of expansion and contraction. Plants with habitat specificity, comparatively, can be illustrated in the genetic record as high diversity within lineages as well as high diversity across distributions with strong phylogeographic structure throughout the species' extent and relatively minimal expansion activity. Patterns of refugia and localised persistence and gene flow are influenced by a complex range of factors including topography, life history characteristics, population size, and temporal scales (Binks *et al.,* 2019; Byrne, 2008).

The age of landscapes accounts for the length of time a species is responding to biogeographical influences which also contributes to genetic variation. The landscapes of the Southern and Northern Hemisphere are widely regarded to be on a spectrum of old, climatically buffered, infertile landscapes (OCBILs) and young, often disturbed, fertile landscapes (YODFELs) (Hopper, 2023; Robins *et al.,* 2021). OCBIL theory situates the unglaciated, ancient landscapes typical of the Southern Hemisphere in contrast to the predominantly glaciated, recently formed landscapes of the Northern Hemisphere, as a means to explain the evolution and ecology of the former for best practice conservation outcomes (Hopper, 2009; Hopper *et al.,* 2020; Robins *et al.,* 2021; Silveira *et al.,* 2021). Recently evolved plants in post-glaciated landscapes in the Northern Hemisphere typically have low genetic diversity and differentiation across their extent (Gugger *et al.,* 2010; Laricchia *et al.,* 2015). This is due to glaciation severely bottlenecking species during range contraction to refugial habitat, leading to a loss of genetic variability and not yet having had time to re-accumulate and re-distribute genetic variation across their more recently expanded range (Binks *et al.,* 2019; Grivet & Petit, 2003). Conversely, plants with prolonged persistence in the landscape, those typical of the Southern Hemisphere, tend to exhibit high genetic diversity within and among populations and strong population structure throughout their distribution (Byrne *et al.,* 2014). This is largely because species persisting and evolving in old landscapes unaffected by major disturbance regions (e.g., glaciation, tectonic activity, and volcanism) have had more time to accumulate genetic diversity and diverge into deep lineages (Binks *et al.,* 2019).

Members of the *Podocarpus* genus have distinctive demographic properties and provide key insights to evolutionary and eco-physical responses to large-scale geological and climatic shifts due to their long-term persistence in old landscapes (Biffin *et al.,* 2011; Kahn *et al.,* 2023; Llorens *et al.,* 2017; Tomlinson *et al.,* 1991). The genus belongs to one of the oldest extant conifer families, Podocarpaceae, as demonstrated in early Triassic fossil records (Biffin *et al.,* 2011; Brodribb & Hill, 2004). With over 120 species, it is the most species-rich genus within this family (Kahn *et al.,* 2023). Peaking in diversity in the Southern Hemisphere in the late Eocene (~35mya), these southern conifers thrived in the wet, temperate rainforests dominating the climatic conditions at the time (Brodribb & Hill, 2004). Though species of *Podocarpus* are found globally, its origins on the Gondwanan supercontinent determine its widespread distribution as the most successful conifer in the Southern Hemisphere (Biffin *et al.,* 2011). The breakup of this vast landmass eventuated in *Podocarpus* occurrence throughout Southern Hemisphere continents, including Australia, New Zealand, South America, and south-east Asia, with many species favouring high-rainfall climates that defined margins of Gondwana (Gibbs, 2006; Hill & Brodribb, 1999; Kelch, 1997; Ornelas *et al.,* 2010).

Phylogeographic studies of *Podocarpus* have been conducted on limited taxa of this genus in the Southern Hemisphere and are described here to briefly contextualise similar studies to this one. Ornelas et al. (2010) focused their research on *P. matudae* and its evolutionary divergence during the Quaternary, a period defined by heightened biogeographic activity, on either side of a late arriving land bridge in Northern Mesoamerica. Through phylogeographic analysis of chloroplast markers, the authors set out to determine the historic extent and dispersal of *P. matudae*, whether as remnant populations or via migration on either side of the land bridge. Population structure between the regions was distinguishable whereby the lack of structure in the western regions was likely attributed to *P. matudae* seeking suitable refuge during significant glacial expansion and contraction during the Pleistocene. Populations on the eastern side with stronger phylogeographic structure persisted comparatively unaffected. Prolonged isolation and localised endemic seed and pollen dispersers may also contribute to the distinction in genetic variation of populations (Ornelas *et al.,* 2010). This study illustrates the different evolutionary responses of species to landscapes under increased biogeographic activity and those relatively unaffected by major disturbance, especially intriguing within a *Podocarpus* species. Ornelas et al. (2019) revisited *P. matudae* and the closely related *P. guatemalensis* and *P. oleifolius,* to further test persistence scenarios of cold-tolerant, cloud forest-adapted species. Integrating information from chloroplast markers, phylogenetic, population and spatial analyses, and ecological niche modeling (ENM), the authors largely found in-situ persistence was a common strategy of these species during interglacial periods. ENM showed these species' preference of suitable habitat varied between each other, and phylogenetic analyses suggested long-term maintenance of genetic diversity with some potential hybridisation. Ornelas et al. (2019) highlight the complexities of analysing cloud forest-adapted species responses to a dynamic geological and climate atmosphere over a large temporal scale (Byrne, 2008).

In southern South America, Quiroga and Premoli (2009) predicted the cold-tolerant *P. nubigena* persisted through climatic oscillations within refugia during Quaternary glaciations. Their hypothesis was supported by significant latitudinal divergence due to a palaeobasin. Populations south of the substrate indicated long-lasting persistence with the highest genetic diversity. Conversely, lower genetic variation was presented in the northern mountain populations that sought montane refugia in response to climate shifts. Further north in South America, Bernardi et al. (2020) integrated phylogeography and species distribution models to infer the ways *P. lambertii* responded to climatic fluctuations in the same period. The authors documented this species also expanded and contracted from refugia defined by favourable temperature and altitude. Quiroga et al. (2012) used similar methods integrating modelling techniques with phylogeographic analysis to further understand the effects of glacial-interglacial climate periods on *P. parlatorei*, a cold-tolerant conifer found in naturally fragmented populations in the montane Yungas forests of the central Andes. These authors found contraction to montane refugia during warm climatic cycles was a persistence strategy of *P. parlatorei*. In addition, Bernardi et al. (2020) and Quiroga et al. (2012) demonstrated *P. lambertii* and *P. parlatorei*, respectively, each had continuous gene flow across the landscape historically which was evident in the shared haplotypes across their respective distributions. Historical barriers to gene flow were suggested to explain the current disjunct populations within each species. In another study of *P. parlatorlei*, Quiroga et al. (2019) incorporated phylogenetic analysis of this species with other unrelated endemic species in north-western Argentina for the conceptual development of integrated biogeographical conservation units. The authors proposed that concordant genetic patterns of a range of biota within a region strengthens conservation efforts.

Genetic studies of *Podocarpus* in Australia are limited to two, both conducted on *P. elatus* (Illawarra plum), a dioecious tree with a broad, fragmented distribution along the eastern coast. The 2011 study by Mellick et al. focused on whether historic or contemporary drivers influenced the genetic diversity and structure of *P. elatus* using the nuclear genome and ENM. Mellick et al. (2011) determined that the moderate differences in genetic diversity and divergence in the northern and southern regions of the species' distribution, bisected by the Clarence River Corridor, were most likely attributed to historic processes. The authors mention, however, significant contemporary land clearing in the central range may have impacted gene flow, increasing the rate of regional divergence (Mellick *et al.,* 2011). The authors emphasised the importance of phylogeographic studies to determine gene flow and diversity of endemic species with limited range in fragmented habitats for species' resilience and conservation (Mellick *et al.,* 2011). The second study of *P. elatus* also used ENM and analysis of the nuclear genome to examine range expansion and contraction dynamics during the last glacial cycle. Mellick et al. (2012) found that northern populations persisted in refugia during the Last Glacial Maximum (LGM) and expanded during the post-glacial period whereas populations south of the Clarence River Corridor were widespread during the LGM and subsequently contracted. The modelling and genetic analyses were consistent in these scenarios. Overlaying environmental modelling with genetic analysis, this study challenged the idea that broadly distributed species respond in a similar way to climate change (Mellick *et al.,* 2012), indicating that individual species need to be assessed on a case-by-case basis to inform effective conservation strategies.

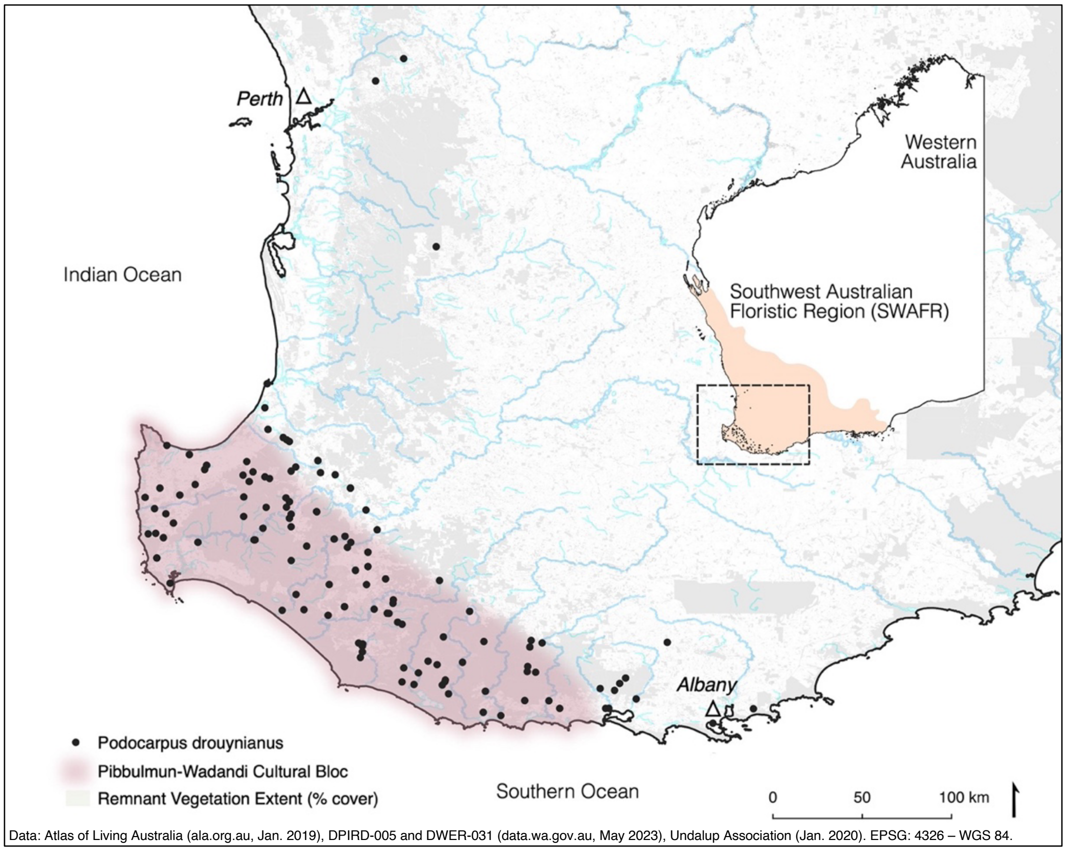
These studies provide examples of persistence strategies utilised by some species of *Podocarpus* during periods of dynamic geologic and climatic activity*,* which demonstrate that contraction to refugia was a common strategy. The signatures apparent in the genetic composition of this genus provide key insights to evolutionary and eco-physical responses of species persisting for prolonged periods in landscapes largely unaffected by major disturbance regimes.

The Southwest Australian Floristic Region: An Ancestral Biome

The ancient landscapes of the Southwest Australian Floristic Region (SWAFR *sensu* Gioia & Hopper, 2017) provide a worthy canvas for phylogeographic analyses of species that have persisted through a long history of climate change (Byrne, 2007). Globally recognised for its exceptional biodiversity, the SWAFR harbours over 8,000 native plant species, both relictual and recently evolved, nearly half of which are endemic (Beard *et al.,* 2000; Gioia & Hopper, 2017; Yates *et al.,* 2019). The SWAFR boundary is defined by biogeographical characteristics of southwestern Australia. It is a mesic floristic region bordered by an arid landscape along the north-southeastern edge and ocean on its western and southern margins (Figure 2) (Byrne *et al.,* 2011; Hopper & Gioia, 2004). Resting on a deeply weathered, geologically stable substrate, the interior of this region's subdued, low-relief topography is attributed to the large granitic Yilgarn Plateau (Byrne, 2007; Llorens *et al.,* 2017; Nistelberger *et al.,* 2021). Pibbulmun-Wadandi Country is encompassed entirely by the SWAFR boundary.

This floristic region offers notable examples of plant evolution as determined by long-term persistence in an ancient landscape unaffected by significant disturbance regimes that have been experienced in other parts of the world (Binks *et al.,* 2021; Byrne *et al.*, 2014; Hopper *et al.,* 2020). While not glaciated, the formation of the biome we see today is a result of large-scale climatic oscillations that significantly contributed to the current distribution and restriction of flora to southwestern Australia (Byrne, 2008; Byrne *et al.,* 2011). A gradient of temperature and rainfall defines the current Mediterranean-type climate of this region, from the low-rainfall (<300mm) zones in the arid northeast to the mesic zones in the extreme southwest (Byrne *et al.*, 2014). The geographic scope of this rainfall is derived from large-scale climatic oscillations and aridification of the late Miocene (10-6mya). During this time, the abundance of rainforest species, including those with Gondwanan ancestry, shifted to a domination of sclerophyllous species that were better adapted to the drier and more arid conditions (Byrne *et al.,* 2008). Glacial-interglacial climate periods defined the mid Pleistocene (0.8-0.5mya) that saw the expansion of arid zones during the glacial intervals and subsequent progressive aridification through the late Pleistocene (~0.25mya) solidified the rainfall patterns and vegetation composition and distribution that we see today (Byrne *et al.,* 2008).

Across Australia, the contemporary distribution of high rainfall forests followed a similar pattern of contraction due to this aridification (Byrne *et al*., 2011). These remnant mesic forest communities across the continent host the seven species of *Podocarpus* endemic to Australia (Mellick *et al.,* 2011). In the SWAFR, these fluctuations in the climate and increased aridification restricted mesic plant taxa of Gondwanan ancestry to the high-rainfall zone in the southwestern corner of the region (Binks *et al.,* 2019; Byrne *et al.,* 2011; Markgraf *et al.,* 1995). The only species of *Podocarpus* found in Western Australia exists entirely within the SWAFR, concentrated in this southwestern most corner with a few northern outliers (Figure 2) (Florabase, accessed July 2021). Its nearest relatives occur eastward across the continent some 4,000 km away, separated by the arid Nullarbor Plain (Byrne *et al.,* 2014; Mellick *et al.,* 2011). *Kalloora* (*Podocarpus drouynianus*), commonly known as emu plum, is a dioecious coniferous shrub endemic to this region. The spelling of *kalloora* is determined by Pibbulmun-Wadandi Elders, indicating a regional dialect, whereas an alternative spelling includes *koolah* (SERCUL, 2022). As this research is focused in Pibbulmun-Wadandi Country, encompassing the main range of *P. drouynianus*, the former spelling is used interchangeably with its scientific name.



Data: Atlas of Living Australia (ala.org.au, Jan. 2019), DPIRD-005 and DWER-031 (data.wa.gov.au, May 2023), Undalup Association (Jan. 2020). EPSG: 4326 – WGS 84.

Figure 2. The natural range of *Podocarpus drouynianus*, based on collection records from the Western Australian Herbarium, is shown in the southwestern corner of Western Australia with a few outlier populations near Perth. The Pibbulmun-Wadandi cultural bloc encompasses much of the natural range of *P. drouynianus*. The major towns of Perth and Albany are identified, and the inset map illustrates the area covered by the SWAFR in Western Australia.

Kalloora is a common and widespread component of the understory vegetation in the Jarrah (*Eucalyptus marginata*) – Marri (*Corymbia calophylla*) dominated wet sclerophyllous forests of the extreme southwest (Figure 3) (Chalwell & Ladd, 2005). While species of *Podocarpus* are typically trees found in wet montane or humid rainforest environments, *kalloora*, and its closest relative *P. spinulosus*, are unique in their persistence as shrubs that thrive in more arid environments to their counterparts (Hill & Brodribb, 1999; Ladd & Enright, 2011; Ornelas *et al.,* 2010). In line with their distinctive survival in drier, more drought and fire-prone climates, *kalloora* and *P. spinulosus* developed survival mechanisms, such as resprouting from a lignotuber and post-fire coning (Kahn *et al.,* 2023; Ladd & Enright, 2011; Mellick *et al.,* 2011; Nistelberger *et al.,* 2021). By synchronising flowering and subsequent coning en mass, this trait is purportedly an adaptation to enhance dispersal mechanisms, such as improved wind pollination efficiency and increased attraction to seed-dispersing animal species (Chalwell & Ladd, 205; Ladd & Enright, 2011; Tomlinson *et al.,* 1991; Wright *et al.,* 2022). The recalcitrant seeds of *kalloora* are borne on a large fleshy podocarpium, the purple aril commonly referred to as a fruit, that emerges about one year after disturbance (such as fire) and timed with seasonal wet conditions (Chalwell & Ladd, 2005; Ladd & Enright, 2011). These ‘fruit’ are a sought-after food source of a key seed disperser, the emu (*Dromaius novaehollandiae*) (Chalwell & Ladd, 2005; Nield *et al.,* 2020). The seeds of *kalloora* can be retained in the gut of an emu for a full two days, during which time these large flightless ratites can travel several kilometres, suggesting long-range seed dispersal (Chalwell & Ladd, 2005; Kahn *et al.,* 2023; Ladd & Enright, 2011; Nield *et al.,* 2015). The potential of anthropogenic driven seed dispersal, apparent in other species with similarly large seed, might also suggest long-distance dispersal (Lullfitz *et al.,* 2020b).

Figure 3. Examples of *kalloora* (*Podocarpus drouynianus*) characteristics and preferred habitat. All photos were taken by Genevieve Carey unless otherwise noted. (a) New growth of kalloora after a recent burn in Jarrah (*Eucalyptus marginata)* – Marri (*Corymbia calophylla*) forest; (b) two purple seed cones of *kalloora* showing the large seed borne on the apical end (photo: Andy McGregor); (c) a mature *kalloora* plant in Jarrah dominated forest; (d) pollen cone formation on the upper stem of *kalloora*; (e) *kalloora* growth in established Jarrah-Marri Forest; (f) seeds of *kalloora* in emu (*Dromaius novaehollandiae*) scat.

Pibbulmun-Wadandi and Kalloora

Pibbulmun-Wadandi recognise the evolutionary qualities of *kalloora,* namely its survival mechanisms in fire-prone environments and long-distance seed dispersal, within various aspects of cultural practice and lifeways, including practical techniques, social-economic interaction, and landscape-scale management (I. Webb pers comms 2018). This sheds light on the intimate understanding of the requirements to maintain viable and resilient sets of interconnected ecosystems through species management. Maintenance of resources encompasses the complex understandings required to ensure continued gene flow and support survival mechanisms, such as embedding habitat corridor management in cultural practice and timing the use of fire for predictable production of seed (Lullfitz *et al.,* 2022; Neale & Kelly, 2020; Rossetto *et al.,* 2017; W. Webb pers comms 2019; Wright *et al.,* 2022). *Kalloora* harvest events are celebrated by the Pibbulmun-Wadandi community whereby an abundant harvest verifies cultural land management practices, including seasonal burning techniques, have been carried out effectively, ensuring sufficient resources for the community and other species (Bond *et al.,* 2019; I. Webb pers comms 2018). Conversely, where harvest events are limited, Pibbulmun-Wadandi custodians articulate this as a broader issue related to a lack of integrated cultural management systems (Guilfoyle *et al.,* 2015; W. Webb pers comms 2019). In which case, subsistence requirements, social elements, and ecological aspects are embedded within Pibbulmun-Wadandi land management and overall worldviews (Amundsen-Meyer, 2013). While not currently listed as a threatened species by Australian legislative criteria (DCCEEW, 2022), the Pibbulmun-Wadandi community have expressed concerns for the viability of *kalloora* (I. Webb pers comms 2018). This is due to transgenerational observations of a shift in the species' distribution and behavioural traits, broadscale land clearing and habitat fragmentation, a noticed change of land management regimes, including the application of fire on the landscape, and an underrepresentation of Pibbulmun-Wadandi input within land management policy since colonial settlement (Bunbury, 2015; Monks *et al.,* 2019; Nield *et al.,* 2019; W. Webb pers comms 2019). These factors may impact the future persistence of *kalloora,* and being a significant cultural plant, potential impacts to *kalloora* persistence and resilience so too influence cultural wellbeing (Lullfitz *et al.,* 2020b).

Impetus for Research and Expectations

A greater understanding of the persistence strategies and dispersal mechanisms of *kalloora* aims to address concerns from Pibbulmun-Wadandi custodians, who have a strong connection to this cultural plant (W. Webb pers comms 2018). Further, *kalloora* harbours unique potential to provide insight to the effects of long-term persistence – in turn, responses to vast environmental change – on genetic patterning and adaptive capacity in this ancestral biome (Byrne *et al.,* 2014; Ornelas *et al.,* 2010). Realising the persistence strategies and extent of gene flow of *kalloora* gives us a measure of resilience of this cultural plant species. With a clearer picture of a species mechanisms of survival, as shaped by evolutionary and biogeographical processes through previous periods of climate change, we can better understand its ability to persist through future climate change, sharpening the focus of conservation efforts (Bond *et al.,* 2019; Byrne, 2007; Quiroga *et al.,* 2019).

The widespread distribution and long-term persistence of *P. drouynianus* in the mesic zone of the SWAFR, in combination with its cultural and social significance, makes it an ideal plant taxon to examine genetic variation and integrate shared understandings, fundamental to evidence-based conservation priorities (Bobo-Pinilla *et al.,* 2022; Bell *et al.,* 2014; Premoli *et al.,* 2012). While aspects of *kalloora* biology, including certain reproductive traits and dispersal requirements, have been investigated (Chalwell & Ladd, 2005; Ladd & Enright, 2011; Nield *et al.,* 2016), this species has not been analysed phylogeographically. Significant factors influencing *kalloora* genetic diversity include its long-term persistence in the landscape, widespread distribution, and long-distance seed dispersal. Phylogeographic analyses of individual taxa with similar distributional range to that of *kalloora*, such as *E. marginata* (Jarrah), *C. calophylla* (Marri), and *Allocasuarina humilis* (Dwarf Sheoak), have stressed the importance of assessing species with widespread distribution (Llorens *et al.,* 2017; Nistelberger *et al.,* 2021; Tapper *et al.,* 2014; Quiroga *et al.,* 2016). More specifically, species within the mesic environments of the SWAFR require acute attention as mesic ancestry is poorly understood in this region, especially in southern conifers and species with Gondwanan ancestry, and to interpret and facilitate evolutionary processes for species' resilience (Byrne, 2011; Sampson *et al.,* 2018; Tomlinson *et al.,* 1991; Wheeler & Byrne, 2006). Further, as a key component of the understory vegetation, phylogeographic analysis of *kalloora* may be a useful indicator of overall forest function and structure (Chalwell & Ladd, 2005).

In carrying out a phylogeographic study in southwestern Australia, we might expect certain results from the genetic analysis based on studies of species with comparable distribution and similar characteristics to *kalloora*. Relative to surrounding regions, the mesic biome in the SWAFRs extreme southwest has experienced prolonged geological stability (Bradbury *et al.,* 2016; Byrne *et al.,* 2011). *Kalloora* has maintained a long-term presence in this 'ancestral biome', which may be reflected in high or low intraspecific genetic diversity, depending on whether populations remained locally stable or contracted to refugia during periods of less mesic climate (Bradbury *et al.,* 2016; Byrne *et al.,* 2011). Current phylogeographic studies within the SWAFR have examined the implications of historical and future climatic influences on taxa for species adaptation (Byrne *et al.,* 2011; Wheeler & Byrne, 2006). Persistence within refugial habitat with characteristic recent expansion events has been observed in species within the SWAFR, albeit in a limited number of taxa (Dalmaris *et al.*, 2015; Nistelberger *et al.,* 2014). While other species of *Podocarpus* have demonstrated contraction to refugia as a viable persistence strategy through climate fluctuations, this has been documented in typically wet montane environments (Adie & Lawes, 2010; Bernardi *et al.,* 2020; Mellick *et al.,* 2012; Quiroga & Premoli, 2009). Although *kalloora* is better suited to drier climates than other species in this genus, it may still have utilised refugial habitat as a persistence strategy historically in times of more extreme arid cycles. While relatively stable, geologic variation within this region is apparent in the large granitic plateau defining the interior contrasting with the coastal plain along the western margin, which may contribute to distinct phylogeographic lineages in *kalloora* particularly for outlier populations, as has been seen in other southwest Australian species (Nistelberger *et al.,* 2021; Wheeler & Byrne, 2006). Dependent on potential historical range fragmentation and recent expansion events, we might observe species with widespread distributions exhibiting intraspecific lineage divergence or minimal genetic structuring, respectively (Byrne *et al.,* 2002; Llorens *et al.,* 2017).

Phylogeographic studies of plants typically analyse a combination of both the chloroplast DNA (cpDNA) and the nuclear genomes (in this case, using single nucleotide polymorphisms; SNPs). These two types of DNA offer distinct but complementary information, namely due to the different ways the genes are inherited. CpDNA is uniparentally inherited and does not undergo recombination, leading to a much slower mutation rate than the biparentally inherited nuclear genome (Petit & Vendramin, 2007; Schaal *et al.,* 1998). The higher mutation rate of the nuclear genome offers a more contemporary, individual-level evolutionary insight while the slower to evolve cpDNA is applied in a historical, landscape-scale context (Petit & Vendramin, 2007). Analysing a combination of the chloroplast and nuclear genome contextualises the evolutionary processes of plant species, contributing to our understanding of the historical and contemporary influences on genetic diversity and distribution. Genetic patterning at the landscape scale through cpDNA provides an indication of a species' long-term response to biogeographical patterns and historical persistence strategies, whereby individual-scale patterns of contemporary genetic variation illustrate the evolutionary potential of species and more fine-scale aspects of their gene flow (Bradbury *et al.,* 2019; Mellick *et al.,* 2011; Sampson *et al.,* 2018). As a dioecious conifer, it is assumed that the chloroplast genome of *kalloora* is paternally inherited, which is consistent with other podocarps and gymnosperms in general (Bernardi *et al.,* 2020; Ornelas *et al.,* 2010; Petit & Vendramin, 2006), and its nuclear genome inherits both the maternal and paternal lineage. Dispersal of pollen by wind and long-distance animal-dispersed seed are likely to show as high gene flow and low population divergence through the main distribution of *kalloora* (Allendorf, 2017; Ornelas *et al.,* 2010). However, the geographically isolated outlier populations may or may not factor into the potential high gene flow of *kalloora* and the genetic patterns in these populations are more difficult to predict. These populations may be included in the gene flow and show limited genetic divergence, or they may be excluded entirely from the typical range of seed dispersal and will be significantly divergent from the main distribution of *kalloora*. It is worth noting that most phylogeographic studies within the SWAFR to date have interrogated sclerophyllous angiosperms with relatively limited dispersal capacity that have been able to persist locally without contraction to refugia (Byrne & Hopper, 2008; Robins *et al.,* 2021). In which case, the long-distance dispersal potential of this relictual conifer of an otherwise typically rainforest genus may leave a unique signature across its genome and provide broader insight to the evolution of flora in this ancient landscape (Byrne *et al.,* 2014).

Aims and Hypotheses

Through analysis of the nuclear and chloroplast genomes, the aim of this study is to determine the level of genetic diversity and phylogeographic pattern across the natural distribution of *kalloora* within a culturally guided framework for its conservation and management. The development of hypotheses for this study was based on previously established factors and characteristics of *kalloora*; namely, its long-term presence on the landscape, long-distance seed dispersal, and to address concerns raised by Pibbulmun-Wadandi custodians related to the long-term conservation prospect of this cultural plant.

This study will investigate the spatial genetic patterning of *kalloora* and shared understandings by testing the following hypotheses:

1) *Kalloora* persisted through historical climatic and geologic shifts by contracting to refugia.
2) Gene flow is extensive across the geographic range of *kalloora*.
3) A community-based framework can increase shared understandings among research collaborators.

Chapter 2: Methods and Materials

Sampling and Extraction

The distributional range of *kalloora,* based on collection records from the Western Australian Herbarium, was considered in the sampling strategy design. The populations chosen for sampling were based on an even spread of representation across *kalloora's* range. Leaves were sampled from an average of 10 mature plants, with a minimal sampling distance of seven metres between plants, in each of the 22 *P. drouynianus* populations spread across its known distribution in southwestern Australia, but also two outlier populations east of metropolitan Perth (AVO and SAW) (Table 1). There was initial difficulty in locating the outlier populations near Perth. Drawing on the local network, Fred and Jean Hort were identified as community naturalists who potentially knew of these outlier populations. Fred and Jean Hort accompanied the researcher in the field for successful location and sampling of the two outlier populations. Sampling in the main geographic range was conducted with Pibbulmun-Wadandi Elders, Knowledge Holders, cultural facilitators, and the Wadandi Cultural Conservation Corps alongside the researcher. At least one herbarium voucher specimen and one DNA voucher from each sampled population were lodged with the Western Australia Herbarium and Biodiversity and Conservation Science at the Department of Biodiversity, Conservation, and Attractions (DBCA), respectively. In the field, herbarium voucher specimens were held in a plant press and DNA samples were stored on silica gel until delivered to the Western Australia Herbarium and the Sid James Conservation Genetics laboratory by the researcher and representatives from the aforementioned Pibbulmun-Wadandi community groups. Flora collection licenses, Regulation 4 and Regulation 61 (under approval numbers CE006517 and FT61000955), were obtained through DBCA.

DNA was extracted from freeze-dried material using a 2% CTAB protocol (Doyle & Doyle, 1987) with the addition of 1% w/v polyvinylpyrrolidone to the extraction buffer by geneticists in the Sid James Conservation Genetics laboratory (DBCA) in Perth. DNA samples were sent to Diversity Arrays Technology Pty Ltd (DarT, Canberra, Australia) for DarTseq analysis. Briefly, library preparation involved DNA digestion using two methylation-sensitive restriction enzymes, PstI and HpaII, and the fragments were ligated with uniquely barcoded adaptors. SNP calling and quality checks were performed using DarT's proprietary pipelines that resulted in a small dataset consisting of 9554 SNP loci with 46.62% missing data and average read depth of 23.67x across 182 individuals. Upon receiving this dataset, further filtering was applied using the dartR, package v.1.8.3 (Gruber *et al.,* 2018) in R v.4.0.4 (R Development Core Team, 2021) as follows: removal of secondary loci, depth 5-100, reproducibility 0.9, SNP call rate 0.60, maf 0.02 and individual call rate 0.5. This generated a dataset of 1462 SNPs with 20.75% missing data and 32.01x average read depth across 160 individuals. Principal component analysis (PCA) was performed on both the unfiltered (9554 loci) and filtered (1462 loci) datasets using the gl.pcoa function in dartR. Due to obvious issues in the data (see Results), no further analysis on these datasets was performed.

Table 1. Summary of 22 *Podocarpus drouynianus* populations from southwestern Australia sampled for both nuclear and chloroplast DNA sequencing.

Population	Code	n	Latitude	Longitude
Avon Valley	AVO	8	-31.641382	116.311591
Bibbulmun Track	BIB	9	-34.778003	116.185861
Blackwood	BLA	9	-34.120437	115.552907
Blue Lake Road	BLU	9	-34.771948	117.453691
Boyanup	BOY	9	-33.598778	115.752026
Cambray	CAM	8	-33.883028	115.724374
Coronation Road	COR	9	-34.203837	115.883284
Donnelly Mill	DON	8	-34.071311	116.134104
East River Road	ERV	8	-34.942436	117.39243
Kalloora 01	KL1	9	-34.563598	116.573965
Kalloora 02	KL2	9	-34.680728	116.853205
Kordabup	KOR	8	-34.961654	117.159677
Lullfitz Property	LUL	9	-33.820014	115.374327

Mordalup	MOR	8	-34.314938	116.498511
Mountain Road	MTN	8	-34.780257	116.956949
Osmington	OSM	9	-33.9226	115.119882
Rocky Gully	RGU	8	-34.593336	116.960043
Sawyers Valley	SAW	9	-31.922893	116.222323
Vasse Highway	VAS	8	-34.353263	115.781314
Vlam Road	VLA	8	-34.141561	115.090709
Walpole	WAL	9	-34.952092	116.608875
Wheatley Coast Road	WHE	9	-34.398748	116.277454

n – number of samples; Location – site latitude and longitude.

Sequencing and Analysis

Four intergenic spacer regions, *atpE-rbcL, psbA-trnH*, *trnL-trnF,* and *trnS-trnG,* from the chloroplast genome were chosen for amplification based on regions that have shown intraspecific variation in other *Podocarpus* species (Bernardi *et al.,* 2020; Ornelas *et al.,* 2010), as well as Australian plants more universally (Byrne & Hankinson, 2012). Sequencing was performed on the same set of samples as the SNP dataset, using the primers and polymerase chain reaction (PCR) conditions detailed in previous studies (Bernardi *et al.,* 2020; Byrne & Hankinson, 2012, from Shaw *et al.,* 2005/2007; Byrne & Hankinson, 2012, from Tate & Simpson 2003; Ornelas *et al.,* 2010, from Taberlat *et al.,* 1991 and Shaw 2005; Sang *et al.,* 1997). The PCRs were conducted by the Australian Genome Research Facility (AGRF) (Perth, Australia). The resulting sequences were received by the researcher and the remainder of analyses were conducted by them. The sequences were aligned, trimmed, and edited for miscalls using MEGA 5.05 (Tamura *et al.,* 2007) and concatenated in FASconCAT (Kück & Meusemann, 2010) to generate a total sequence length of 3021 base pairs (bp). Insertion–deletions (indels) were manually coded as binary characters, although mononucleotide repeat length differences were ignored due to the high likelihood of read errors.

Chloroplast haplotypes were identified, and the resulting haplotype (H_D) and nucleotide diversity (π) were calculated using DNASP 5.10.01 (Librado & Rozas, 2009). A median-joining maximum parsimony network was developed in NETWORK 4.6.1.1 (Bandelt *et al.,* 1999), to examine the evolutionary relatedness of chloroplast haplotypes. Estimates of population differentiation (NST, GST) were calculated using PERMUT 2.0 (Pons & Petit, 1996). While GST only considers haplotype frequencies (unordered analysis), NST considers the distance between those haplotypes (ordered analysis). Significant phylogeographic structure is indicated when haplotypes within populations are on average more similar to each other than to a random set of haplotypes (NST > GST), suggesting genetic differentiation among populations is influenced by a mutational process rather than genetic drift alone (Bradbury *et al.,* 2016; Llorens *et al.,* 2017). Neutrality and expansion tests, which assess the likelihood of departures from neutrality and population growth (Bradbury *et al.,* 2016), were calculated with Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997), and R_2 (Ramos-Onsins & Rozas, 2002) using DNAsp. The distribution of haplotypes was mapped to visualise their geographic arrangement and look for a signal of refugia (i.e., areas of high haplotype diversity surrounded by low diversity).

Incorporated Understandings

A ‘yarning’ methodology provided a structure to incorporate information provided by Pibbulmun-Wadandi. This methodology entails relaxed discussions of places and topics, often informed by the immediate place of interest with relevance to the research study (Bessarab & Ng’andu, 2010). Thus, yarning encapsulates methods of listening, learning, and responding to information from ones surrounds as much as the interaction and discussion between researcher and Knowledge Holder (Hughes & Barlo, 2021), further balancing knowledge sets. Insights shared during the semi-structured interviews were recorded and are included as quotes throughout this paper and summarised in Table 4 with interpretations from the researcher. Human Research Ethics were approved through the University of Western Australia (RA/4/20/6165).

Chapter 3: Results

Single Nucleotide Polymorphisms

“The Old Girls are holding onto their secrets.” Wayne ‘Wonitji’ Webb, 2022

The SNP dataset returned from DarT was unusually small, had excessive missing data, and many samples were removed due to poor quality. These are all indications of problematic input data such that alignment in the SNP calling process was hindered to result in a small, low-quality dataset. Upon exploration of both the unfiltered and filtered datasets using PCA, there was poor resolution such that these analyses were not particularly informative, and the dataset was not used to inform the study. After this result, the Pibbulmun-Wadandi community offered the view that the maternal lineage of *kalloora* may not be ready to divulge information held in its nuclear genome, unlike the paternally inherited chloroplast genome which sequenced successfully, and would reveal itself in time, pointing to potential explanations outside western science. Although the SNP data were not used to inform this study it is worth pointing out that the PCAs on both the unfiltered and filtered datasets did return a low resolution yet clear signature of differentiation between the outlier populations (AVO and SAW) and the rest of the sampled *kalloora* populations (Figure 4), drawing similar inferences to the chloroplast DNA results discussed in further detail below.

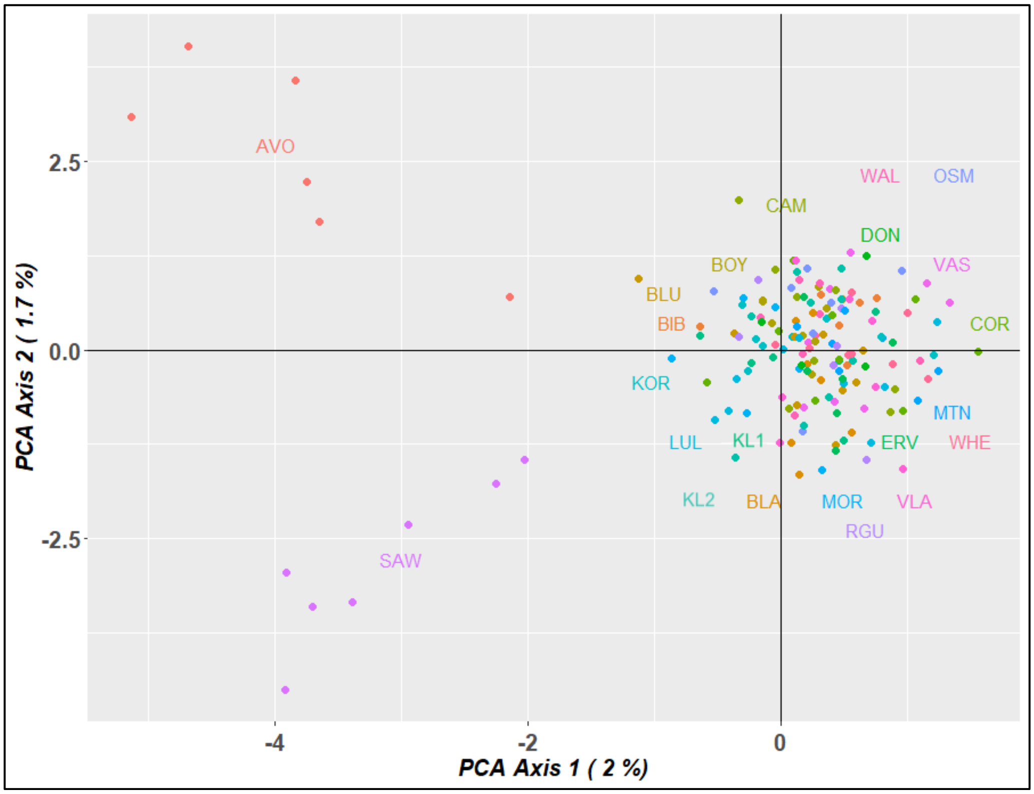


Figure 4. Principal Component Analysis ordination showing clustering of individuals from 22 *Podocarpus drouynianus* sampled populations based on similarity of 1462 SNP markers. Data derived from poor resolution SNP results, shown here to demonstrate the distinction between the outlier AVO and SAW populations from the main range of the species' distribution.

Chloroplast Diversity and Phylogeographic Patterns

The trimmed lengths of the *atpE-rbcL, psbA-trnH, trnL-trnF,* and *trnS-trnG* intergenic regions were 963 bp, 742 bp, 382 bp, and 934 bp respectively. Across all 3021 bases of sequences in 188 *P. drouynianus* individuals there were 27 polymorphic sites and two indels were scored across the dataset. A total of 28 unique haplotypes were identified and all populations exhibited at least two haplotypes, with a mean of 4.14±0.27 haplotypes per population (Table 2). Three haplotypes were more widely distributed than the rest, occurring across 74% of individuals. Of the 28 identified haplotypes, 17 occurred as singletons. Interestingly, H01, which comprised the majority of the two outlier populations, was not common but was broadly dispersed in populations across the main distribution.

Table 2. List of haplotypes derived from chloroplast DNA sequence analysis of *Podocarpus drouynianus* and their frequencies based on four combined regions, *atpE-rbcL, psbA-trnH, trnL-trnF,* and *trnS-trnG*.

Haplotype	Location (number of individuals)	Frequency (%)
H01	Avon Valley (4), Mountain Road (1), Vasse Highway (1), Walpole (8), Donnelly Mill (2), Blackwood (1), Kalloora 01 (1), Lullfitz Property (1), Coronation Road (1), Kordabup (1), E River Road (1), Sawyers Valley (8)	12.77
H02	Avon Valley (3)	1.6
H03	Avon Valley (1), Rocky Gully (2)	1.6
H04	Mountain Road (3), Blue Lake Road (5), Bibbulmun Track (5), Vasse Highway (4), Walpole (5), Cambray (1), Osmington (3), Boyanup (5), Rocky Gully (1), Wheatley Coast Road (7), Kalloora 02 (5), Kalloora 01 (2), Vlam Road (5), Lullfitz (5), Coronation Road (4), Kordabup (1), East River Road (1)	36.7
H05	Mountain Road (1), Bibbulmun Track (1), Cambray (1), Blackwood (2), Kalloora 01 (1), Vlam Road (1), Mordalup (1)	4.26
H06	Mountain Road (1), Blue Lake Road (1)	1.06
H07	Blue Lake Road (2), Bibbulmun Track (1), Vasse Highway (2), Walpole (2), Cambray (3), Osmington (4), Blackwood (2), Boyanup (4), Rocky Gully (2), Wheatley Coast (1), Kalloora 02 (3), Kalloora 01 (2), Lullfitz Property (2), Coronation Road (1), Kordabup (5), East River Road (3), Mordalup (6), Sawyers Valley (1)	24.47
H08	Blue Lake Road (2), Bibbulmun Track (1), Cambray (1), Rocky Gully (2), Lullfitz Property (1), East River Road (1)	4.26
H09	Bibbulmun Track (1)	0.53
H10	Bibbulmun Track (1)	0.53
H11	Vasse Highway (1), Osmington (1)	1.06
H12	Cambray (2)	1.06
H13	Osmington (1)	0.53
H14	Donnelly Mill (1)	0.53
H15	Donnelly Mill (1)	0.53
H16	Blackwood (1), Mordalup (1)	1.06
H17	Rocky Gully (1)	0.53
H18	Wheatley Coast Road (1)	0.53
H19	Kalloora 02 (1)	0.53
H20	Kalloora 01 (1)	0.53
H21	Kalloora 01 (1)	0.53
H22	Kalloora 01 (1)	0.53
H23	Vlam Road (1)	0.53
H24	Vlam Road (1)	0.53
H25	Coronation Road (1)	0.53
H26	Coronation Road (1), East River Road (1)	1.06
H27	Coronation Road (1)	0.53
H28	Kordabup (1), East River Road (1)	1.06

Measures of total haplotype diversity were high-moderate (0.7881), as was diversity within populations. Nucleotide diversity was very low ($\pi = 0.001$), indicating haplotypes were not highly divergent in terms of nucleotide composition. Fu's F_S and Tajima's D were both insignificant ($F_S = 0.33$, $D = -0.082$; $P > 0.05$) indicating neutrality, while Ramos-Onsins & Rozas value was low and significant ($R_2 = 0.161$; $P < 0.05$) indicating the possibility of some population expansion. Tests of phylogeographic structure resulted in low GST and NST values, suggesting little among-population differentiation (Table 3). The value of NST was greater than GST, by a minimally significant margin ($P = 0.047$), indicating haplotypes co-occurring in a population are more likely to be related than haplotypes occurring in different populations albeit at weak phylogeographic structure.

Table 3. Haplotype and nucleotide diversity and differentiation statistics. Statistics calculated from chloroplast DNA sequence data of *Podocarpus drouynianus* based on four combined regions, *atpE-rbcL, psbA-trnH, trnL-trnF, trnS-trnG,* for 188 samples from 22 populations.

Test	Statistic	Value
Diversity and differentiation		
Haplotype diversity	H_D	0.788
Nucleotide diversity	π	0.001
Within-population diversity (unordered)	*hS*	0.701 (0.037)
Within-population diversity (ordered)	*vS*	0.66 (0.059)
Total diversity (unordered)	*hT*	0.795 (0.026)
Total diversity (ordered)	*vT*	0.797 (0.071)
Population differentiation (unordered)	*GST*	0.118 (0.051)
Population differentiation (ordered)	*NST*	0.172 (0.08)
Phylogeographical structure	*NST* > *GST*	**P = 0.047**
Population size change		
Tajima's *D*	*D*	-0.082 P = 0.545
Fu's F_S	F_S	0.33 P = 0.444
Ramos-Onsins & Rozas R_2	R_2	**0.161 P = 0.000**

Standard errors in parentheses. Bold values represent a significant ($P<0.05$) result.

The haplotype network was relatively simple with the three most common and widespread haplotypes, H01, H04, and H07, forming three main nodes (Figure 5). With the exception of one haplotype, H08, branching off between H01 and H07, all other haplotypes expanded from these three nodes and the majority represented singleton haplotypes, with five to seven branches per node. The H04 and H07 nodes were more closely related than H01, as determined by the number of mutational steps separating haplotypes in the network.

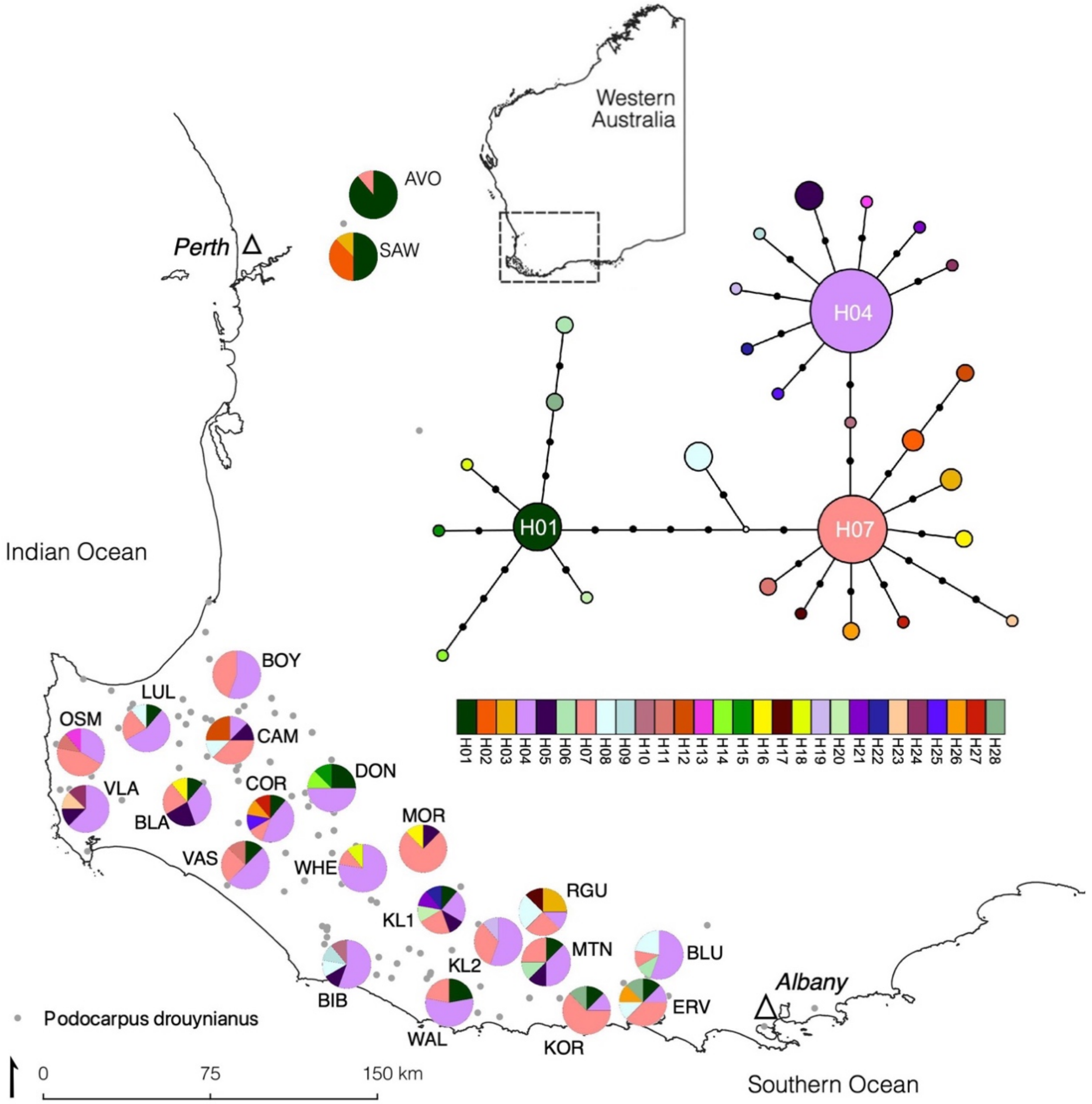


Figure 5. Median-joining maximum parsimony haplotype network of 28 chloroplast haplotypes observed in *Podocarpus drouynianus* alongside the distribution of haplotypes overlaid on a geographical map of sampling locations in southwestern Australia. Collection records of the species from the Western Australian Herbarium are represented as grey circles. Haplotypes were identified from analysis of *atpE-rbcL, psbA-trnH, trnL-trnF,* and *trnS-trnG* chloroplast sequences in 188 samples from 22 populations. Pie charts present the frequency of haplotypes in each sampled population. Population name codes correspond to those in Table 2.

The outlier populations sampled near Perth (AVO and SAW) exhibited a unique haplotype assemblage with H01 as the dominant haplotype. While H01 was also present in the main range, it was in much lower frequency than H04 and H07, which occurred in almost every population. Other than this contrast, the remaining populations exhibited little to no obvious geographic haplotype patterning (Figure 5). No signal of refugia was detected as indicated by the high haplotype diversity across all populations and no obvious geographic regions of high or low diversity.

Shared Insights

The community-based framework provided an opportunity for the collection of perspectives from the team throughout the study. A summary of shared learnings from various stages of the research are collated in Table 4 and are included throughout the document in quotations. The delivery of samples and vouchers to the genetics lab and the Western Australian Herbarium by the researcher and representatives from the Pibbulmun-Wadandi community provided further exposure to the western science process and allowed knowledge sharing between the community and researchers (Figure 6) (Collier-Robinson *et al.,* 2019). Preserved specimens of *P. drouynianus* were set aside by the researcher for the research team to view during the visit. During the viewing, critical Pibbulmun-Wadandi understandings were shared when a Knowledge Holder related certain preserved *kalloora* specimens, collected as early as 1898, to the place and time of individual ancestral family relations, an observation that provided immense insight to the connection between people, family, and plants (Lullfitz *et al.,* 2023; Pyke *et al.,* 2018; Vaughan, 2018). This observation placed the study in a deeper context of Pibbulmun-Wadandi understandings of place, time, and plant-people-landscape connections. Table 4 presents a summary of the key learnings as quotes from the cultural supervisor of this study which frame much of the discussion presented in Chapter 4.

Table 4. Brief description of learnings by the researcher based on insights shared by Pibbulmun-Wadandi at different stages of the study.

Stage of study	*Key insight(s)*	*Interpretations and learnings*
Impetus for research	“We have concerns for our *kalloora*, our harvests are becoming less bountiful, less predictable – this is a worry for us, our lands are under pressure, and so are our food sources. We need to re-instate our ways of caring for Country.” *Wayne ‘Wonitji’ Webb, 2nd March 2019*	This describes the deeply felt concern for the health of *kalloora* and illustrates the custodial responsibility towards plants. Ecosystem maintenance is a core cultural practice whereby the health of a Country is reflected in those responsible for its management. The current state of land management where *kalloora* grows is not currently adequate for sustainable harvests and the return of cultural practice is essential for the restoration of balanced ecosystems.
Impetus for research	“Mother nature we need her, we gotta let her do her job. Take things out of the Country and you’ll find the Country will start dying off slowly, and if we don’t do something now, it’ll be too late.” *Wayne ‘Wonitji’ Webb, 2nd March 2019*	Altering landscapes without a deep understanding of how an ecosystem functions has consequences for the long-term health of Country. This quote describes a sense of urgency to care for Country which is inherent in this community. This urgency is amplified by the custodial responsibilities of descendent communities to look after inherited cultural landscapes. These concerns should centralise research and land management priorities.

Fieldwork	"Looking after *kalloora* is looking after our *moort*, our family. Everybody helps, these plums will go to our Aunties." *Iszaac 'Waalitj' Webb, 14th October 2021*	This quote embeds the study within a community-based framework where *kalloora* is acknowledged as a cultural plant. The management and care of cultural plants often entails looking after the wider community, a cyclical practice of care. The distribution of a harvest is an important cultural practice to ensure a strong community and *kalloora* is tended to with this consideration.
Fieldwork	"We tell our stories, of our connection to Country, how the Country works, and how it all goes hand in hand." *Wayne 'Wonitji' Webb, 14th March 2022*	This widens the lens of *kalloora*'s place within the context of a cultural landscape and illustrates the sustained ecological presence and transgenerational knowledge systems of Pibbulmun-Wadandi custodians.
Delivery of samples to the genetics lab and herbarium	"These plants are our *moort,* our family." *Iszaac 'Waalitj' Webb, 27th May 2022*	This quote embodies the connection between people, plants, ancestors, custodianship, and cultural practice. To look after cultural plants is to look after family, they are treated in the same respect.
Return of inconclusive SNP data	"They'll tell us when they're ready." *Wayne 'Wonitji' Webb, 27th May 2022*	This situates *kalloora* as an individual and hints at the notion that timescales are relative. Perhaps we need to treat *kalloora* as a person-like entity and work beyond specific timeframes to further understand why the SNP data did not work.
Return of inconclusive SNP data	"The Old Girls are holding onto their secrets." *Wayne 'Wonitji' Webb, 27th May 2022*	The 'Old Girls' referred to here may be the Pibbulmun-Wadandi women that traditionally managed and cared for *kalloora.* In managing *kalloora,* and thus shaping current populations, women may have a strong influence on the genetic record. In a deep connection with this cultural plant, it could be seen as these Ancestors being held in the maternally inherited DNA within the nuclear genome. These interpretations require further unpacking with custodians. This quote proposes to the research team that we may need to look to sources outside the realm of western science for further understandings.
Analysing results	"DNA is a bridge between two knowledge systems." *Wayne 'Wonitji' Webb, 27th May 2022*	In many ways, DNA is unifying in its sincerity, in that genetic material is the essence of life. The interpretations offered in the analysis of genetic diversity are derived from the core truth of a species. Each knowledge system has a depth of understanding, and both immensely

		value information held at the molecular level. Commonalities naturally arose between knowledge systems in this process as there are certain understandings that are essential to maintaining a species genetic viability.

Figure 6. Stages of the project conducted with research partners. All photos were taken by Genevieve Carey unless otherwise noted. (a) Wadandi Cultural Conservationists sampling *kalloora* (*Podocarpus drouynianus*); (b) Wadandi custodian conducting fieldwork under cultural guidance (photo: Andy McGregor); (c) Binalup Cultural Rangers standing with *kalloora*; (d) Pibbulmun-Wadandi custodians view specimens of *kalloora* at the Western Australian Herbarium; (e) supervisors of the researcher discuss cross-cultural botanical understandings within southwestern Australia; (f) research collaborators deliver samples of *kalloora* to the genetics lab.

Chapter 4: Discussion

In this study, we set out to determine whether 1) *kalloora* persisted through historical climatic and geological shifts by contracting to refugial areas, 2) there is extensive gene flow is across the geographic range of *kalloora,* and 3) a community-based framework can increase shared understandings among research collaborators. This was achieved via phylogeographic analysis of *kalloora* and embedding the study within a community-based framework informed by a Pibbulmun-Wadandi Elder. Phylogeographic analysis of chloroplast markers was used in this study as the SNP dataset did not deliver a clear pattern and the dataset was discarded. While the high haplotype diversity of *kalloora* illustrates prolonged persistence in the landscape, the haplotype patterning does not suggest major contraction to refugial areas. This is a pattern consistent with other plant taxa in the Southwest Australia Floristic Region (SWAFR) that have been shown to generally persist within localised habitat. The second hypothesis is plausible due to the haplotype patterning indicating extensive gene flow across the species' main distribution. Finally, community-based frameworks can increase understandings among research partners, demonstrated in the key insights shared by collaborators throughout stages of the study and in Table 4.

Persistence in an Ancient Landscape

Plants with a prolonged presence in the landscape employ a range of persistence strategies, including contraction and expansion from refugia and developing specific habitat requirements, during biogeographic activity that either strain or favour species proliferation (Binks *et al.,* 2019; Byrne *et al.,* 2014; Yates *et al.,* 2019). We hypothesised that *kalloora* persisted through historical climatic and geological shifts by contracting to refugial areas. We can conclude from the genetic results that contraction and expansion from major refugia was not an evolutionary survival strategy of *P. drouynianus.* This was evident in the widespread distribution of haplotypes across the sampled populations and minimal expansion activity. No clear evidence of *kalloora* utilising refugia as a persistence strategy is a somewhat unexpected result as it contrasts with other *Podocarpus* species that demonstrably persisted through major climatic oscillations in refugia, albeit in typically wet, montane environments (Adie & Lawes, 2010; Bernardi *et al.,* 2020; Mellick *et al.,* 2012; Quiroga & Premoli, 2009). Although contraction to refugial habitat has been observed in the SWAFR, it is a relatively uncommon strategy in this region (Dalmaris *et al.*, 2015; Nistelberger *et al.*, 2014). In which case, *kalloora* is consistent with the flora of the landscape in which it occurs.

As expected, the cpDNA genetic structure of *kalloora* is consistent with patterns of long-term persistence in a stable landscape, as demonstrated by the high haplotype diversity overall (H_D = 0.788), as well as the widespread haplotype diversity retained within populations. *Kalloora* exhibited similar haplotype diversity and population persistence to other species in the region with comparable range where variation in the chloroplast genome has been analysed. *Corymbia calophylla* (Myrtaceae) (Marri)*, Banksia nivea* (Proteaceae), and *Allocasuarina humilis* (Casuarinaceae) had similar levels of haplotype diversity to *P. drouynianus.* However, these species differed in that they showed signals of expansion that indicated progression southward during major climatic oscillations of the late Pleistocene (Llorens *et al.,* 2017; Sampson *et al.,* 2018; Sampson & Byrne, 2022). The aridification of the region at this time saw an influx of northern, more arid-adapted species encroaching on the rainforest environments of the extreme southwest (Byrne *et al.,* 2011). While the low R_2 value (Table 3) indicates recent population expansion of *kalloora*, taken in consideration with the widespread circulation of haplotypes across the main distribution and low differentiation, it does not suggest significant population fluctuation of *kalloora* populations. Rather, this may be explained by gradual contraction with minor expansion episodes due to oscillations in rainfall during the late Pleistocene (Byrne *et al.*, 2008; Sampson *et al.,* 2018). Limited evidence of expansion in *kalloora* supports our understanding that this species is a relic of a historically rainforested region (Byrne *et al.,* 2011). The patterns evident in the genetic analyses of these species further our understanding of broad and intricate vegetation dynamics during periods of variable climate. Additionally, while the maintenance of genetic diversity is a consistent pattern among species persisting in the landscape, as with dioecy and wind-mediated pollen dispersal (Llorens *et al.,* 2017; Mellick *et al.,* 2013), these factors are also typically associated with population structure (Sampson *et al.,* 2018). In the SWAFR, species demonstrably colonise landscape and geological features, such as large granite inselbergs, and, without methods of widespread pollen and seed dispersal, diversify within localised habitat over a long period of time (Byrne & Hopper, 2008;

Hopper *et al.,* 2020; Nistelberger *et al.,* 2014; Yates & Ladd, 2004; Yates *et al.,* 2019). The distribution of haplotypes may also be demarcated by significant features in the landscape, such as riverways and plateaus, as well as historical climate change events which act as barriers to gene flow (Bradbury *et al.,* 2016; Byrne *et al.,* 1999; Wheeler & Byrne, 2006). Strong population structure is a common result of this insulation, whereby genetic divergence is spatially evident (Byrne *et al.,* 2002; Sampson *et al.,* 2018), which includes species with widespread distribution (Llorens *et al.,* 2017; Nistelberger *et al.,* 2021; Tapper *et al.,* 2014).

The outlier populations, however, warrant discussion as these populations did exhibit distinct haplotype composition and divergence from the main range and may account for the weakly significant phylogeographic structure result (Table 3; P=0.047). The distinct composition of haplotypes is indicative of isolation of these populations from the main range. However, there are shared haplotypes between these two populations and the main range, which was an unexpected result. Further, the composition of haplotypes between the two outlier populations is also unique, whereby H01 accounts for the majority of both and yet the other haplotypes within each population are distinct and not closely related. There are two potential explanations for the genetic structure of these populations, the former more likely than the latter. It is possible that as aridification expanded in the interior of the continent, the high-rainfall forest, which included *kalloora*, contracted to the southwest corner of this region. This resulted in these remnant, outlying populations of *kalloora* outside the main current distribution with effectively random haplotype frequencies as a subset of the main range. Potentially, this may be a demonstration of *kalloora* utilising broadscale refugia apparent as its main distribution and the outlier populations persisting in minor outlying refugia in their current extent after major contraction of the main range, without subsequent re-expansion. The contraction of the high-rainfall forest to the southwest corner of Western Australia is well established in the palaeoclimatic record (Byrne, 2007; Byrne *et al.,* 2014; Elliot & Byrne, 2003; Quiroga *et al.,* 2016) as is the historical distribution of Gondwanan ancestral species (Brodribb & Hill, 2004; Kelch, 1997). Additionally, the maintenance of genetic diversity across *kalloora* generally, but also within these smaller outlying populations, is indicative of maintaining substantial population sizes in the landscape over a prolonged period. This scenario is supported by species distribution modelling that has shown *kalloora* distribution was once more widespread in the region (Carey, 2019). Long distance migration events are another potential explanation for the distinct haplotype composition of the outlier populations, entailing transportation of seed from one location to another outside typical dispersal patterns. Due to the distance between these outlier populations and the main range and considering the large size of the seed, it is assumed historical transport (i.e., pre-European) would require a similarly large dispersal agent, e.g., either emu or human (Calviño-Cancela, 2012). Moreover, the assemblage of the haplotypes between these two populations suggests that at least two separate migration events would have needed to occur, as demonstrated in the assemblage of unrelated haplotypes stemming from different nodes of the haplotype network. It is worth noting that these considerations are based on known occurrence records for *kalloora* from the Western Australian Herbarium (Florabase, accessed July 2021) that suggest the outlier populations are geographic outliers; however, *kalloora* may be more abundant in the Perth region than is currently known. Although, even if additional populations do exist in between the two outlier populations and the main distribution, it is unlikely that many populations have gone unrecorded, and moreover, the distinction in haplotype composition indicates that dispersal is not a frequent occurrence between the main distribution and these northern areas, suggesting genuine geographic isolation. Further research targeting the geographic gap between outliers and the main range may narrow down the scenarios discussed above.

The steady contraction of mesic forests restricted *kalloora* distribution to the high rainfall south-western corner of Australia. Habitat specificity, in this case, may be demonstrated by the main distribution of *kalloora* aligning with the high rainfall zone of the SWAFR throughout climatic oscillations. Here, the evolutionary success of *kalloora* may be attributed to an early development of mechanisms to survive in a drying climate prior to the onset of major aridification, including improved water use efficiency and post-fire flowering attributes (Ladd & Enright, 2011). This is supported by the strong resprouting ability of *kalloora* and resprouting from a lignotuber. A strong resprouting ability is a trait found in other gymnosperms with old lineages (e.g., *Wollemia nobilis*, *Macrozamia riedlei*, and *Ginkgo biloba*) (Pausus & Keeley, 2014) and resprouting from a lignotuber is a trait tied to fire-prone environments (Ladd & Enright, 2011; Nield *et al.,* 2016; Russell-Smith *et al.,* 2012). Both properties contribute to *kalloora's* evolutionary success as the only species of its otherwise rainforest genus to maintain widespread presence in an increasingly fire-prone and arid landscape (Pausus & Schwilk, 2012). The low population structure of *kalloora* suggests extensive gene flow across its main distribution in historically continuous suitable habitat, likely facilitated by high dispersal of seed by emus. In this case, further consideration of a measure of gene flow may be appropriate to understand whether extensive gene flow by seed has eroded signals of contraction to refugia and other potential persistence strategies. Studies in this area to date have generally targeted angiosperms with limited dispersal capacity whereas *kalloora*'s long-distance seed dispersal and prolonged persistence in the landscape may contribute strongly to its high genetic diversity and weak population structure. It is worth noting, *M. riedlei* is also a widespread ancient gymnosperm that resprouts strongly after fire and bears a large seed that is dispersed by emu (Byrne & James, 1991; Nield *et al.,* 2019). Relevant studies targeting the genomic structure of *M. riedlei* are limited to one conducted by Byrne and James (1991) which indicated high genetic diversity and effective and widespread distribution of genes. This study was limited in scope, however, and the conservation management of these two species may benefit from further research targeting genetic variation and persistence strategies, namely the implication of post-fire resprouting and long-distance seed distribution (Byrne & James, 1991; Nield *et al.,* 2019; Pausus & Keeley, 2014; Premoli & Steinke, 2008).

Preservation of Gene Flow and Ecosystem Maintenance

The spatial patterns of haplotype distribution suggest the maintenance of a large population size and extensive gene flow of *kalloora* within its main range. This is indicated by the widespread distribution of common haplotypes across its geographic range and weak phylogeographic structure, evidence to support our second hypothesis. This is most likely explained by effective and frequent long-distance seed dispersal during its prolonged lifespan. While this result was expected, the extensiveness of haplotype distribution was unforeseen and demonstrates a level of efficacy that distinguishes the genetic patterning of *kalloora* from other species with long-term persistence and broad distribution in this region (Broadhurst & Coates, 2002; Byrne *et al.,* 2002; Hines & Byrne, 2001). The widespread distribution of *kalloora* haplotypes suggests critical dependence on long-distance and extensive seed dispersal as a long-term evolutionary survival mechanism to distribute and maintain genetic diversity that is supported and enhanced by wind-mediated pollen dispersal and dioecy (Byrne *et al.,* 2014; Llorens *et al.,* 2017). The abundance of *kalloora* in suitable habitat is also indicative of long-distance and widespread seed dispersal (Chalwell & Ladd, 2005; Nield *et al.,* 2015).

Spatial patterns of seed dispersers are well recognised as critical to plant population dynamics (Cain *et al.,* 2000; Nield *et al.,* 2015). This suggests that impacts to disperser habitat, such as land fragmentation and altered land management strategies, may have major implications for plant species that are reliant on these dispersers for maintaining extensive gene flow (Burbidge & Whelan, 1982; Calviño-Cancela *et al.,* 2006; Lullfitz *et al.,* 2020a; Nathan *et al.,* 2000; Nield *et al.,* 2020). Habitat fragmentation has the potential to interfere with this symbiotic relationship between *kalloora* and emus*,* interrupting long-evolved natural processes. Using a simulation model to examine changes in landscape connectivity to emu movement and in relation to seed dispersal, Nield et al. (2019) determined that habitat fragmentation severely limits seed dispersion distances and alters the typical movements of emu, especially so in a landscape fragmented by multiple, small patches of clearing. The loss of genetic variation due to fragmentation occurs namely through bottlenecking, increased inbreeding, and genetic drift, leading to the erosion of genetic diversity through the gradual loss of alleles (Binks *et al.,* 2018; Young *et al.,* 1996). Corrosion of genetic diversity weakens a species' capacity for adaptation, leading to vulnerability and limited resilience to threats in the long-term (Boogert *et al.,* 2006; Cristobal-Perez *et al.,* 2021; Nistelberger *et al.,* 2021). The high genetic diversity and low phylogeographic structure of *kalloora* is indicative of long-term persistence in the landscape and reliance on long-distance seed dispersal during that time. Disruptions to these long-evolved survival mechanisms has the potential to severely impact the genetic diversity and adaptive potential of *kalloora*.

"Mother nature we need her, we gotta let her do her job. Take things out of the Country and you'll find the Country will start dying off slowly, and if we don't do something now, it'll be too late."
Wayne 'Wonitji' Webb, 2018

Since European incursion on the landscape, southwestern Australia has experienced a significant disruption to ecological services (Bunbury, 2015). The forced removal of Pibbulmun-Wadandi people and cultural practice from the landscape dramatically altered the maintenance of ecosystems (Bunbury, 2015; Guilfoyle *et al.,* 2015) and simultaneous broadscale land clearing abruptly severed habitat continuity (Byrne *et al.,* 2014; Ford, 2011). Fragmentation of landscapes severely restricts the range of long-distance seed dispersers, especially large flightless frugivores (Ford, 2011; Mellick *et al.,* 2016). With once widespread and continuous habitat, emus were the predominant disperser of large seed (Chalwell & Ladd, 2005). The disruption of the habitat continuity of emus has implications for the array of species which depend on this movement (Chalwell & Ladd, 2005; Nield, 2014). This is especially so in common and widespread flora which comprise fundamental elements of broad vegetation dynamics and forest composition (Ahrens *et al.,* 2019; González *et al.,* 2020; Nield *et al.,* 2019). With its heightened dispersal capacity, *kalloora* has successfully maintained its widespread distribution and large population size in this region throughout major climatic fluctuations. This is evident in its high haplotype diversity and widespread circulation of haplotypes. Additionally, the presence and use of fire on the landscape has been drastically altered post-European settlement. Notably, Pibbulmun-Wadandi fire-based land management practice was severely suppressed, if not momentarily eliminated (Fletcher *et al.,* 2021). Contemporary prescription-based fire regimes endeavour to suppress natural fire and intentional burns maintain a strict schedule (Bradshaw *et al.,* 2018). These regimes are largely based on knowledge sets and understandings derived from mainstream fire practice in the Northern Hemisphere, the vegetation dynamics of which often differ drastically to the Southern Hemisphere (Hopper, 2023; Zylstra, 2011; Zylstra, 2018). Mechanisms developed by *kalloora,* notably resprouting from a lignotuber and post-fire coning to enhance seed dispersal, have ensured its long-term survival in this region. These mechanisms are developed in long-evolution and sudden changes could have major implications for reproduction and subsequent gene flow. Ecosystem processes with these dependencies are most sensitive to the isolation effects of habitat fragmentation and abruptly altered land management regimes (Bennet, 2003), implications of which are further exacerbated in confined biomes (Byrne *et al.,* 2011; Byrne *et al.,* 2014), such as Pibbulmun-Wadandi Country. Implementing conservation and land management practices which recognise these inherent sensitivities may enable more resilient ecosystems.

Incorporated Understandings Through Community-based Frameworks

The genetic analyses undertaken in this study complement existing understandings held by Pibbulmun-Wadandi. The survival mechanisms developed by *kalloora,* including post-fire flowering and widespread distribution of seed, are recognised by Pibbulmun-Wadandi who nurture these sophisticated elements on practical, social, and intangible levels within cultural practice (e.g., through the seasonal application of fire, community resource distribution, and oral tradition) (Guilfoyle *et al.,* 2015; W. Webb pers comms 2019). A truly cultural plant, *kalloora* is deeply embedded in Pibbulmun-Wadandi lifeways and the placement of this study within a community-based framework provided a platform for the parallels between genetic results and cultural connections to emerge. Insights documented throughout the research process demonstrate shared understandings can develop from these frameworks, revealing unique perspectives between knowledge systems. Two of which, elaborated on here, include the response to the inconclusive SNP results and the other from the visit to the Western Australian Herbarium (the Herbarium).

"They'll tell us when they're ready." Wayne 'Wonitji' Webb, 2022

Western and Pibbulmun-Wadandi cultural traditions often operate in distinct worldviews, themes of which are summarised in Barnhardt and Kawagley (2005). Broadly, distinctions are apparent in concepts of time (i.e., linear and cyclical), dissemination of information (i.e., oral and written), and origin of explanations (i.e., physical and metaphysical worlds). When the initial sequencing of SNP markers was deemed unsuccessful, the response varied between overlapping disappointment and understanding among the research partners. Pibbulmun-Wadandi offered the insight that *kalloora* will 'tell us when they're ready' to divulge information in their nuclear genome (W. Webb pers comms 2022). As an offering of support, this interpretation prompted the research team to consider expertise outside a western scientific framework. It served as a reminder there may be other factors and responsibilities underpinning *kalloora* conservation management (Country *et al.,* 2019). In addition, this insight presented an animate identity to *kalloora* and in relation to the familial relationship between this community and this cultural plant. This understanding is situated within a knowledge system that emphasises a social connectivity that encompasses people, other species, and ancestors, and a cultural responsibility to maintain these relationships (Country *et al.,* 2019; Weiss *et al.,* 2012). During the fieldwork undertaken alongside Pibbulmun-Wadandi community, it was made known *kalloora* has associations with women in the community typically looking after this plant (W. Webb pers comms 2022). In this sense, Pibbulmun-Wadandi may look to maternal lineages, both ancestral and current, for further perspective in this area. Additionally, the way *kalloora* is strongly tied to functionalities in the broader landscape (e.g., the application of fire and unimpeded movement of emus) may indicate ensuring these aspects are considered first before *kalloora* is ready to divulge information in its nuclear genome. This aligns with the understanding landscape-scale conservation and protection is often prioritised by Pibbulmun-Wadandi (Guilfoyle *et al.,* 2015) and concepts of which are advocated for within the field of conservation biology (Bobo-Pinilla *et al.,* 2022; Byrne, 2007).

While the reason for the unsuccessful sequencing of the SNP markers is uncertain, per advice received from the lab, difficulty in sequencing the nuclear genome is an issue apparent in other coniferous species (Mellick *et al.,* 2011; Nistelberger *et al.,* 2021). In general, gymnosperms have a large genome and complex chromosomal arrangements, which may contribute to difficulty in sequencing. To say 'they'll tell us when they're ready' does not intend to stop attempts at sequencing. Rather, it proposes alternative timeframes and methodologies to consider in parallel (Ahuriri-Driscoll *et al.,* 2007). The attempts to sequence a uniquely challenging genome by the genetics lab were recognised by the Pibbulmun-Wadandi community. The skills and technology offered by the genetics team and the lab provide critical understandings of the health and viability of cultural plants. The field of conservation biology and the study of phylogeography provide service to the protection of plants via analysis of genetics. The examination of cultural plants at the molecular level can be understood as a way western science methodologies provide a voice and identity to flora. This illustrates the ways western science and Pibbulmun-Wadandi knowledge systems each provide novel approaches and understandings to the analysis of information. Utilising the strengths of each knowledge system expands our cumulative understanding, allows for complementarities to arise, and levels potential asymmetries (Tengö *et al.,* 2012; Zurba *et al.,* 2022). In this way, the integrity of each knowledge system is maintained (Ahuriri-Driscoll *et al.,* 2007). The community-based framework in which this research was based provided the interface for these understandings to be shared.

"These plants are our moort*, our family." Iszaac 'Waalitj' Webb, 2022*

The collective visit to the Herbarium to turn over the samples provided another example of insights that arise from these opportunities. The process itself, of Pibbulmun-Wadandi community physically handing over voucher specimens to the Herbarium, framed in the context of 'passing custodianship', offered a depth of cross-cultural understandings. *Kalloora* is *moort*, 'family', for Pibbulmun-Wadandi. It was essentially this understanding that was communicated to the genetics lab and Herbarium when handling the samples. There was some uncertainty around whether showing specimens within the Herbarium collected by early colonisers would be upsetting. This was discussed as a team and it was decided these histories are well-acknowledged and, while potentially confronting, the collection of specimens at the Herbarium offers a wealth of value. The preservation of *kalloora* provided the opportunity for the team handing over samples to make direct connection with the plants nurtured by Pibbulmun-Wadandi ancestors, the 'Old Girls'. While viewing select preserved *kalloora*, a Pibbulmun-Wadandi Knowledge Holder related the individual specimens to the time and location of individual family relations. Equating the Herbarium *kalloora* specimens of different ages and locations to specific Pibbulmun-Wadandi family members of those times and places who, we can safely assume, would have cared for those particular *kalloora,* further illustrates the deep connection and understanding Pibbulmun-Wadandi custodians have with cultural plants. This insight demonstrates at least four generations of family connection to the *kalloora* specimens preserved within the Herbarium.

An understanding which connects individual family members to specific places and time, draws on a complex spatial and temporal database maintained by cultural practice (Country *et al.,* 2019). Although the preserved *kalloora* were long removed from their place of origin, the Pibbulmun-Wadandi Knowledge Holder was able to access a cultural archive that is deeply embedded in place. The ease with which the insight was shared was derived from millennia of generations of Pibbulmun-Wadandi practicing and passing down understandings and maintaining culture. Thus, this observation illustrates the cultural responsibilities embedded in transgenerational knowledge transmission (Country *et al.,* 2019) and demonstrates a continual connection to Country. These connections to people and place underpin the responsibility to continue to look after Country, as determined by cultural understandings. The observations shared among the research team were made possible in part by the foresight to establish herbaria and the technologies and methodologies available in long-term biological preservation. Exposure to these processes and records was initiated by the community-based framework which structured this study, and these insights strengthen partnerships and form new understandings as a collective (Country *et al.,* 2019).

Kalloora Bidiwah *(Emu Plum Pathways)*

Community-based frameworks demonstrate the opportunities that arise for shared learnings which apply to conservation techniques. Founded in the impetus for this research was the concern for the long-term viability of *kalloora*. To mitigate the potentially deleterious effects of habitat fragmentation on people and plants, we can look to shared understandings, integrated methodologies, and embedding adaptive techniques that complement natural processes in conservation design. A considered approach to conservation is driven by evidence-based understanding, informed observation, and integrated knowledge systems (Gavin *et al.,* 2018; Monks *et al.,* 2019). Conservation imperatives that prioritise the preservation of genetic integrity and species' adaptive potentials have flow on effects for ecosystems (Byrne, 2007). The field of conservation biology, while grounded in a western scientific framework, often incorporates other disciplines to draw interpretations, typically fostering receptiveness and which guide holistic conservation approaches (Weiss *et al.,* 2012). This expansion of disciplines aligns with aspects of Pibbulmun-Wadandi knowledge systems which consider the whole of landscape, on social and ecological scales, to carry out management of Country. Additionally, these knowledge systems both operate within experimental, systematic, and observational principles which guide conservation approaches (Ahuriri-Driscoll *et al.,* 2007; Weiss *et al.,* 2012).

In globally-recognised biodiversity hotspots, such as the SWAFR, it is critical that we implement informed conservation schemes to preserve the population dynamics and adaptive potential of species in a landscape under anthropogenic and climatic pressure (Bobo-Pinilla *et al.,* 2022; Bradbury *et al.,* 2019; Bunbury, 2015; Byrne, 2007; Cristobal-Perez *et al.,* 2022); as articulated by cultural custodians (Lullfitz *et al.,* 2017; Ottewell & Byrne, 2022; W. Webb pers comms 2019). Academic research is utilised by Pibbulmun-Wadandi custodians to support caring for Country priorities (Ahuriri-Driscoll *et al.,* 2007; Guilfoyle *et al.,* 2015) and in this case, *kalloora*, one cultural plant of many, served as a proxy to provide the basis for shared understandings of landscape conservation. This may then support adaptive management actions related to cultural landscape and ecological connectivity. Acknowledging the acute attention millennia of generations of Pibbulmun-Wadandi have paid to *kalloora* by factoring its survival mechanisms into practical and spiritual cultural practice is required for contemporary conservation of this significant cultural plant. Pibbulmun-Wadandi recognise the importance of interconnected landscapes for ecosystem health and embed these understandings in societal and cultural life. Interconnected landscapes form fundamental conceptual and practical elements within Pibbulmun-Wadandi knowledge systems, manifest as Songlines, which retain and transmit knowledge archived in the land (Neale & Kelly, 2020) and are often visualised as corridors or pathways through landscapes (Page & Memmot, 2019; Rossetto *et al.,* 2017). The sacrosanct information comprising these knowledge systems is the custodial responsibility of Indigenous communities (Hernandez, 2022). Framing research and conservation priorities and practice within a framework of habitat connectivity, however, aligns with culturally informed land management. In this way, Elders have agency in how conservation biology research and conservation practice is implemented, enabled by community-based frameworks.

"DNA is a bridge between two knowledge systems." Wayne 'Wonitji' Webb, 2022

Evidence-based conservation schemes which integrate practical and conceptual frameworks of understanding, in balanced and constructive ways (Hernandez, 2022), promote the integral health of biomes (Gavin *et al.,* 2018). Population connectivity, defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor *et al.,* 1993 from Bennet, 2003), embeds mechanisms developed through evolution within conservation concepts (Ahrens *et al.,* 2019; Petit & Vendramin, 2006; Renton *et al.,* 2012). Studies in the field of conservation biology often advocate for the imperative of population connectivity in conservation action to maintain the functional heritage of ecosystems based on implications at the molecular level (Bobo-Pinilla *et al.,* 2022; Quiroga *et al.,* 2012). The connectivity of landscapes recognises the critical survival mechanisms developed in deep evolutionary time, especially so in mutualisms with dependence on long-distance seed dispersal by large, flightless frugivores (Calviño-Cancela, 2012; Chalwell & Ladd, 2005). A significant feature in Pibbulmun-Wadandi knowledge systems, the emu is the sole ratite and largest frugivore in the region, evolved from ancestral flightless birds as a key seed disperser for *kalloora* and other plants with large seed (Byrne *et al.,* 2003; Nield *et al.,* 2015; Sampson *et al.,* 2018; W. Webb pers comms 2018). Recognising this slowly evolved, critical mutualism in conservation schemes of landscape connectivity, *kalloora bidiwah* (emu plum pathways), maintains these fundamental disperser assemblages (Moran, 2008), preserving genetic variation, unifying knowledge systems, and centralising culturally informed land management designs in community-based frameworks for biocultural resilience.

Chapter 5: Conclusion

Further Research

The results from the phylogeographic analysis further illuminate the uniqueness of *kalloora* in southwestern Australia. As the only *Podocarpus* in the region, *kalloora* has maintained its prolonged presence in the landscape by developing survival mechanisms in an increasingly drier and more fire-prone environment and capitalising on a long-distance seed disperser. A more comprehensive understanding of *kalloora* phylogeographic structure and lineage, and broader *Podocarpus* persistence strategies, may benefit from genomic research on its closest known relative, *P. spinulosus*. *P. spinulosus* is the only other species within this genus known to have evolved traits to survive through increasing aridification and thrive in a drier climate (Ladd & Enright, 2011). Comparatively, other species of *Podocarpus* in the Southern Hemisphere that have responded to climatic shifts by expanding and contracting from refugia (Bernardi *et al.,* 2020), exhibit significant population structure (Mellick *et al.,* 2011; Mellick *et al.,* 2012; Ornelas *et al.,* 2010), favour wet, montane climatic environments (Migliore *et al.,* 2020), and grow as trees that are unequipped to survive fire (Mellick *et al.,* 2011; Mellick *et al.,* 2012). Phylogeographic studies on *P. spinulosus* would broaden our understanding of the paleoclimate of this continent (Byrne *et al.,* 2014) and the genomic structure and evolutionary context of Podocarpaceae and plants with Gondwanan ancestry in general (Brodribb & Hill, 1998; Ladd & Enright, 2011; Quiroga *et al.,* 2016), as this genus is underrepresented in Australian genomic studies (Mellick *et al.,* 2011; Tomlinson *et al.,* 1991). In addition, comparisons of phylogeographic structure and biogeographical responses (e.g., post-fire resprouting activity) of these closely related species, would lend insight on the evolution and survival techniques of plant taxa in general to drier and more fire-prone landscapes for informed conservation strategies in a changing climate. For instance, research considering the contribution of resprouting from a lignotuber on the genetic fitness of *P. drouynianus* and *P. spinulosus* may provide further understanding of the effect of this evolutionary trait to the long-term persistence and adaptive capacity of these species (Ladd & Enright, 2011; Pausus & Keeley, 2014; Pausus & Schwilk, 2012).

Integrating fields of research further enhances our ability to implement informed conservation action in the face of large-scale and drastic climate change. Assessing influences on a species historical distribution and addressing species adaptive potential in a changing climate may be supported by Species Distribution Modeling (SDM) (Mellick *et al.,* 2012). SDM incorporates spatio-temporal data, historical and predictive, with statistical analysis, providing a platform to analyse interactions between a species' past and projected distribution and suitable habitat (Reese *et al.,* 2019; Renton *et al.,* 2012; Stewart *et al.,* 2018). Unpublished SDM research of *kalloora* using historic climatic variables suggests much wider widespread distribution further north and east of the current distribution (Carey, 2019) but future modelling projections for *kalloora* have not yet been done. The incorporation of predicted climatic variables in SDM may provide a more comprehensive application of evidence-based conservation schemes for this species resilience in current and future climate change (Draper *et al.,* 2003; Kahn *et al.,* 2023; Premoli *et al.,* 2012; Sharma *et al.,* 2018).

Targeting phylogeographic studies on other biota in the high-rainfall area of the SWAFR, especially those connected with the emu, may contribute to a stronger understanding of the elements required for the maintenance of this mesic biome (Byrne, 2008). In the analysis of *P. parlatorlei* and other nearby unrelated species, Quiroga et al. (2019) proposed that integration of genetic studies of endemic species in proximity to each other strengthens conservation efforts and contributes to the conceptual development of integrated biogeographical conservation units. This may be especially insightful in other relictual species with Gondwanan ancestry and those that have relationships with the emu within the SWAFR. Studies in this area may illustrate evolutionary responses of mesic taxa to prolonged biogeographic activity (Byrne, 2008) and elucidate the potential impacts of changes to emu habitat may have on species that rely on the long-distance movement of this flightless frugivore.

Additionally, human-mediated propagule dispersal (Bell *et at.,* 2014; Kondo *et al.,* 2012; Lullfitz *et al*., 2020b; Rangan *et al.,* 2015; Rossetto *et al.,* 2017) and environmental engineering by human societies (Amundsen-Meyer, 2013; Dortch *et al.,* 2014; Lullfitz *et al.,* 2017; Smith, 2011) is increasingly documented in literature. Considering the influence of people on vegetation communities and the genetic variation of plants broadens our understanding of how people interacted with, altered, and maintained ecosystems historically. Similar to *kalloora*, the taxa studied in the phylogeographic studies considering people as dispersers exhibited high gene flow, widespread common haplotypes, and low population structure. Anthropogenic driven dispersal of seed was deduced as the likely means for these results whereby people had an important role in preserving gene flow and genetic variation. Human niche construction (HNC) theory posits behaviour patterns, both deliberate and inadvertent, modify the environment in a range of ways (Smith, 2011). Further research that considers *kalloora* within HNC theory, including Pibbulmun-Wadandi fire management techniques, may complement and elaborate on existing studies in southwestern Australia (Dortch *et al.,* 2014; Lullfitz *et al.,* 2017; Lullfitz *et al.,* 2020b). Of note, is the alignment between the natural range of *kalloora* and the cultural boundary of Pibbulmun-Wadandi (Figure 2) which may suggest mutualisms between the two for consideration in studies within niche construction. These areas lend avenues for further research and insight into *kalloora*, especially due to the cultural importance of this plant and its position as a key component of the understory in southwestern Australia. Undertaken within community-based frameworks, studies in these areas create avenues for further collaborations between knowledge systems to gain a greater understanding of viable and effective conservation schemes for the contemporary and on-going preservation and maintenance of ecosystems.

Finally, identifying community research priorities with Pibbulmun-Wadandi custodians may provide areas of further study related to *kalloora*. Working within pre-existing community structures on projects aimed at caring for Country often provide opportunities to share and develop priorities for further research. The development and support of community-driven projects within an adaptive framework focused on the conservation of *kalloora* may catalyse further research priorities of this significant cultural plant and ensure socially relevant outcomes.

Concluding Thoughts

Initiated by concerns within the Pibbulmun-Wadandi community, this study aimed to determine persistence strategies of *kalloora*, the extensiveness of gene flow across its main range, and if a community-based framework can increase shared understandings among research partners. The haplotype diversity confirms the long-term persistence of *kalloora* in the landscape as a large and widespread population. However, haplotype patterning did not suggest refugia as a persistence strategy, evident in its weak population structure and minimal expansion activity. Habitat specificity as a persistence strategy in historical climate shifts may be apparent in the suitable habitat of *kalloora* aligning with the high rainfall zone of southwestern Australia. Here, it is possible the extensiveness of gene flow may have eroded potential signatures of refugia. The widespread circulation of haplotypes across its main range is indicative of extensive gene flow and maintaining a large population size, suggesting deep time reliance on long-distance seed dispersal. This level of variation across *kalloora* distribution deepens our understanding of the vital role long-distance seed dispersers play in ecosystems, contemporarily and in deep-time evolution, and highlights the critical need to maintain their habitat connectivity, as well as that of *kalloora* itself. Finally, this study demonstrated that community-based frameworks increase understandings among research partners and that culturally informed, integrated land management practice is critical for the maintenance of ecosystems.

Phylogeographic analysis of the cpDNA provided a pathway to address concerns about the health of *kalloora.* The analyses placed this species in its evolutionary context, elaborated on its survival mechanisms, indicated a measure of its resilience, and supported a culturally informed avenue of conservation practice. *Kalloora bidiwah* (emu plum pathways) describes foundational elements of cultural knowledge systems, as informed by Pibbulmun-Wadandi custodians and concepts embedded in conservation biology. Establishing a conservation concept of habitat connectivity, integrates shared understandings of the survival mechanisms critical to *kalloora* resilience. Interpretations of the results derived from the three hypotheses that shaped this research led to the unique integration of understandings for the management of *kalloora.* As the first interrogation of the chloroplast genome of *kalloora,* and, to our knowledge, the first attempted sequencing of its nuclear genome, this research contributes to our understanding of the genomic structure, genetic diversity, and methods of genomic extraction and sequencing of a long-lived Gondwanan gymnosperm. From these analyses, we can infer historical persistence strategies of this species in an increasingly fire-prone and arid landscape. Conducting the study within a community-based framework exposed a level of shared understandings that may arise from such a collaboration. In doing so, *kalloora bidiwah,* named by the Pibbulmun-Wadandi Elder, presented itself as an integrative approach for *kalloora* conservation management. Land management schemes which embed community-based frameworks into the implementation of conservation practice may successfully integrate vital understandings of plant-animal mutualisms. The remarkable mesic biome of the southwest corner of Australia, a shrinking window to Gondwana, is a landscape cared for over millennia, and requires special consideration of contemporary, culturally informed conservation practices. These results offer insight to a species with deeply rooted ancestry in this region alongside Pibbulmun-Wadandi and future generations.

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