

Retracing the dispersal of rainforest food trees by east Australian Indigenous Peoples with genomic data



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Declarations

This thesis entitled “Retracing the dispersal of east Australian rainforest food trees by First Nations Peoples with genomic data” is an original piece of research which is the result of my own work and includes nothing which is the outcome of work done in collaboration except where this is specifically indicated in the text. This thesis has been substantially accomplished during enrolment in this degree. The research contents have not been submitted for a higher degree to any other university or institution. Any help and assistance that I have received in this research and the preparation of the thesis itself have been appropriately acknowledged. All information sources and literature used are indicated in the text. This thesis does not violate or infringe any copyright, trademark, patent, or other rights whatsoever of any person.

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Signed

Monica Fahey (Student number 45056757)

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Abstract

Over millennia, Indigenous peoples have dispersed the propagules of non-crop plants intentionally or accidentally via trade, seasonal migration or attending ceremonies. This has potentially increased the geographic range or abundance of many “wild” edible plant species around the world. However few phylogeographic studies have investigated anthropogenic dispersal as a factor of the distribution and demographic history of plant populations. It remains a challenge to separate the signal of anthropogenic versus non-anthropogenic dispersal with genomic data alone. This thesis showcases multidisciplinary research that incorporates plant genomics, historical research, and collaboration with Indigenous Biocultural Knowledge (IBK) holders to retrace the dispersal of culturally significant and edible rainforest trees by Indigenous Peoples in eastern Australia.

Chapter 1 outlines the development of an ethical and culturally appropriate research protocol for collaboration with First Nations peoples. Chapter 2 outlines a genomic screening method that can be used to identify non-crop plant species with edible fruit that show putative signals of dispersal by ancient Indigenous peoples. Chapter 3 revealed genomic patterns within *Araucaria bidwillii* (Bunya Pine) consistent with IBCK evidence that pre-colonial and colonial First Nations peoples translocated the species in its southern range. Chapter 4 demonstrated genomic evidence that First Nations peoples facilitated an upland expansion of *Castanospermum australe* (Black Bean) in its southern range. These findings illustrate that plant genomics can be deployed as a tool to rediscover Indigenous histories disrupted by colonial dispossession. It also yields insights to the long-term demographic and evolutionary impacts of plant translocations and raises questions about restoration goals and values.

Chapter 1. Introduction

General introduction

Dispersal is one of the most important processes that influence species' persistence and distribution in the face of environmental change, as it allows species to track the geographic shift suitable conditions (1–3). In addition, historical dispersal processes affect gene flow and the accumulation or loss of genetic diversity amongst populations, partially determining a species' *in situ* adaptive potential (4). For instance, invasive plant populations have managed to overcome environmental constraints on genetic diversity through multiple human-mediated long-distance dispersal events (5). In various parts of the world, ethnobotanists have long speculated that ancient Indigenous Peoples¹ translocated culturally significant non-domesticated trees (6, 7), potentially altering the geographic range, environmental niche and population dynamics of many species. However most biogeographic studies do not consider how past human activities have impacted species' present-day distributions (8).

In recent years, the ecological sciences have undergone a conceptual shift to recognise that plant populations and landscapes previously thought of as “wild”, have in fact been shaped by human activity over hundreds to thousands of years (9, 10). New developments in archaeology and palaeoecology have deepened our understanding of the antiquity and technological advancement of Indigenous cultures, hinting at a range of interventions that directly or indirectly impacted the geographic range of useful plants and animals (11, 12). This included translocations and domestication (13, 14), as well as the alteration of fire regimes and forest structure (15), soil composition (16) and atmospheric carbon (17). These findings align with the ancient custodial relationships that Indigenous Peoples have with the natural world (18).

Recognition of past human influences on species and landscapes, has also led to the uptake of human niche construction theory as a framework to investigate human-mediated ecological change (for example (19, 20)). Human niche construction theory posits that as people interact with and modify the environment, two-way ecological and cultural feedback processes are triggered (21–23). In this regard,

¹ I adopt the term “Indigenous Peoples” or “Indigenous groups” to refer to people who are the descendants of those who inhabited a geographical region at the time when people of different cultures or ethnic origins arrived. I use this term as it is the most broadly accepted internationally, and was adopted by the United Nations (107). Some chapters may also use the term “First Nations” or in the Australian context, “Traditional Owners” or “Aboriginal”. These terms refer to the Indigenous Peoples of Australia, who occupied the continent at least 60 000 years prior to European colonisation and settlement in 1788.

humans may exert cultural pressures that shape the evolutionary pathway of culturally important species and their environmental niche (24, 25), with inadvertent ecological consequences for their own human evolution (23). However, the extent that Indigenous Peoples shaped present-day plant distributions in places like Australia and the Americas continues to be debated (26–28). This highlights the need to develop new multidisciplinary approaches to revisit old questions about people-plant interactions (18).

Retracing the dispersal of plants by ancestral human populations may elucidate the geographic diffusion of technologies and lifeways, or how they were adapted through time (see (24, 29)). In Australia, authors like Bill Gammage (30) and Bruce Pascoe (31) have popularised long-standing debates over the extent to which ancient Indigenous Peoples managed the land and cultivated edible and useful plants. However, most ecological research that recognises the influence of Indigenous Peoples has focused on Indigenous burning practices. “Firestick farming” (32) was recognised by early colonisers and scholars as a widely-used mechanism to promote the growth of fire-adapted vegetation for human consumption (33), green pick to attract game for hunting (32), and more recently as a method to protect fire-sensitive resources from wildfires (34–36). Furthermore, these perspectives have tended to focus on ecosystem-level and indirect anthropogenic impacts on plant assembly processes (11, 37), although see (38). In Australia, information on direct Indigenous interventions on plant communities and populations, such as intentional or incidental propagule dispersal, is lacking (although see (39, 40)).

Oral histories told by Indigenous knowledge holders and colonial-era ethnographic or historical accounts describe the translocation of non-domesticated plants by precolonial Indigenous Peoples in various parts of the world (6, 41–43), but the paucity of such data makes it difficult to assess the extent to which these activities shaped the biogeography of species. The concentration of culturally important resource plants around historical Indigenous settlements, middens or along well-utilised transport routes supports Indigenous claims of ancient translocations in Australia (38, 44–49), North America (6, 43, 50–52), and South America (28, 53). Additionally, the disjunct distribution of culturally important plants has raised speculation of long-distance dispersal by Indigenous Peoples in Australia (7, 42, 54, 55), and in North America where there has been a sudden appearance of plant remains of particular species in the archaeological record (6, 43, 56). However, without more information, it is often difficult to assess whether it was the plants or the human settlements that originated first. Further, the role of non-anthropogenic dispersal vectors cannot be eliminated, such as seed caching or movement by animals (6). Molecular analysis of plant populations can provide important insights to the role of human dispersal, by differentiating between dispersal patterns expected of faunal versus anthropogenic vectors (see Chapter 3 for details).

Meanwhile, the contemporary restoration industry routinely employs plant translocations, either as part of habitat restoration projects to mitigate the impacts of development or to bolster populations of threatened species (57). Researchers have begun to evaluate the potential of mixing provenances and maximising genetic diversity of seed stock to establish resilient plant populations that can adapt to future climatic conditions (4, 58). However, there is considerable debate amongst geneticists about the fitness consequences of mixing genotypes, with some advocating that seed should be sourced locally to minimise the risk of outbreeding depression (59, 60). The use of genetic data to reconstruct the demographic history of long-lived tree populations established or impacted by ancient human translocation practices can enhance our understanding of the long-term adaptive potential of admixed populations over a timeframe that cannot be tested experimentally.

In response to these gaps in the literature and advancements in molecular techniques, the work presented in this thesis employs high-throughput DNA sequencing to retrace the species-specific and population-level impacts of historical rainforest tree dispersals by Indigenous groups in eastern Australia. A handful of Australian-based studies have attempted to retrace Indigenous dispersals using microsatellites (61), short-read sequences (40) or pooled-plastid sequence data (42), though the high volume of Single Nucleotide Polymorphisms (SNPs) generated by Next Generation Sequencing techniques has made it possible to reconstruct the demographic history of species in greater detail (62). Reconstructing ancient plant translocations by Indigenous Peoples is important for recognising biocultural heritage and understanding the biogeographic history of plant species. Furthermore, it establishes pathways for the development of cross-cultural restoration workflows and can yield insights to the long-term outcomes of plant translocations applicable to the restoration industry. Examining ancient translocation practices may contribute to the ethics of ‘assisted migrations’, when species need to be moved outside their current range in order to meet habitat requirements under projected climate change.

Indigenous arboriculture and translocations in Australia

The earliest dated evidence for arboreal exploitation on the Australian continent is approximately 40 Kya (63) and archaeological work has revealed that for at least the past 5 Ky, tree nuts were an important part of the diet for various Indigenous groups that inhabited the northeastern rainforests (12, 64–66). Early Holocene cultivation practices have been inferred from the archaeological records of Papua New Guinea, including the introduction of bananas and other plants to the highlands (67). Though despite the extensive historical interchange between the two regions, including various Papuan pre-domesticated crop species, there is no archaeological or ethnographic evidence that these horticultural practices were

imported to northern Australia (13, 68). However, ethnographic sources indicate that intentional arboreal translocations were historically practiced by some Indigenous groups that fall within the study area in northern and eastern Australia (42, 44). Geographically adjacent to the study area, the Gidjingali people in Arnhem Land are known to have casually dispersed the seed of *Syzygium* and other fruit species in the midden-enriched soils of abandoned campsites, with the expectation that they would grow into fruit trees (68, 69). Casual broadcasting of seed is hypothesised to explain the conspicuous presence of woody vine scrub species on archaeologically recovered middens in the Cape York Peninsula (47) and *Erythrina vespertilio* (Bat's Wing Coral Tree) around wells in the Northern Territory (70).

However, on the whole, the ethnographic evidence for intentional propagule dispersal by Indigenous Peoples in Australia is patchy and most sources refer to grasses and tuberous plants (41), though early colonial references and contemporary Indigenous knowledge holders have cited seed dispersal of trees and shrubs in various parts of the continent (20, 55, 71). Additionally, a non-exhaustive search of the literature revealed multiple accounts of creation stories and other oral legends by contemporary Indigenous knowledge holders that hint at past intentional translocations (72, 73). While some have argued that these accounts should be seen as "spiritual propagation" rather than taken literally (27), a handful of Australian studies identified a correlation between Indigenous oral histories and ancient environmental events (74, 75). This suggests there is likely value in investigating ethnographic accounts of plant translocations with molecular data.

Retracing historical arboreal translocations with genomic data

Genomic methods can be used to reconstruct historical translocations and have been widely employed to investigate domestication processes and identify wild pre-domesticate populations, with significant discoveries in the diffusion history of some root-crops and cereals (for example, 74–78). Whether intended or not, anthropogenic translocation is a form of human-induced selection that alters the genotype frequencies within and between populations of a given species. Here, taking a limited sample of a population's genetic material will either result in founder effects (or bottlenecks) in a newly established population or admixture if combined with material from other genetically distinct populations (25). This leaves a genetic legacy of dispersal in populations that can be detected with molecular markers, and often regarded as incipient domestication (81).

As an emerging field of study, there are few examples in the literature that demonstrate how to employ molecular data to retrace past Indigenous dispersals of non-crop species (the exception of (26, 40, 42, 82, 83)). Although domestication is not the focus of this thesis, patterns observed in incipiently domesticated

tree species can provide an initial set of expectations on the potential genetic legacies of Indigenous translocations. Except in cases of interspecific hybridization and clonal propagation, selection through dispersal-induced admixture and bottlenecks are often more protracted in fruit and nut trees, owing to their generally long generation times (i.e., fewer generations of selection) and capacity for outcrossing with less selected individuals via faunal dispersal (53, 84, 85). This is particularly pertinent as gene flow between incipiently domesticated and wild populations often obscures the signal of human influence (86). Therefore, in the present study, it was anticipated that dispersal-limited species with larger seed would be more likely to exhibit genomic evidence of human influence.

A range of dispersion histories have been uncovered over the past decade, often contradicting previously held beliefs about the modes, antiquity and genetic legacies of Holocene translocations (for a review, see (86)). Recent SNP-based studies have revealed highly reticulate migration and admixture scenarios amongst pre- and partially-domesticated populations of various arboreal crop species (53, 87, 88), and overturned the assumed prevalence of bottlenecks in the early stages of domestication (86). It is now understood that human selection, including Indigenous silviculture practices, can yield variable impacts on the genetic diversity of managed plant populations (89–91). These discoveries provide incentive to expand our genotyping efforts in other poorly studied systems to better understand the full range of human influences.

In Chapter 3, I described and tested for broadly defined genetic patterns expected to arise from each translocation scenario, however the strength of these signals was expected to depend on the biogeographic history and overall genetic diversity of the study species. Previous molecular studies have demonstrated that even when there is robust biocultural evidence of translocation, it is difficult to detect low intensity anthropogenic dispersal signals in species that have weak population structure facilitated by natural dispersal (61, 92). In particular, the concurrent timing of human activity and climate warming in the Holocene presents a challenge to differentiate between the two drivers of vegetation shifts (93, 94). By contrast, semi-domesticated tree species like cacao (*Theobroma cacao*) and Brazil nut (*Bertholletia excelsa*) show population structure associated with Pleistocene climate refugium, enabling researchers to retrace the human-mediated migration of these distinct lineages (95, 96). This highlights the importance of carefully selecting a study system where non-anthropogenic modes of dispersal can be controlled or accounted for.

The culturally important rainforest food trees in eastern Australia present both a challenge and opportunity to broaden our understanding of the genomic signatures created from past anthropogenic

dispersals, and how it can be differentiated from non-anthropogenic dispersal. For instance, it is not evident from the archaeological record whether precolonial arboreal translocations were practiced over a sufficient timeframe or scale to produce clear patterns of reinforcement and admixture. However there are rich data on the phylogeographic patterns generated by climatic shifts and faunal dispersal for many rainforest species across the study area (97–101), and a clear relationship has been demonstrated between life history traits and the capacity for climate-induced dispersion (1, 101, 102). In this regard, unusual dispersal patterns putatively facilitated by human activity were expected to stand out.

Biocultural protocols and Indigenous Biocultural Knowledge

The research presented here affected and engaged Indigenous Peoples in numerous ways. First it focussed on tree species that are culturally significant to many Indigenous groups of the study area and required the collection of plant genetic material from Indigenous lands. Additionally, the questions and interpretations were partially based on knowledge provided by Indigenous Peoples. As this type of scholarship can run the risk of further entrenching colonial dispossession of Indigenous lands and cultures, the collaborators on this project deemed it essential to develop an ethical and culturally respectful framework for engaging Indigenous Peoples in our research (see Chapter 2 for details).

The term Indigenous Biocultural Knowledge (IBK) is used to refer to the body of knowledge that Indigenous Peoples have about the cultural connections between people and the biophysical world (103). In the words of Gerry Turpin, *Mbabaram* Traditional Owner and cultural advisor to this research project, IBK is ‘*knowledge that encompasses people, language and culture and their relationship to the environment*’ (103). IBK, also known as ‘Indigenous Ecological Knowledge’ (104) or ‘Traditional Ecological Knowledge’ (105), is handed down through the generations, and accumulates and evolves through socio-ecological adaptive processes (106). IBK that pertains to the use or dispersal of culturally significant trees is utilized throughout this thesis, to either develop anthropogenic dispersal hypotheses (Chapter 4), or to interpret genomic signals of dispersal (Chapter 5). Relevant IBK was either obtained through the literature or attributed to the work of project collaborator and Gangalidda man, Patrick Cooke. Chapter 2 describes the process by which Cooke obtained IBK, and the protocols we developed to engage with Indigenous Peoples and obtain plant genetic material from Indigenous lands.

Thesis aims and structure

The overarching aim of this thesis was to evaluate evidence of historical arboreal translocations by Indigenous Peoples in eastern Australia by studying the genomic patterns of two culturally significant tree species: *Araucaria bidwillii* (Bunya Pine) and *Castanospermum australe* (Black Bean). Retracing historical

propagule dispersal by Indigenous Peoples can yield insights into the long-term demographic and evolutionary impacts of plant translocations and may help raise awareness or potentially rediscover human histories and biocultural knowledge that has been disrupted by settler colonialism. I use the terms “human-mediated dispersal”, “anthropogenic dispersal” or “translocation” interchangeably. All terms refer to the movement of seed propagules by people, whether intentional or incidental.

Thesis structure

This thesis comprises six chapters, including the current introduction (Chapter 1) and a synthesis of the data (Chapter 6). Chapters 2-4 address the research objectives described above and have been prepared as a series of papers for publication. Chapter 5 is prepared as a data chapter and the research presented here is yet to be submitted for publication. I employed a multidisciplinary approach that primarily utilised genomic data to infer the dispersal history of the study species, and incorporated biocultural knowledge obtained from the literature or related ethnographic research conducted by collaborator Patrick Cooke. As this is a “thesis by publication”, there is some repetition in the introductions and methods between chapters. Each chapter is constructed in the format of a research paper, with a referencing system, writing style and structure following journal requirements. The division of labour regarding the data chapters is broken down in Table 1. Chapter 6 summarises the contribution of my research findings to the broader academic literature and discusses future directions.

My main objectives were to

- 1) Determine a protocol for collecting genomic material from culturally significant plant species with the consent of relevant Indigenous groups and in collaboration with Indigenous researchers.
- 2) Identify generic genomic signatures that can be created from anthropogenic dispersals, and in what contexts this can be differentiated from non-anthropogenic dispersal (such as dispersal by animals).
- 3) Integrate molecular data with ethnohistoric and biocultural information (where available) to test for genomic signatures of anthropogenic dispersal in Bunya Pine and Black Bean.

Objective 1 was addressed through collaboration with Indigenous student researcher Patrick Cooke and is outlined in Chapter 2. Using this research project on Indigenous plant translocations as a case study, Chapter 2 summarises the legal and customary protocols for conducting biocultural research (including

use of plant genetic material) with Indigenous Peoples and/or on Indigenous Country² in an Australian context. With Patrick Cooke as lead author, here I described my experiences as a non-Indigenous researcher in a cross-cultural space, to provide insights to other non-Indigenous researchers, and to contrast with the unique issues affecting Indigenous researchers.

Objective 2 was addressed in Chapter 3 and outlined a first-step genomic workflow that can be used to identify species with dispersal signatures that warrant an in-depth investigation of putative human influence. The chapter achieves this by testing four signals of dispersal with different results expected for three dispersal histories: (1) ongoing faunal dispersal, (2) post-megafauna isolation and (3) post-megafauna isolation followed by dispersal of putative human influence. I conceived of and produced this chapter with guidance from my supervisors.

Objective 3 was addressed in Chapters 4-5, each of which outlined a genomic investigation of species-specific anthropogenic dispersal hypotheses derived from biocultural evidence. Chapter 4 compared nuclear DNA patterns within and between disjunct distributions of Bunya Pine, with the expectation that anthropogenic dispersal was restricted to the southern range of the species. Chapter 5 combined nuclear and whole-plastid DNA to test for evidence of long-distance dispersal in Black Bean, with the expectation that Indigenous Peoples facilitated a southern range expansion. I conceived of and produced these chapters with guidance from my supervisors.

² Indigenous Peoples throughout Australia use the term Country to refer to their homelands. Country is multidimensional and not only refers to the land and its features, but all the organisms (including people) that inhabit it and the Dreaming stories that describe its origin and the connections between all beings (108). See Chapter 2 for a description of the meaning that Country holds for Indigenous Peoples in Australia.

Author contributions to data chapters

Table 1. Contribution of authors to each of the thesis data chapters.

Key to author initials: MF=Monica Fahey; PC=Patrick Cooke; EE=Emilie Ens; MR=Maurizio Rossetto; PAC=Phillip Clarke; MRa=Margaret Raven; GT=Gerry Turpin; AF=Andrew Ford; RK=Ray Kerkhove.

Data chapter	2	3	4	5
Conception and design	PC, EE	MF, MR	MF	MF
Planning and implementation	PC, MF, EE, GT, MRa	MF, MR	MF, EE	MF, EE
Data collection	PC, MF	AF, MF	MF, RK	MF, AF, MR, EE
Analysis and interpretation	PC, MF, EE	MF	MF	MF
Writing	PC, MF, EE, MRa, PAC, GT, MR	MF, MR, EE	MF, MR, EE, RK	MF, MR, EE
Overall responsibility	PC	MF	MF	MF

List of original publications

This thesis is partially based on the following original publications, which are referred to in the text by their order of appearance (Chapters 2-4).

Chapter 2 - Cooke P., Fahey M., Ens E. J., Raven M., Clarke P. A., Rossetto M., and Turpin G. (2022) Applying biocultural research protocols in ecology: Insider and outsider experiences from Australia. *Ecological Management & Restoration*, 23 (81): 64-74. doi:10.1111/emr.12545.

Chapter 3 - Fahey M., Rossetto M., Ens E. J., and Ford A. (2022) Genomic screening to identify food trees potentially dispersed by precolonial Indigenous Peoples. *Genes*, 13(3): 476. doi:10.3390/genes13030476.

Chapter 4 - Fahey M., Rossetto M., Ens E. J., and Kerkhove R. (submitted) *Araucaria bidwillii* (Araucariaceae) genomics suggest Indigenous Peoples adapted plant translocation practices under settler colonialism. *Proceedings of the National Academy of Sciences*.

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Chapter 2. Applying biocultural research protocols in ecology: insider and outsider experiences from Australia

Summary

Collaborations between Indigenous and non-Indigenous scientific researchers are increasingly mandated by global to local conservation policy and research ethics guidelines. Break downs occur due to misunderstandings around expected protocols of engagement and cooperation, which are compounded by lack of broader awareness of differences in cultural values, priorities and knowledge systems. Using first hand experiences, we outline eight key protocol and guidelines that researchers should consider when undertaking research with Indigenous peoples, or on Indigenous Country, through exploration of biocultural protocols and guidelines within Australian and Indigenous Custsomy laws. We use the onion as a metaphor to highlight the layers of protocols and guidelines that researchers can peel back to guide their research from international to local scales with ethics around the research question at the core. This paper draws on the perspectives and experiences of an Indigenous researcher (as “insider”/“outsider”) and non-Indigenous researcher (“outsider”), working on a cross-cultural and multidisciplinary investigation of past Aboriginal dispersal of rainforest trees.

Introduction

The surge of ecologists embracing work with Indigenous peoples is important for ethical and sustainable approaches to conservation (Pierotti, 2000; Usher, 2000; Berkes, 1993; Horstman and Wightman 2001; Clarke 2008; Walsh et al. 2013; Ens et al. 2015). We have previously found that non-Indigenous ecologists often lack awareness or empathy towards the social dynamics and cultural governance structures that must be followed to work with Indigenous communities in a respectful and collaborative way (Smith 1999; Christie 2008; Kwaymullina 2016). Equally, research teams may not be cognizant of the unique cultural complexities that Indigenous researchers face when working with other Indigenous peoples as both an “insider” (close familial ties) and “outsider” (institutional connection) (Smith 1999; Kwaymullina 2016; Dew et al. 2019). The cultural obligations that an Indigenous researcher must fulfil are more ambiguous than the expected ethical obligations of a non-Indigenous researcher. Indigenous researchers often have their own framework or set of guiding principles, driven by cultural and social welfare expectations, while working within Indigenous groups and communities; however, in our experiences the objectives of Indigenous-led research and the role of researchers is not often explicit enough in Indigenous engagement strategies. A notable exception was developed by Darlene Oxenham, who produced a set of protocols for Curtin University in Western Australia that, clearly highlighted the roles

and processes for researchers from both Indigenous and non-Indigenous backgrounds, who were undertaking research with Aboriginal and Torres Strait Islander people and communities (Oxenham, 1999).

Under international law, Indigenous people have a right to be negotiated with when ecologists (Indigenous or non-Indigenous) are researching Indigenous people, their knowledge or on any aspect involving their Indigenous ancestral estates (Davies et al. 2004; United Nations 2007; AIATSIS 2020). Many researchers do not recognise that for many contemporary Indigenous peoples, all of Australia is morally Aboriginal land, because of the early European indoctrination of the fallacy of *Terra Nullius*. It is not apparent to many non-Indigenous Australians that they need to consult or negotiate with Indigenous People. At a minimum, some researchers believe that they only need to engage with Indigenous people while actually on declared Aboriginal land under Australian legislation.

Despite the fact that many Indigenous groups aspire to work with ecologists, some non-Indigenous researchers have stated that it is too hard to work with Indigenous people or if they have tried it once, and had a bad experience, they will not do it again (Roughley and Williams 2007). This paper aims to raise awareness of the expectations that Indigenous Australians have of researchers and how these expectations and preferred ways can be navigated to facilitate effective and mutually beneficial research, alongside adherence to mandated protocols and institutional guidelines. Kwaymullina (2016) outlined three essential considerations that non-Indigenous researchers must consider before initiating Indigenous research: 1. should it be conducted at all and what is its relevance to the community or individuals being researched?; 2. researcher positionality, where researchers position themselves within the research from a bias or non-biased framework; and 3. ethical principles of free and prior informed consent and intellectual property rights (Walsh and Mitchell 2002). To work effectively, ecologists also need to understand the spiritual, familial, cosmological meanings behind Country from an Indigenous perspective (Kwaymullina 2005; Kingsley et al. 2013; Maclean et al. 2013).

Tuhiwai Smith (1999), in her book, *Decolonizing Methodologies: Research and Indigenous Peoples*, provided a perspective of “insider” and “outsider” researcher roles. An “insider” is described as someone who is perceived as coming from within the studied community, and an “outsider” as someone who originates from outside the community and whose interests are largely external to that of the Indigenous community. These positions require different practices and behaviours to be performed based on existing relationships and connections the researcher has with communities. They offer a more nuanced approach to research that, appreciates that Indigenous people can also be researchers of their own communities.

Researchers must take into consideration the social dynamics and cultural governance structures of Indigenous communities to be able to work in a respectful and collaborative way (Christie 2008).

What are cultural protocols?

For Indigenous people, protocols may be considered as guiding principles that set out a way for non-Indigenous people to conduct business or research with other Indigenous peoples and on Country (Piquemal 2000). As Swiderska (2012) stated, biocultural community protocols are: 'Charters of rules and responsibilities in which communities set out their customary rights, values and worldviews relating to biocultural resources, natural resources and land, as recognised in customary, national and international laws'. Perhaps spurred on by the United Nations Convention on Biological Diversity Nagoya Protocols, Indigenous people are developing and designing biocultural protocols for setting the parameters for those who aspire to do 'business' with other Indigenous people and on Indigenous Country (Bavikatte and Robinson 2011; Hill et al. 2011; Kohli et al. 2012; Ens et al. 2015; Pert et al. 2015).

Additionally, in Australia, Indigenous Protected Areas, 'Healthy Country' plans and Traditional Use of Marine Resources Agreements (TUMRAs) are all part of the bigger picture for gaining cultural authority in research. While general protocols for cross-cultural collaborations exist in Australia (Byrne et al. 2005; Janke 2009; Janke et al. 2009; AIATSIS 2020; Moggridge 2020), clear step-by-step processes designed to guide Australian ecologists and their navigation of both institutional and Indigenous protocols are lacking. Within a local framework Indigenous organisations, however corporations and community groups are developing steps forward for collaborative research, as exemplified by CSIRO and NAILSMA's *Our Knowledge Our Way in Caring for Country* (Woodward et al. 2020).

When conducting research with Indigenous people the researcher initially requires an understanding of the local community protocols and, if formal corporations or organisations are established, then of the locally defined Indigenous Terms of Reference and associated frameworks. It is essential for researchers to explore and unpack the layers of protocols and guidelines relevant to their research field and the location/s of study to ensure best practice ethical research and to reduce the potential for unintended impacts on the community, organisation or researchers themselves (AIATSIS 2020).

First Nations Peoples understanding of Country

For Australian Indigenous peoples, Country is the basis behind everything. 'Country is family, culture, identity, Country is self' (Kwaymullina 2005). As Aboriginal elder Duncan McInnis stated: 'Culture is everywhere. Culture is situated in the Land and on the Country, in our rivers and sea, and within our

people, it is everywhere'. Country builds your culture, your belief systems, your lore's and songs; it maintains life through hunting and gathering (Rose et al. 2002; Kwaymullina 2005; Dietsch et al. 2011).

The emotions attached to the term Country (Stanner 1965; Davies et al. 2013), from Indigenous peoples' perspectives, are hard to comprehend from a non-Indigenous perspective. From a non-Indigenous standpoint, Country is primarily bought or sold; it is a commodity (Langton 2020). While non-Indigenous families have responsibility to maintain and look after the land, that they have "bought" or "rented", Indigenous peoples have ties to land that are thousands of years old with clan-based rights inscribed through kinship systems and spiritual connections (Graham 1999; Kwaymullina and Kwaymullina 2010). European settlers have only been in Australia for 232 years and do not have the depth of ancestral and cultural connection to Country as Indigenous peoples do. Indigenous peoples have lived in Australia for over 50,000 years (Broome 1994; Tobler et al. 2017), or from time immemorial as Indigenous peoples believe (Perry 2010). They have survived and adapted to the shifting of land masses, rising and falling of seas, climate change, fire, arrival of exotic plants and animals, and many other landscape influences. During this time, the Aboriginal custodians worked and lived well off natural and cultural resources (Kingsley et al. 2013). Now, Indigenous peoples emphasise that Country is sick and it is telling us how sick it is (Morgan et al. 2010).

First Nations people are striving to maintain their rights to ancestral clan estates (their Country) through Land Rights acts, the national *Native Title Act 1993*, and Indigenous customary law (McCorquodale and John 1987; Altman et al. 2006; Davis 2008). As stated by Kwaymullina and Kwaymullina (2010) "[Aboriginal] Law flows from the living hearts of Aboriginal countries, and in this sense, is location specific. The purpose of Aboriginal legal systems is to sustain the pattern of creation". In contemporary Aboriginal societies, Aboriginal Law and spirituality has been challenged by non-Indigenous people and due to the pervasive impacts of colonisation and assimilation, there are a range of feelings about what Country means for different contemporary Indigenous peoples (Morgan et al. 2010).

Beyond cultural awareness, towards mutual benefits of ecological research

Much has been written about the need for greater Indigenous cultural awareness (Bean et al. 2006; Parmenter and Trigger 2018), Indigenous intellectual property and knowledge rights (Janke 2009; Janke et al. 2009), cultural connectivity (Rose 2001, Rose and Robin 2004) and Indigenous research methodologies (Smith 1999; Kwaymullina 2016). The disciplines of health, education and law are now routinely embracing cultural protocols (Dunstan 2019). These disciplines, however, are physically 'detached' from the biophysical aspects of Country. The cultural awareness requirements in the scientific disciplines of

ecology, biology or natural resource management demand greater awareness of the linked biological and cultural protocols that are required for respectful access and interaction with Country, as well as greater acceptance of Indigenous cosmologies, ontologies and epistemologies (ways of knowing and doing). Menzies (2001) described the need for respectful Indigenous research protocols that emphasise the rights, responsibilities and obligations of research partners. Perhaps even more important is co-design, which incorporates “the right” research questions, goals and planned outcomes that align with Indigenous research methodologies, reciprocity and ensuring that benefits flow back to Indigenous peoples who provide valuable knowledge and time to research projects (Smith 1999; Clarke 2008; Kwaymullina 2016). Best practice guidelines for work with Indigenous people advocate for transparency and agreed benefits that should be received by all parties (Carter 2010; Kamau et al. 2010; AIATSIS 2012; Trigger et al. 2014; AIATSIS 2020; Woodward et al. 2020).

There is much important ecological research taking place, and scientists are increasingly working to integrate different scientific pursuits that include Indigenous knowledge and peoples (see for example those reviewed by Ens et al. (2015)). To move forward, the fields of ecology and biology will benefit from the clarification of effective cross-cultural research approaches, including advancement of Indigenous led research. This paper unpacks the layers of cultural and institutional protocols for Indigenous biocultural research and demonstrate application of these protocols from an “insider” and “outsider” perspective.

Methods

In order to unpack the biocultural guidelines, laws and protocols required to conduct respectful ecological research with Indigenous groups, this paper draws on the experiences of a multidisciplinary and multi-institutional project, ‘Retracing the dispersal of rainforest food trees by pre-colonial Aboriginal Australians’, which was funded by the Australian Research Council Discovery Project scheme (2018-2021). Funded were two PhD students: Patrick Cooke an Indigenous (Gungalida) man focused on collating historical and ethnographic biocultural data from an “insider”/ “outsider” perspective; and Monica Fahey, a non-Indigenous female researcher investigating plant genetic data. The PhD students are the lead authors of this paper. The research team worked with east coast Australian Aboriginal groups from northern New South Wales to Cape York Peninsula, which forms the study region of the present paper. This project crosses 19 Australian Indigenous language groups (Figure 1).

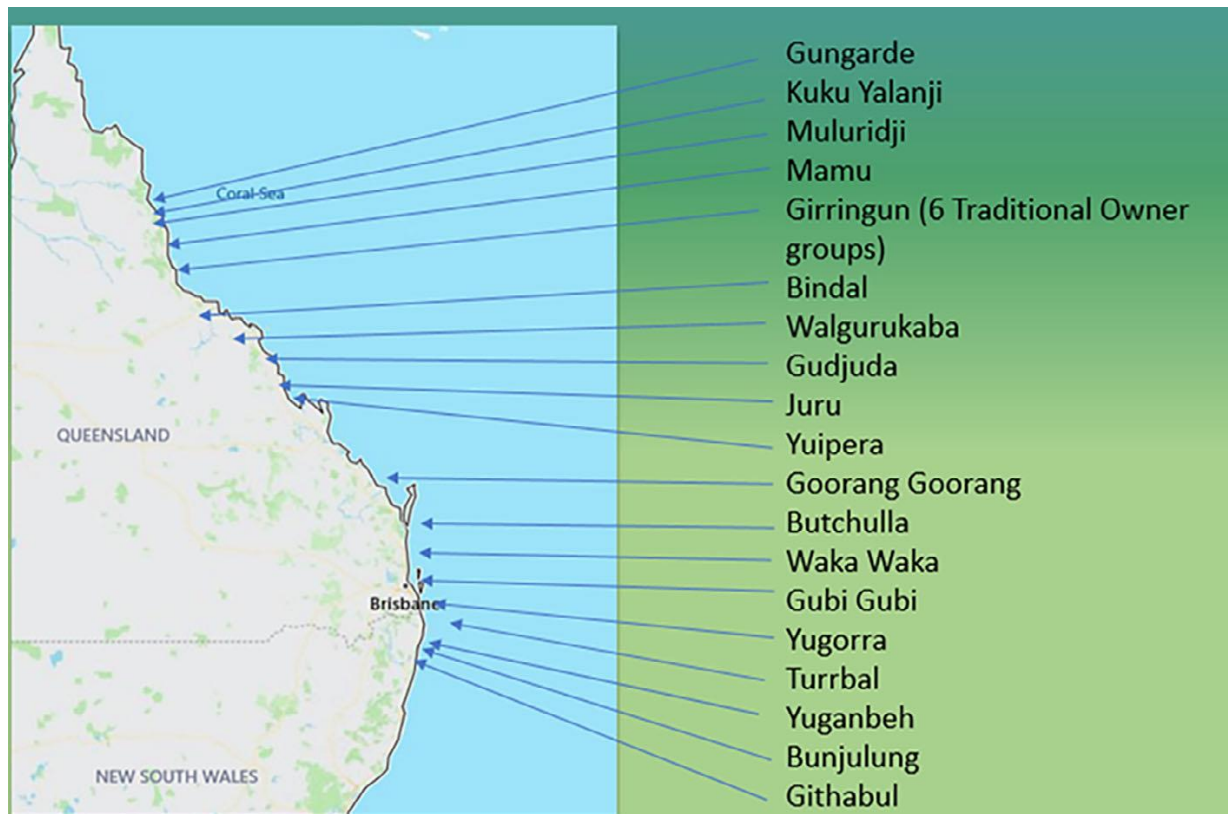


Figure 1. Indigenous groups relevant to this project (Map produced by P. Cooke).

The ‘Retracing the dispersal of rainforest food trees by pre-colonial Aboriginal Australians’ project aimed to 1. investigate evidence for pre-colonial human dispersal of rainforest trees using multidisciplinary methods; and 2. develop an ethical and culturally sensitive research protocol for working with Traditional Owners (TOs).

Familising ourselves with guidelines, law and protocols

Prior to initiating the project, Cooke and Fahey explored the Research Questions (Layer 8, Fig 2) and researched international, national and state guidelines, law and protocols - including those specific to their research institution (Layers 1-4; Fig 2) (Macquarie University, Human Research Ethics)), as directed by the *National Statement on Ethical Conduct in Human Research* (2007) and *AIATSIS Guidelines for Ethical Research in Australian Indigenous Studies* (AIATSIS 2020).

We developed a conceptual model based on the ‘onion’ as a metaphor (see Fang 2005; Kristensen 2018), to help unpack and apply information from these protocols, laws and guidelines in our research. We explored biocultural protocols from a range of sources, including, legislation, guidelines, informal protocols, and local customary engagement practices. In the Australian research context, we identified

Table 1. Layers of Biocultural guidelines, law and protocols requiring consideration when working with Indigenous people and Country in Australian ecology.

Layer	Examples
1	International
2	National
3	State
4	Institutions
5	Community Organisations/ groups
6	Participants
7	Researcher
8	Research Question

Researcher perspectives: as method

This paper discusses and develops a biocultural protocol framework from three perspectives drawn from Smith (2012):

- (1) An Indigenous “insider” perspective of Cooke: an Indigenous person who has pre-existing relationships and understandings of Indigenous Peoples, Country and lore.
- (2) An Indigenous “outsider” perspective of Cooke: an Indigenous researcher without a previous long-term connection to Indigenous peoples, Country and lore.
- (3) An non-Indigenous “outsider” perspective of Fahey: a non-Indigenous person without previous long-term or short-term connections to Indigenous peoples, Country and lore.

Below we describe how researchers from each of these perspectives established research collaborations with two different Aboriginal groups (Mamu and Githabul), with reference to the protocols framework (Fig 2; Table 1). Note that here we only describe how the researchers established the collaboration, and not the entire research process.

Results

Perspective 1: Indigenous “insider” research with Mamu

Following identification of the research questions and a literature review of existing research to understand the layers of protocols (Figure 2, Table 1), Indigenous researcher Cooke commenced establishing the research partnership with a known Indigenous group, the Mamu, invoking personal and participant protocols (Layers 6, 7 Fig 2, Table 1). First, he made contact with a recognised Elder (Yarning, Fig 3a) over the phone. The conversation followed a culturally respectful approach by firstly re-establishing previous connections and making time to have a ‘yarn’ (i.e., less formal talk – see Bessarab and Ng’andu 2010) in order to exchange information on each other’s family and personal life. After this, Cooke asked about the best time to meet face to face. Later yarning took place at the Elder’s home, where the two had a cup of tea and discussed life in general, and after this they got down to business and discussed the research. During this discussion the Elder conveyed the importance of Country, being on Country and how research can affect what happens on Country and the importance of doing research well on Country. From this informal yarning around participant and researcher protocols, it was decided to progress conversations with the Chief Executive Officer (CEO) of the local Indigenous group’s Prescribed Body Corporate (PBC) (Office-yarning, Fig 3a) to organise a meeting on Country (on-Country trip, Fig 3a).

The CEO had organised through their TO constituents, that included Elders, the board of directors, rangers, board members and workers of the corporation, to meet with Cooke and the research team on Country (on-Country trip, Fig 3a). Upon arrival on country there was a quick ‘meet and greet’, and while lunch was being prepared the group did a bit of yarning around a cup of tea and the sharing of food as an “ice-breaker”. After lunch, the TOs formally welcomed the group to Country, followed by self-introductions about who we were, where we came from, what work we do and then an explanation of the research (Layers 6, 7 Fig 2, Table 1). This was conducted so that the individuals could fit everyone into their worldviews and develop understandings and expectations of future behaviours.

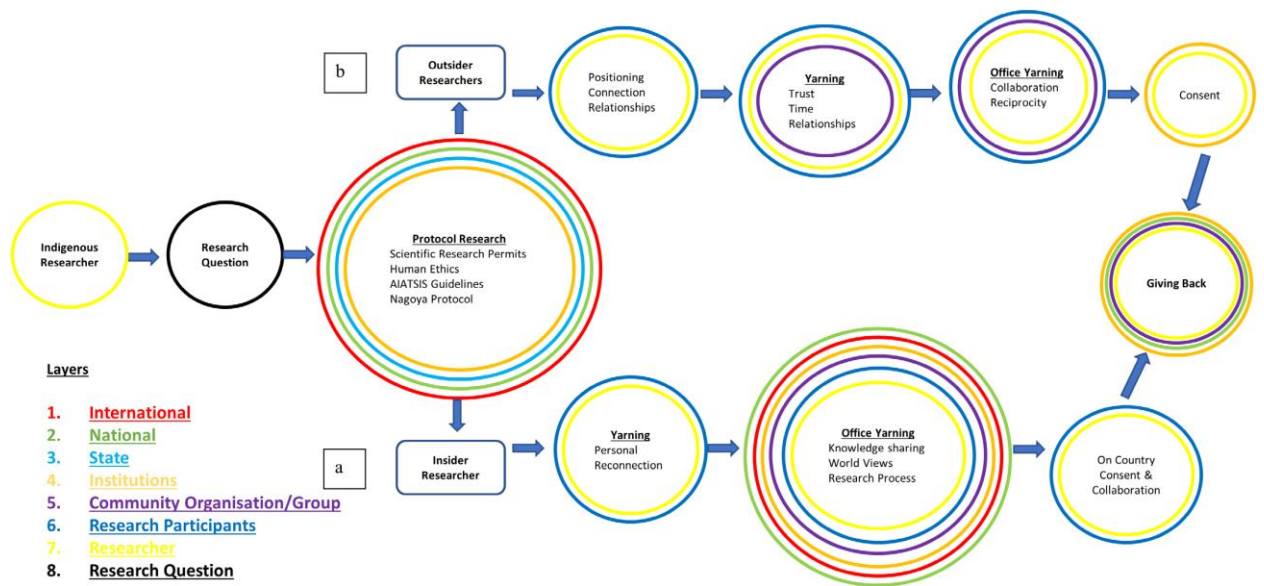


Figure 3. Multiple layers of cultural protocol during the establishment phase of the ‘Retracing the dispersal of rainforest food trees by pre-colonial Aboriginal Australians’ project according to the Indigenous “insider (a)” and “outsider (b)”.

As part of doing business on Country (On-Country, Fig 3a), Cooke talked to the TOs about ethical protocols relevant to the research question, including the need for prior informed consent forms (Layers 1-7 Fig 2, Table 1). Time was given for the TOs to consider and to ask questions around the project and processes, being mindful not to pressure anyone into signing straight away. Once participants were given time to consider whether to sign the prior informed consent forms, which was done, the group was happy to start sharing some of their knowledge by giving examples of the significance of the trees and the importance of preserving these sites for future generations.

After the initial meeting and recording of preliminary information, Cooke established further meetings with the CEO and Elders in order to provide them with a field report of the previous meeting, including photos (Giving back, Fig 3a). Further to this, Cooke offered his research skills to the group to facilitate a reciprocity process. From these discussions, Cooke was asked to assist in the development of a draft research agreement for the corporation. This should have long term benefits by enabling negotiations with institutions or government departments regarding research on their Country. This giving back process invoked national to institutional, organisational and researcher protocols (Layers 2, 4, 5 and 7 Fig 2, Table 1).

Perspective 2: Indigenous “outsider” research with the Githabul

As a Gungalida man and an Indigenous Researcher who had not worked with the Githabul or on their Country, Cooke was first required to conduct background research on the group and determine whether

he could be connected to the community (Positioning, Fig 3b). This process invoked personal and research participant protocols (Layers 6, 7 Fig 2, Table 1).

Following the desktop analysis of the group on the internet, Cooke made phone calls and sent emails to the organisation with initially mixed success in establishing contact. Through his connections he heard that there was a public event (Bunya Festival) where a Githabul TO was doing a welcome to Country. Cooke attended the festival and waited until after the TO had finished his welcome to Country speech. He then approached him personally to introduce himself and have a yarn over a cup of tea (Yarning, Fig 3b). This yarn was about positioning himself and connecting to the Elder's worldview (Bessarab and Ng'andu 2010). Once the Elder had placed him in his worldview the Elder acted as a cultural broker and set about introducing Cooke to other members of his group who were prominent figures in the community and who had deep and intimate knowledge of their Country. It turned out that these community members were Githabul Rangers and were happy to exchange numbers and emails for Cooke to visit their Country.

Allowing time to yarn and build relationships and trust through continual phone calls and a face-to-face catchup resulted in Cooke being invited to go on Githabul Country and experience first-hand the importance of what their Country meant to them (Geia et al. 2013). Upon arrival on Githabul Country, Cooke arranged to meet face to face with the rangers, who then introduced him to their CEO who was another Githabul Elder (Office Yarning, Fig 3b). After yarning with him around the project and having a personal introduction, he gave permission for the rangers to show Cooke around their Country and to introduce him to other Elders within the community.

To build trust and integrity within the community, it took Cooke three visits to be able to undertake interviews with key knowledge holders. Once the trust was gained, Cooke talked with participants to see who was willing to participate in the research, as some people had the knowledge but did not want to openly share it. This process of voluntary participation in research is integral to the national and institutional prior informed consent process of ethical Human Research (Layers 2, 3 Fig 2, Table 1).

Once Cooke had established who would be a willing participant, he then talked through the process of how the interviews would be conducted and mentioned that he would need their signed consent forms to participate in the research. He further explained the importance of the consent forms, not only from the institutional perspective around the intellectual knowledge protection and ethical guidelines, butfor

giving participants the opportunity to voice their intent to protect certain knowledge and to determine who was allowed to access this information in the future through the research project.

After being on Country, yarning, spending time sitting and listening with individuals and groups, and gaining consent to conduct the research, Cooke offered his services to the CEO (Giving back, Fig 3b), invoking institutional and research protocols (protocols 3, 7; Fig 2, Table 1) of reciprocity. This demonstrated that Cooke wanted to share his skills with the community, as they had shared so much with him. From these conversations with the CEO, Cooke was asked to develop a draft community market garden program and a draft Junior Ranger program as a way of giving back to the community.

Perspective 3: Non-Indigenous researcher with Mamu and Githabul

In this case study (Fig 4), researcher Fahey outlines how she applied biocultural protocols to her research as a non-Indigenous person working with Mamu and Githabul people, as well as with Indigenous researcher Cooke. After the process of a literature review, exploration of the research question and consultation with the project research team, Fahey worked with project Indigenous cultural brokers and decided on a procedure of: first, meeting with research participants; second sending a formal project invitation letter to the board of each study group; and third, if the board accepted the invitation, she would send a written agreement for consent to obtain and analyse genetic data of culturally significant trees. This process aligned with the Institutional and community organisation's researcher protocols (Layers 4, 5, 7; Fig 4, Table 1). In order to be as inclusive as possible, Fahey sought out both unaligned TOs as well as PBCs to conduct fieldwork.

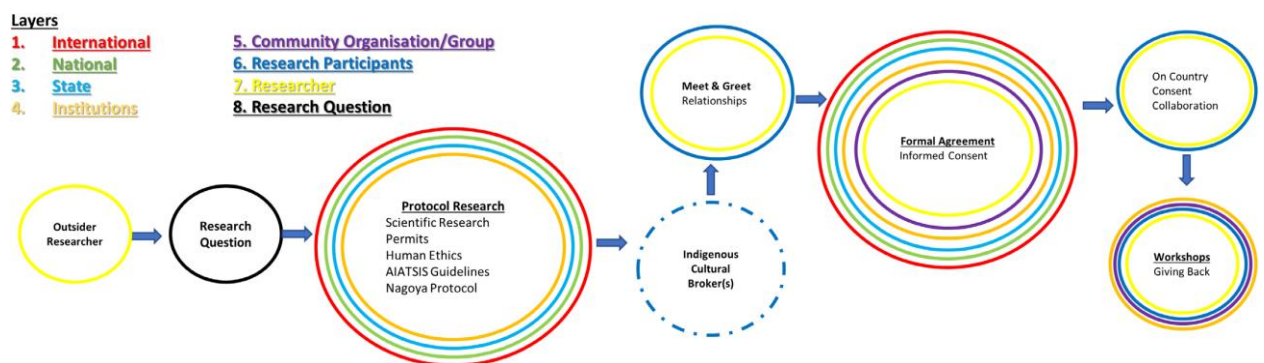


Figure 4. Application of biocultural protocols during the initial phase of the rainforest dispersal project by a non-Indigenous “outsider” researcher.

Fahey's PhD research focused on genotyping culturally-significant rainforest trees. For genetic research involving Indigenous People, Knowledge and Country, there is an obligation for researchers to comply with international and Australian protocols (Layer 1 and 3, Fig 2, Table 1). Fahey drafted a written agreement with Indigenous cultural broker (project team member/co-author), Gerry Turpin, with the intention to obtain permission from PBCs to collect genetic material from their native title determination areas. This agreement is in line with the international *Nagoya Protocol* (Layer 1; Figure 2, Table 1) and served to: first, provide evidence that permission was obtained from TOs to collect plant genetic material; second to hold the researcher to account; and third, help the PBC with their own internal accountability in terms of approving activities on Country. The agreement stipulated the conditions under which the genetic material would be used and the terms to be negotiated by the PBC before signing. For transparency, unaligned TOs were made aware of the agreement with the PBC, though written permission was not sought from such individuals.

Following this process with, Fahey, and the initial contact with Githabul as described above by Cooke, feedback was sought from the Githabul Rangers on how best to draft a locally meaningful project information sheet. The project information sheet is an important communication tool, as it can be passed between interested parties and allows research participants to revisit the project concept. As research participants sometimes express fears and misconceptions that genetic data can be exploited for commercial uses, the information sheet needed to explain that the data are not sufficient to allow for any genetic engineering or other biotechnical applications. Fahey followed the standard procedures to apply for permits to collect plant genetic material from protected reserves across the study sites as managed by the Queensland and New South Wales governments (Layer 3, Figure 4). Fahey also sought human ethics approval through Macquarie University in order to conduct research activities associated with the project (Layer 4; Figure 4).

Prior to fieldwork, Fahey and the research project team discussed the cultural protocol and ethical sensitivities of the project. Fahey articulated the Indigenous researcher's particular perspectives and preferred approaches to the project as Aboriginal knowledge custodians and cultural brokers. For instance, Cooke's family could be affected if an unresolved conflict were to arise during fieldwork in the area that they live. Fahey found value in spending a couple of days outside of the office to contemplate and discuss these issues, and without the pressures of trying to achieve objectives such as collecting samples.

It was important for Fahey to collaboratively develop an ethical protocol for consent agreements, as she and Cooke initially had differing expectations on what and when written permission should be obtained. They also had separate ideas on what the most 'sensitive' aspect of the research was: taking genetic samples of culturally-significant trees versus recording the associated biocultural knowledge. These discussions were highly valuable for Fahey and informed development of a respectful research protocol that aligned with the values of both researchers (Layer 7, Figure 4).

The first fieldtrip to each collection location was scheduled as a 'meet and greet' (Layers 5-6, Fig 4) with the local ranger group (Githabul) or PBC (Mamu) and this was brokered by Cooke. The aim of these trips was to establish relationships before signing a formal consent agreement. A flexible agenda for these trips allowed time for the Githabul Rangers to build trust before taking researchers out on Country. On the last day of the trip, Fahey was invited to a big cook-up. This helped to break down some of the barriers with people who had expressed a general mistrust of researchers. This experience allowed time for the participants to air grievances about past research projects and this gave Fahey the opportunity to demonstrate her willingness to listen to these critiques, which in turn, helped build trust (Baskin 2005). The 'meet and greet' also provided opportunities to further discuss the aims of the project and nature of the genetic data. Fahey found that this eased the concerns of some participants who saw risks associated with genotyping culturally-significant trees. It also allowed for participants to raise hypotheses that they hoped the genetic data could investigate, and thus fostered a more collaborative and reciprocal relationship (Layers 5-7, Fig 4). To further cultivate collaboration and reciprocity, participants were invited to further contribute to the research through participation in conference presentations and cultural/scientific skill sharing workshops. The degree of interest in socialising and engaging in the project varied between groups, as not all groups were willing to discuss intellectual property and only wanted a certain degree of familiarity with the non-Indigenous "outsider" researcher.

Discussion

New biocultural protocol framework

This paper identified eight layers of biocultural guidelines, law and protocols relevant to ecological research in Australia. International, national and to some extent state bodies have developed directives that benchmark 'best practice' research in cross-cultural and Indigenous research. These policy directives, in tandem with more localised and institutional priorities and processes as well as personal and specific research question ethics, can be used to guide biocultural research projects.

Nations have a responsibility to respond to international directives, although progress in Australia has been slow, as evidenced by the delayed ratification of the Nagoya Protocol and UN Declaration on the Rights of Indigenous People. As outlined here in “the onion” metaphorical layering of protocols (Fig 2) and application of this schema from Indigenous insider and outsider perspectives (Fig 3 and 4), national and international protocols offer a starting point for non-Indigenous and Indigenous researchers working together in cross-cultural spaces. Personal values from the researcher and research participants also come into effect and can influence how ethical the process of Indigenous engagement might be. The addition of personal ethics into the biocultural protocols framework presented here is unique; however, is at the core of effective engagement from our perspective.

The multiple perspectives we presented in the case studies demonstrate the existence of core values and previous relationships (or lack thereof) that can benefit effective research in Indigenous spaces. The way in which protocols are applied will differ, depending on whether the researcher is Indigenous or non-Indigenous, and an insider or outsider. Non-Indigenous researchers who are “outsiders” need to build their capacity for understanding Indigenous knowledge epistemologies and Indigenous cultural Lore, while recognising responsibilities and demonstrating flexibility in their approaches to allow for Indigenous ways of knowing and doing. This can be facilitated by cultural brokers who are individuals with working knowledge of the local community dynamics and are willing to guide others while undertaking research on Indigenous peoples lands (Michielil 2003; Maru and Davies 2011). In the non-Indigenous “outsider” case study presented here, a cultural broker played a pivotal role in breaking down the barriers for the non-Indigenous researcher, enabling progression to the next stage of research and meet ‘face to face’ with members of the local communities.

Central to establishing the research from both perspectives was the importance of allowing for time, gaining prior informed consent and establishing reciprocity (Ens et al. 2012; Preuss and Dixon 2012; AIATSIS 2020). We share the view with other cross-cultural researchers, that these core values need to be taken into consideration in the development of a “personal protocol” of researchers if they are to develop sustainable working relationships with Indigenous research partners (Pretty and Smith 2004; Maru and Davies 2011; Holmes and Jampijinpa 2013). Both researchers explicitly deployed reciprocity at several points of the research project, and extended this by offering assistance with tasks outside the scope of the project.

The case studies also highlight that application of the different layers of biocultural protocols does not need to proceed in a linear order, and researchers moved back and forward between them. It was like

peeling back the layers of a 'onion', and yes it will make you cry, but what it does do is meaningfully embed the researcher within the research in a culturally appropriate way, according to both Western and Indigenous Law/Lore. In the inner layers, the framework needs to be flexible so researchers and participants both have opportunities to stop and reflect and draw in information from different layers as required. Essential to effective deployment of this process is communication between all parties. Communication is critical as this forms part of relationship building and making time to work with participants helps build rapport and trust in moving forward with the research.

Moving towards culturally respectful ecological research

As this paper demonstrates, one approach is unlikely to fit all stakeholder needs and must therefore be tailored to the specific research questions, researcher and context. Different stakeholders have different perspectives and aspirations that may result in vastly different expectations of knowledge sharing, collaboration and consent. We found in our research that 'yarning' in order to establish trust on a personal level needed to precede the development of formal agreements we had with the two Indigenous groups.

Currently, it is generally up to the goodwill of researchers to follow through to ensure there are benefits to Indigenous research participants (see Goolmeer *et al.* this issue). There are no enforced consequences for not following legal protocol, for example by-passing consent to enter or remove biological material from Indigenous managed lands. However, there are increasing calls from Indigenous leaders for enforceable protocols for work on Indigenous land, with Indigenous people and with Indigenous knowledge (Goolmeer *et al.* this issue).

Currently, Indigenous representation in academia is low, so it may not always be possible to have "Indigenous-led" research, as is recommended by AIATSIS (2020). It is therefore important for non-Indigenous researchers to think about whether the research question is appropriate after consulting with Indigenous research participants or Elders/leaders in the community even before research starts and then assess whether it will be beneficial to participants or the community (Kwaymullina 2016). Ideally the research should reflect Indigenous values and aid Indigenous researchers and participants in asserting the right to self-representation, self-definition, self-identification and self-determination. Development of mutually beneficial research when working with Indigenous people, knowledge and Country is imperative.

Importantly, we also argue that researchers need to assess their own individual protocols and ethics. This is best done in collaboration with the Indigenous peoples that researchers desire to work with so all parties can gain an understanding of the dynamics of the layers of protocols they work in, akin to the “shared learning” or “learning by doing” philosophies of community development (Borrini-Feyerabend et al. 2004).

As more Indigenous research moves toward being Indigenous-led, a lesson learnt from this research was that although the Indigenous “outsider” perspective benefited from having strong awareness of Customary law, cultural protocols and indirect connections and was somewhat absolved of the personal relationship accountability of the “insider”, there was still the need to take extra precautions to prevent indirect personal and professional risks associated with doing research with “other” Indigenous groups. The experiences outlined in this paper indicate that Indigenous researchers are highly valuable, if not essential, for cross-cultural ecology, although they carry additional social obligations when working with their own and other communities. Research teams need to support or allow space for Indigenous researchers to navigate such challenges and remain flexible to allow for alternative ways of doing and knowing throughout ecological research projects that aspire to empower Indigenous people, knowledge and Country.

Conclusion

Biocultural protocols are an important means for Indigenous communities to uphold governance structures while adhering to international and national legal requirements, institutional ethical guidelines and local customary practices. Given the diversity of Indigenous cultures and the different government and institutional legal systems, navigating these layers of protocols in ecological research can be overwhelmingly complex, sitespecific and highly dependant upon whether the researcher operates from an Indigenous, non-Indigenous, “insider” or “outsider” perspective. Ecologists who wish to engage in cross-cultural research will benefit from exploring the layers of biocultural protocols relevant to the research question, research location and the Traditional Owner group(s), while reflecting on their own ethical processes and those incumbent to their organisation.

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Chapter 3. Genomic Screening to Identify Food Trees Potentially Dispersed by Precolonial Indigenous Peoples

Abstract

Over millennia, Indigenous peoples have dispersed the propagules of non-crop plants through trade, seasonal migration or attending ceremonies; and potentially increased the geographic range or abundance of many food species around the world. Genomic data can be used to reconstruct these histories. However, it can be difficult to disentangle anthropogenic from non-anthropogenic dispersal in long-lived non-crop species. We developed a genomic workflow that can be used to screen out species that show patterns consistent with faunal dispersal or long-term isolation and identify species that carry dispersal signals of putative human influence. We used genotyping-by-sequencing (DARTseq) and whole-plastid sequencing (SKIMseq) to identify nuclear and chloroplast Single Nucleotide Polymorphisms in east Australian rainforest trees (4 families, 7 genera, 15 species) with large (>30 mm) or small (<30 mm) edible fruit, either with or without a known history of use by Indigenous peoples. We employed standard population genetic analyses to test for four signals of dispersal using a limited and opportunistically acquired sample scheme. We expected different patterns for species that fall into one of three broadly described dispersal histories: (1) ongoing faunal dispersal, (2) post-megafauna isolation and (3) post-megafauna isolation followed by dispersal of putative human influence. We identified five large-fruited species that displayed strong population structure combined with signals of dispersal. We propose coalescent methods to investigate whether these genomic signals can be attributed to post-megafauna isolation and dispersal by Indigenous peoples.

Introduction

Historical plant dispersal by Indigenous peoples has been recorded in many parts of the world and there is a growing recognition that ancient Indigenous populations had a significant influence on the composition and distribution of ecosystems [1–8]. However, the literature is sparse, due to a lack of published research, loss of cultural knowledge following colonisation, or because historical and academic observations have been blind to the diversity of Indigenous planting practices [9–11]. Contemporary Indigenous knowledge holders and colonial-era observations indicate that Indigenous groups from around the world have cultivated, traded and dispersed useful or culturally-significant plants across the landscape [10,12–17]. Whether intentional or incidental, these plant translocation events would have expanded the abundance and geographic range of many species, and many populations of so-called “wild” species are therefore likely to represent living cultural artefacts (for example [9,18–21]).

Molecular studies have sought to reconstruct the demographic history of food plant species to investigate the origins and processes of domestication [22–25]. These studies generally focus on crops that have been extensively genotyped and for which different cultivars are well-described (for example [26–30]). However, little work has been done on the human-mediated dispersal of non-crop species (although see [31–35]). This could be in the form of “assisted migration” – the movement of a species outside its natural range, “introduction” – the establishment of new populations within a species’ existing range and “reinforcement” – the planting of propagules from one population into another [36]. Retracing propagule dispersal by pre-colonial Indigenous peoples (hereon referred to as ‘Indigenous dispersal’) is important for cultural resource recognition and management and can yield insights to the long-term evolutionary impacts of translocations that can be applied to restoration activities.

To advance this field of study, we advocate for the use of simple genomic tests to screen for species that are likely to yield signals of Indigenous dispersal. While there are likely thousands of plant species around the world that have known or unknown histories of Indigenous cultivation, not all these can be successfully uncovered by genomic studies. Even in cases where there is abundant ethnographic evidence of translocation, many species will not carry an easy to interpret genomic signal. For instance, the quantity of propagules dispersed by historical human activities, and the distances over which they were dispersed, may not have been sufficient to create genetic structure that can be readily discriminated from that created by non-human modes of dispersal (as appears to be the case with *Camassia quamash*, [33]).

Our study focuses on the rainforests of eastern Australia. Contemporary Indigenous knowledge and early colonial records reveal extensive movement of various rainforest trees for food cultivation, ceremony and trading across the region [37,38]. However, the antiquity of these activities is not clear from the current state of the research. In a review of the subject, the Australian ethnographic literature is described as scant though detailed accounts of propagule movement, planting, or cultivation, often with ceremonial elements [13]. The archaeological record suggests humans began to permanently occupy tropical rainforests in very low numbers at least 8 kya, with intensive settlement around 2 kya [39]. However, the archaeological record is also sparse, and it is possible that human rainforest occupation is much older. Additionally, the occurrence of pre-domesticates of New Guinea crops such as taro (*Colocasia esculenta*), yam (*Dioscorea alata*) and bananas (*Musa acuminata*) suggests that there was an “experimental horticultural province” [40] in northern Australia (including the northern section of the study region). These rainforest food plants spread to the Australian continent either while it was still contiguous with the New Guinea landmass in the terminal Pleistocene/early Holocene and/or via maritime human dispersal following sea-level rise in the mid-late Holocene [5,21].

Researchers that seek to retrace past Indigenous dispersal need to consider the dispersal capacity of faunal or other vectors in the study area. The relationship between fleshy fruit size and the dispersal potential of woody species has been successfully demonstrated among plants of the east Australian rainforests. Here, plants with small fleshy fruit are widely dispersed by birds and are typically characterised by low population structure and have potential for colonisation of new areas via long-distance-dispersal (LDD) [41,42]. This genomic background would make it difficult to identify populations translocated by humans. In contrast, following the extinction of megafauna from the Australian continent between 50 to 16 kya [43], large-seeded plants lost an important mechanism for LDD and the ability to re-colonise areas of suitable habitat following the end of the Last Glacial Maximum (25-16 kya). Consequently, large-seeded rainforest species generally have greater between-population genomic divergence and occupy smaller geographic ranges than their small-fruited counterparts [42,44]. We anticipate that the strong population structure in large-fruited species would contrast with the genomic signal left by Indigenous dispersal events that post-date the megafauna extinction.

Here we present a screening strategy that employs simple genomic tests to identify signals of dispersal within long-lived non-crop plant species that may be attributed to Indigenous peoples. We sought to investigate whether fleshy fruited species with a known history of Indigenous use carry genomic patterns that are distinctive from expected signatures of widespread faunal dispersal. We were also interested in whether these signatures could be identified in other species that are likely to have been a nutritious food source, but for which we lack historic evidence of their extensive use by Indigenous groups.

We employed an opportunistic sample design to develop nuclear DNA (nDNA) genotyping-by-sequencing and whole-chloroplast (cpDNA) SNP datasets of east Australian rainforest trees that fall into one of five fruit-trait categories that impact dispersal capacity. We tested for four genomic signals of dispersal with different patterns expected for species with a history of long-term isolation, long-term faunal mediated dispersal, or dispersal following long-term isolation (Table 1, Materials & Methods 2.6). Signal 1 “low F_{st} values and the absence of isolation-by-distance (IBD)” is the outcome of recent and/or rapid dispersal, Signal 2 “admixture between sites” is produced by dispersal following long-term isolation, such as across a biogeographic barrier, Signal 3 “genomic outliers within sites” is produced by very recent long-distance dispersal (LDD) between formerly isolated sites and Signal 4 “long-distance dispersal of haplotypes” is produced by recent dispersal following long-term isolation.

Species with signatures of dispersal following long-term isolation were regarded as candidates for further investigation of putative Indigenous dispersal histories. For these candidates, we outline a strategy to test specific dispersal hypotheses using more comprehensive sampling and coalescent analyses.

Table 1. The patterns expected from four tests of dispersal assuming different dispersal traits and histories. For each signal, we expected different results for species with a history of long-term isolation, long-term faunal mediated dispersal or dispersal following long-term isolation. Note that more than one dispersal scenario is hypothesized for species in the small fruit categories. Signal 1 = “low Fst values and absence of isolation-by-distance”. Signal 2 = “admixture between sites”. Signal 3 = “genomic outliers within sites”. Signal 4 = “haplotype long-distance dispersal”. ✓ = expected genomic signal from post-megafauna Indigenous dispersal. ✗ = genomic pattern not consistent with post-megafauna Indigenous dispersal. IBD = isolation-by-distance. LDD = long-distance dispersal.

Dispersal trait	Signal 1	Signal 2	Signal 3	Signal 4
Small fruit faunal dispersed	✗ Low Fst values & IBD (long-term dispersal)	✓ Admixture between sites (dispersal following long-term isolation) ✗ Homogeneity among sites (long-term dispersal)	✓ Within-site outliers (recent LDD) ✗ No outliers (long-term dispersal)	✗ Range-wide haplotype sharing (long-term dispersal) ✓ Single widespread haplotype (recent rapid dispersal)
Small fruit Indigenous dispersed	✓ Low Fst values & absence of IBD (recent rapid dispersal)	✓ Admixture between sites (dispersal following long-term isolation) ✗ Homogeneity among sites (long-term dispersal)	✓ Within-site outliers (dispersal following long-term isolation)	✗ Range-wide haplotype sharing (long-term dispersal) ✓ Single widespread haplotype (recent rapid dispersal)
Large fruit faunal dispersed	✗ High Fst values with or without IBD (long-term isolation)	✗ Structure across barriers (long-term isolation)	✗ Differentiation amongst sites & no outliers (long-term isolation)	✗ Haplotype divergence (long-term isolation)
Large fruit Indigenous dispersed	✓ Low Fst values & absence of IBD (recent rapid dispersal)	✓ Admixture between sites (dispersal following long-term isolation)	✓ Within-site outliers (dispersal following long-term isolation)	✓ Haplotype sharing between differentiated sites (dispersal following long-term isolation) ✓ Single widespread haplotype (recent rapid dispersal)

Materials and Methods

Study System

The study area extended along the coastal plains and ranges of eastern Australia from the tropical monsoonal rainforests of Iron Range (12° 42' S) in the Cape York Peninsula, Queensland (QLD) to the scattered subtropical forests around Glennifer, New South Wales (NSW; 30° 22' S; Figure 1). The study species are primarily located in the Australian Wet Tropics (AWT; 15° 40' to 19° 15' S) or northern NSW (NNSW); and some extend through the intervening regions of Central QLD (CQLD; ~20° to 24° S) and Southeast QLD (SEQ; ~25° to 28° S). There are several breaks in wet forest habitat within and between these regions [45].

During the Quaternary, climate-driven cycles of wet forest habitat contraction and re-expansion led to periods of genetic isolation and admixture for many rainforest species [41,46,47]. The AWT bioregion comprises a mosaic of tropical upland and lowland forests separated by drier corridors of mixed wet/dry habitats that act as “permeable” genetic or distributional barriers for some rainforest species [48–52]. This includes the Black Mountain Corridor (BMC) [49] and Cairns-Cardwell Lowlands (CCL) [44,48,50]. The subtropical rainforests in NNSW are highly fragmented, with upland sites isolated by extensive low-lying river systems. The Clarence River Corridor (CRC) is also a dry habitat break for some mesic species and has played a role in diversification between SEQ and upland regions of the mid-north coast of NSW [46,47,53].

Specialised large-fruit dispersers have been historically absent from NNSW and SEQ, and local dispersal rates are expected to be lower in the region [54,55]. Therefore, it is assumed that large fleshy fruit in southern forests have no means of long-distance dispersal except through human activity. This pattern appears to be less pronounced in the AWT [56], where fruit up to 62 mm can be locally dispersed (≤ 2 km) by non-volant vertebrates such as the southern Cassowary (*Casuarius casuarius johnsonii*) [57,58]. Meanwhile fruit bats (*Pteropus* spp.) and birds would facilitate dispersal of small-fruited species over longer distances across the whole study area.

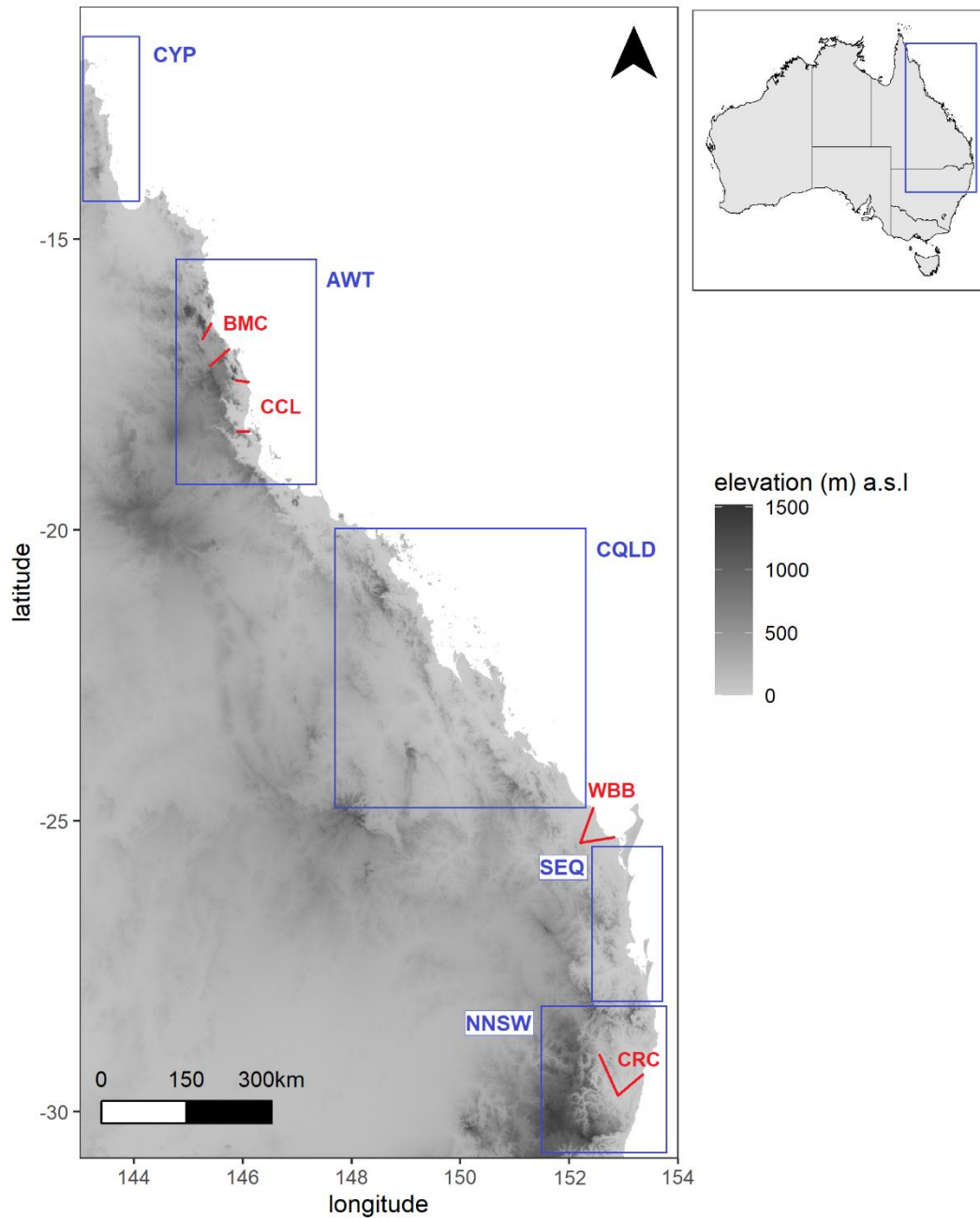


Figure 1. The study area in eastern Australia. Geographic regions separated by disjunctions of rainforest vegetation are indicated by the blue boxes. NNSW=Northern New South Wales, SEQ = Southeast Queensland, CQLD = Central Queensland, AWT = Australian Wet Tropics, CYP = Cape York Peninsula. Low elevation biogeographic barriers that structure the genomic variation in some of the study species are demarcated by red lines. CRC = Clarence River Corridor, WBB = Wide Bay-Burnett, CCL = Cairns-Cardwell Lowlands, BMC = Black Mountain Corridor.

Study Design

For our core analyses, we selected three groups of co-generic or closely related rainforest species with fleshy fruit and/or edible nutritious seed (Table 1). This includes 4 x *Elaeocarpus* (Elaeocarpaceae), 1 x *Pleioluma*, 1 x *Planchonella* and 2 x *Niemeyera* (Sapotaceae); 3 x *Endiandra* and 1 x *Bielschmiedia* (Lauraceae). The fruit of

these species typically contain a single large seed that comprises most of the fruit. Additionally, we included *Castanospermum australe* (Fabaceae), in which the genomic impacts of dispersal by Bundjalung people in NNSW has been previously demonstrated [32]. For broader context, 12 additional species from other families were included in our initial analyses, 3 of which have inedible wind-dispersed fruit. We employed an opportunistic rather than comprehensive sample strategy that captured the core distribution of each of the study species, including their presence across putative biogeographic barriers. All sample sites were located within large stands of remnant rainforest, primarily in protected reserves, excluding a few NNSW sites for *C. australe* (VP, HS, Raz, MP; Figure 3a(i)), *Endiandra globosa* (HS, BH; Figure 3f(i)), *E. pubens* (HS, HH; Figure 3h(i)), *E. discolor* (HS, BH; Figure 3m(i)) and *Elaeocarpus reticulatus* (Ty, BrH, W, Br; Figure 3o(i)), which were taken from small remnant patches and may have been impacted by restoration plantings on site or nearby. Only large adult trees (inferred to be at least 50 years) were sampled to minimise the confounding influence of recent restoration plantings on our sample scheme.

We grouped species according to the following fruit traits: large fleshy and Indigenous-used, small fleshy and Indigenous-used, large fleshy, small fleshy, wind dispersed. Following [38], our fruit-size categories were based on maximum width and defined as large (≥ 30 mm) or small (≤ 30 mm; see Table 2). These categories correspond with the maximum size of fruit that can be ingested whole by the largest volant dispersers in the southern subtropical rainforests [70]. Fruit size was obtained from Australian Tropical Rainforest Plants Edition 8 (<https://apps.lucidcentral.org/rainforest/text/intro/index.html>) or from plantNET (<https://plantnet.rbgsyd.nsw.gov.au/>). Species were categorised as Indigenous used if we found archaeological or ethnographic reports that indicate past or ongoing consumption by Indigenous groups in Australia (Table 2). The other species may also have been Indigenous used, but we could not find reports of this.

Among our study species, *Planchonella australis* is an anomaly since it has large fleshy fruit with 1-5 smaller seeds that can potentially be dispersed by fruit bats. Note that although fruit size is a variable trait, the lower end of the range is generally recorded from fruit with inviable seed or no seed at all and would not contribute to the gene pool of the species. Therefore, although a maximum fruit width of <30 mm has been recorded for *Planchonella australis*, *Niemeyera whitei* and *Elaeocarpus johnsonii*, we included these in the large fruit categories as they are primarily much wider than 30 mm.

Table 2. The study species and their fruit traits, the genomic data used in the study and references that report use of each species by Indigenous Australians. **Fruit traits:** S=Small (<30 mm) L=Large (>30 mm) F=Fleshy W=Woody O=Other. **Seed traits:** L= Large S= Small. **nDNA**=nuclear DNA. **cpDNA**=chloroplast DNA. **Location:** AWT = Australian Wet Tropics NNSW = Northern New South Wales SEQ = Southeast Queensland.

Family	Species	Common names	Fruit trait	Max. fruit width (mm)	Seed number & traits	nDNA markers (SNPs)	cpDNA sequence (bp)	Mantel score (P=0.05) *three sites only	Reported Indigenous use
Study Species									
Fabaceae	<i>Castanospermum australe</i>	Morteon Bay chestnut, Black bean, Bean tree	LO	45	3-5 L	38,124 18,443 (north) 20,705 (south)		0.67 (P=0.04) AWT 0.43 (P=0.18) NNSW	'Black bean was a staple food of many northern rainforest Aboriginal people and is still prepared and eaten today.' (cited[59]). Ethnographic records of consumption by Indigenous peoples (AWT) [60–64]. Seed detoxification described in the AWT [65,66] and in NNSW/SEQ [32,67,68].
Lauraceae	<i>Bielschmiedia bancroftii</i>	Yellow walnut, Yellow nut, Canary ash	LO	75 x 62	1 L	2,080	108,132	0.36 (P=0.33) AWT	Seed preparation described in the AWT [61]. Archaeological evidence of seed processing in the AWT [39,69].
Lauraceae	<i>Endiandra insignis</i>	Hairy walnut	LF	90 x 100	1 L	13,913	106,112	0.99 (P=0.17) AWT*	Seed preparation described in the AWT [61]. Bush tucker guide (AWT)[70]. Archaeological evidence of seed processing (AWT) [69].
Sapotaceae	<i>Planchonella australis</i>	Black apple, brush apple, wild plum, native plum	LF	50	1-5 S	24,873	86,899	0.63 (P=0.17) NNSW*	Ethnographic records [67]. Bush tucker guide [70].
Elaeocarpaceae	<i>Elaeocarpus bancroftii</i>	Kuranda quandong, Ebony heart, Nutwood, Johnstone River almond	LF	55 x 40	1 L	17,085		0.14 (P=0.32) AWT	Ethnographic records [67,71]. Bush tucker guide[68,70]. Archaeological records of seed preparation [72].
Lauraceae	<i>Endiandra compressa</i>		LF	71 x 60	1 L	4,025	107,869	0.91 (P=0.33) AWT	
Lauraceae	<i>Endiandra globosa</i>	Black Walnut	LF	60 x 60	1 L	24,382	107,910	0.99 (P=0.33) AWT	
Lauraceae	<i>Endiandra pubens</i>	Hairy walnut	LF	75 x 75	1 L	23,322	107,371	0.99 (P=0.17) NNSW*	
Sapotaceae	<i>Niemeyera prunifera</i>		LF	50 x 50	1 L	22,778	84,279	0.91 (P=0.12) AWT	
Sapotaceae	<i>Niemeyera whitei</i>		LF	20-50	1 L	10,669	87,841	0.61 (P=0.33) NNSW *	
Elaeocarpaceae	<i>Elaeocarpus johnsonii</i>	Kuranda quandong	LO	40 x 25	1 L	1,274		0.99 (P=0.33) AWT *	Bush tucker guide described the seed as edible [73].
Elaeocarpaceae	<i>Elaeocarpus grandis</i>	Blue quandong, Silver quandong, Blue fig	SF	33 x 33	1 L	10,273		0.54 (P=0.13) NBMC 0.13 (P=0.35) SBMC 0.99 (P=0.33) CQLD*	'You can eat the thin layer of flesh of the ripe purple-blue fruits when flesh is soft.' (cited [59]). Bush tucker guide describes edible fruit[70].
Elaeocarpaceae	<i>Elaeocarpus reticulatus</i>		SF	12 x 12	1 S	14,731		0.56 (P<0.01) NNSW	B. McLeod describes the fruit as "good bush tucker tea" that can be eaten raw or as a jam [74] (NB: reference is from outside of study area).
Sapotaceae	<i>Pleioluma queenslandica</i>		SF	22 x 9	1 S	15,270	85,895		
Lauraceae	<i>Endiandra discolor</i>		SF	17 x 13	1 S	23,081	107,031	-0.05 (P=0.42) NNSW	
FST Only									
Lauraceae	<i>Endiandra introrsa</i>		LF	50 x 50		3,461			

Lauraceae	<i>Bielschmiedia tooram</i>	Brown walnut, Tooram walnut	LF	55 x 35	3,461		Bush tucker guide describes edible fruit [70]. Bush tucker guide describes edible seed[73].
Lauraceae	<i>Bielschmiedia volckii</i>		LF	67 x 65	3,461		
Sapindaceae	<i>Diploglottis australis</i>	Native tamarind, Tamarind tree, Orange tamarind	SF	15	4,640	0.88 (P<0.01) NNSW	Ethnographic sources [60,67] and bush tucker guide [70] describe the culinary properties of the fruit.
Lauraceae	<i>Neolitsea dealbata</i>		SF	11 x 11	2,881	0.91 (P<0.01) NNSW	
Lauraceae	<i>Cryptocaria glaucescens</i>		SF	15 x 18	14,970	0.89 (P<0.01) NNSW	
Elaeocarpaceae	<i>Sloanea australis</i>		SF	17 x 17	7,429	0.59 (P<0.01) NNSW	
Myrtaceae	<i>Tristaniopsis laurina</i>	Water gum, Kanooka	W	10 x 6	13,841	0.59 (P<0.01) NNSW	
Myrtaceae	<i>Tristaniopsis collina</i>	Mountain water gum	W	10 x 6	10,721	0.82 (P<0.01) NNSW	
Cunoniaceae	<i>Ceratopetalum apetalum</i>	Coachwood	W	>8	659	0.75 (P<0.01) NNSW	

Simulation of Hypothetical Dispersal Scenarios

The premise of our screening strategy is that species with a history of post-megafauna isolation followed by recent Indigenous dispersal would produce genomic patterns that are distinct from widespread and long-term faunal dispersal. We sought to verify this assumption by simulating genetic differentiation of a species under 9 hypothetical dispersal scenarios. We calculated the pairwise *Fst* values from each of the simulated scenarios to determine whether patterns of population differentiation are identifiably distinct between long-term faunal and recent Indigenous dispersal (see Appendix A for full description of methods and results).

Nuclear and Chloroplast Genomic Methods

For all samples, nDNA extraction from leaf samples and SNP genotyping using DArTseq technology [75] was undertaken at Diversity Arrays Technology Pty Ltd (Canberra, Australia). We followed [66] and filtered markers according to reproducibility average (proportion of technical replicates for which the marker score is consistent) and call rate (proportion of individuals with non-missing scores). We selected markers with a reproducibility average of at least 0.96 and a minimum call rate of 0.80.

In addition, we obtained comparative cpDNA sequence data for Sapotaceae and Lauraceae to determine the ancestral relationships between populations and samples. Whole-chloroplast sequencing was undertaken at Deakin Genomics Research and Discovery Facility (Geelong, Australia) and we assembled the genomes *de novo* with ORG.Asm [76]. We used CLC Genomics Workbench 20.0 (QIAGEN) to inspect read quality and depth, and map reads against annotated reference sequences obtained from GeSeq[77]. We used the default settings to map Lauraceae samples against *Endiandra globosa* (Accession: KT588614)

and Sapotaceae samples against *Pouteria campechiana* (Accession: NC033501). For read conflicts, we used the quality score and vote options to determine the consensus sequence and we filtered variants with a coverage < 8 or read consensus < 60%. After removing areas of low coverage, the Lauraceae chloroplast sequence alignments ranged between 106,112 and 108,132 bp long (Table 2). The read coverage and quality were generally poorer for Sapotaceae species, and the cleaned alignments were between 84,279 and 87,841 bp.

We aligned the species libraries with the relevant reference sequence using the MEGA alignment function in Geneious Prime 2021.1.1 (<https://www.geneious.com>). To eliminate potential sequence errors, we removed non-synonymous variants in coding regions. To investigate the possibility of contamination in libraries with unexpectedly high variation, we extracted sequences that mapped to the *ycf1* and *ndhH* genes and used the BLAST function in GenBank with default settings to determine if any samples matched with libraries of algae or other distantly related species.

Assessment of Fruit Traits and Genetic Connectivity

We calculated pairwise genetic distances for all 25 species to verify our primary assumption that species with large fruit have lower dispersal rates than wind-dispersed or small-fruit species. Pairwise-Fst values were calculated using the R package BEDASSLE [78] under the Weir & Hill model [79]. Then for each species, we took the average of their pairwise Fst values at 50 km distance intervals, starting from 0-50 km up to 651-700 km. To visualise how fruit traits influence gene flow over each distance interval, we constructed violin plots of results organised by fruit trait. As there were only a few observations above 300 km, we plotted distance classes between 301-700 km together for visual clarity. Small-fruited species were expected to show lower pairwise Fst values than large fruit species.

Genomic Tests of Dispersal Signals

We sought to identify whether the core 15 study species show any of the four signals of putative Indigenous dispersal described in Table 1. For each signal, we expected different results for species with a history of long-term isolation, long-term faunal mediated dispersal, or dispersal following long-term isolation. To identify candidates that warrant an investigation of Indigenous dispersal histories, we sought to eliminate species that show signals overwhelmingly consistent with long-term faunal mediated dispersal or long-term isolation. Signals more consistent with dispersal following long-term isolation were hypothesized to be the outcome of Indigenous-mediated dispersal following isolation driven by the megafauna extinction.

To test for Signal 1 “combination of low F_{st} values and absence of IBD”, we performed a Pearson Mantel test on each species’ genetic and geographic distance matrices with 999 permutations ($P=0.05$). The distance matrices were linearised F_{st} values ($F_{st}/(1-F_{st})$) against log geographic distance (km) and all calculations were made in the R package *vegan* 2.5-7 [80]. Where relevant, we subdivided the datasets to construct distance matrices within the AWT and NNSW. Given the sparse sample design and our aims to develop a screening strategy, we were more interested in identifying overall patterns of IBD than statistical significance.

Signal 1 is produced by recent and rapid radiation. This pattern may be attributed to extensive Indigenous dispersal, although other mechanisms of recent widespread migration cannot be excluded for small-fruited species. In the absence of Indigenous dispersal, large-fruited species were expected to show high F_{st} values consistent with long-term isolation. The impact of IBD was expected only in the absence of barriers. On the other hand, range-wide faunal dispersal in a stable system is likely to yield low F_{st} values in combination with IBD.

For Signals 2-3, we used the STRUCTURE-like genotype assignment algorithm implemented by R package *sNMF* [81] to assess the degree of shared ancestry between samples. We modeled $K=2-10$ ancestral genotypes for each species, with 10 replicates per model. The cross-entropy criterion was used to evaluate model suitability in *sNMF* and we plotted the mean individual genotype assignments for $K=2-4$ models. Given our sparse sample scheme may confound the genotype assignment algorithm, we verified the *sNMF* results with a principal components analysis (PCA) on the genomic variation among samples. Ordination was visualised in the first 3 primary axes of variation, with samples coloured according to latitude to determine whether genetic structure is geographic.

In our assessment of Signal 2 “admixture between sites”, we looked for sites where most samples had admixed *sNMF* profiles (e.g., $\leq 75\%$ of the dominant genotype) in the optimal K model. Admixed profiles are a putative signal of secondary contact and admixture after many generations of isolation and could be facilitated by Indigenous-dispersal or by faunal dispersal amongst small-fruited species. However, admixed profiles could alternatively be the outcome of incomplete lineage sorting due to vicariance, a recent bottleneck or admixture with an unsampled or extinct lineage [82]. We expected large-fruited species to show stronger population structure than small-fruited species, and Indigenous-used species to show some admixture of genotypes separated by barriers or disjunct regions. Regardless of human influence, small-fruited species were expected to show either a single genotype indicative of long-term range-wide connectivity or admixture consistent with post-glacial re-connectivity.

Signal 3 “within-site outliers” refers to samples that show a genotype that is distinct from most of the sample site (in the PCA and sNMF plot). Such a pattern may be produced by recent LDD and is hypothesised to be the outcome of recent Indigenous dispersal (reinforcement). Signals of LDD within small-fruited species may also be attributed to volant faunal dispersers, although this pattern is not expected.

To test Signal 4 “haplotype LDD”, the cleaned cpDNA alignments were exported for a Neighbour-Joining network analysis (epsilon=0) of haplotypes in PopART[83]. We looked for haplotype sharing or closely related haplotypes between otherwise highly genetically differentiated sites and/or disjunct sites as a putative signal of LDD. For large-fruited species, such a pattern is hypothesised to be the outcome of Indigenous-mediated reinforcement between previously isolated sites. Meanwhile assisted migrations or introductions may result in patterns consistent with rapid expansion, such as low haplotype variation between disjunct sites or a single widespread haplotype. Small-fruited species were expected to show extensive haplotype sharing and few mutations between haplotypes, indicative of long-term population connectivity. A single widespread haplotype may be indicative of rapid expansion facilitated by either Indigenous or faunal dispersal. Meanwhile large-fruited species without human influence were expected to retain strong haplotype differentiation between sites or across barriers.

Results

Fruit Traits and Genetic Connectivity

The violin plots of species-mean pairwise F_{st} shows that as a group, species with large fleshy fruit have higher median pairwise F_{st} values than the wind-dispersed or small fleshy-fruited species across all distance intervals excluding 201-250 km (Figure 2). This supports our founding premise that faunal vectors facilitate extensive gene flow within small fruit species, while large fruit species lack a mechanism of long-distance seed dispersal and thus have lower rates of gene flow. The large-fruit though small-seeded *Planchonella australis* has lower F_{st} values than the other categories and may be attributed to Indigenous-assisted dispersal or animal-dispersal (Table S1). Compared with fleshy fruit species, the range of F_{st} values is small in the wind-dispersed category and increases only marginally with geographic distance. This indicates that wind-dispersal is relatively uniform in the study area, while gene flow within fleshy fruit species is sensitive to the type and/or availability of vertebrate dispersers.

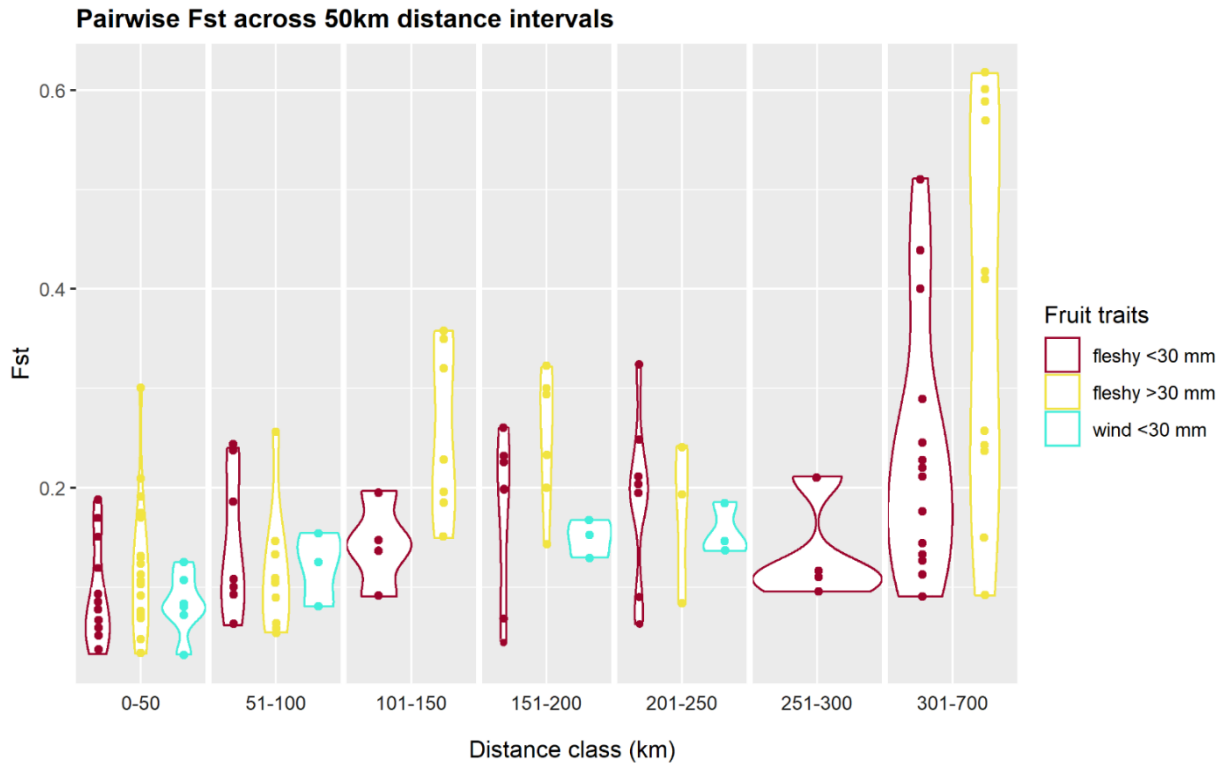


Figure 2. Violin plots of the average pairwise F_{st} values calculated for 25 species at 50 km distance intervals and colored by fruit trait.

Simulation Study

Overall, the 9 simulated dispersal scenarios support the premise that long-term faunal dispersal and post-isolation Indigenous dispersal produce distinct patterns of genetic differentiation. The two hypothetical scenarios of post-glacial volant faunal dispersal show low F_{st} values though a prominent barrier effect (Figure Appendix 1 and Appendix 2). As expected, the post-megafauna isolation model yielded the greatest population structure amongst all dispersal scenarios (Figure Appendix 3).

The Indigenous dispersal scenarios produced varying patterns of differentiation depending on the pattern of migration and the length of the migration period. For instance, the symmetric island model of migration in hd1 and hd2 (Figures A4 and A5) yielded a greater homogenising effect than the distance-weighted migration of the faunal models. Models hd3 and hd6 with Indigenous dispersal 5000-4000 years ago exhibited higher F_{st} values due to the shorter and more ancient period of migration (Figures A6 and A9). In contrast with all other models, the lack of migration combined with the range expansion in hd4 yielded high F_{st} estimates excluding between the two recently diverged deme0 and deme1 (Figure Appendix 7). The directional migration in hd5 and hd6 yielded higher F_{st} values and different population structure to the faunal dispersal scenarios (Figures A8 and A9).

Genomic Tests of Dispersal Signals

We identified five candidates for the investigation of Indigenous dispersal. Four candidates displayed at least two positive signals of dispersal that could not be explained by faunal dispersal: *Castanospermum australe*, *Endiandra insignis*, *Beilschmiedia bancroftii*, *Elaeocarpus bancroftii* (Table 3). Additionally, we identified *Niemeyera prunifera* as a candidate, despite only displaying one signal (Table 3), as the combination of genomic patterns suggest a change in dispersal rates over time that may implicate past anthropogenic influence.

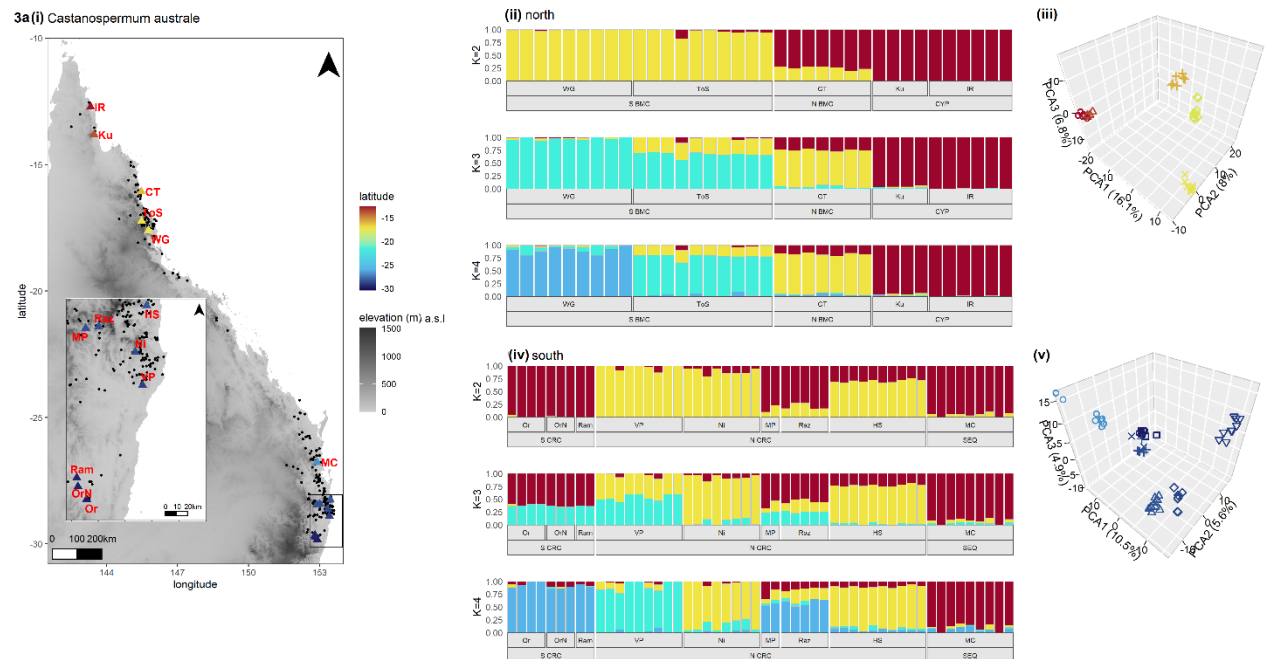
Table 3. Summary of dispersal signals found in the study species. The presence or absence of these signals can be used to evaluate whether a species would make a suitable candidate to investigate the influence of Indigenous dispersal. Signal 1 = “low F_{st} values and absence of isolation-by-distance (IBD)”. Signal 2 = “admixture between sites”. Signal 3 = “genomic outliers within sites”. Signal 4 = “haplotype long distance dispersal (LDD)”. Note that Signal 4 could not be tested for *Elaeocarpus* species due to a lack of cpDNA data. The sample scheme for *E. globosa* (NNSW) was insufficient to test for Signals 1-2. Species identified as candidates for Indigenous dispersal studies have an asterisk*.

Species	Fruit > 30 mm	Verified Indigenous use	Signal 1 nDNA	Signal 2 nDNA	Signal 3 nDNA	Signal 4 cpDNA
<i>Castanospermum australe</i> (CYP/AWT)	✓	✓	✗	✓	✗	✗
<i>C. australe</i> (SEQ/NNSW)*	✓	✓	✓	✓	✗	✗
<i>Endiandra insignis</i> *	✓	✓	✗	✗	✗	✓
<i>Beilschmiedia bancroftii</i> *	✓	✓	✓	✗	✓	✓
<i>Planchonella australis</i>	✓	✓	✗	✗	✓	✗
<i>Elaeocarpus bancroftii</i> *	✓	✓	✓	✓	✗	
<i>Endiandra globosa</i> (AWT)	✓	✗	✗	✗	✓	✗
<i>E. globosa</i> (NNSW)	✓	✗			✓	✗
<i>Endiandra compressa</i>	✓	✗	✗	✗	✗	✗
<i>Endiandra pubens</i>	✓	✗	✗	✗	✗	✗
<i>Niemeyera prunifera</i> *	✓	✗	✗	✗	✗	✓
<i>Niemeyera whitei</i>	✓	✗	✗	✗	✗	✗

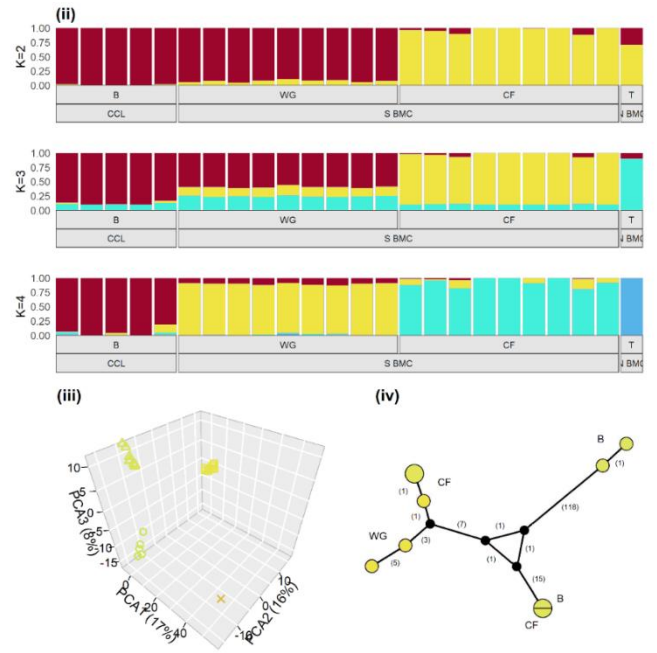
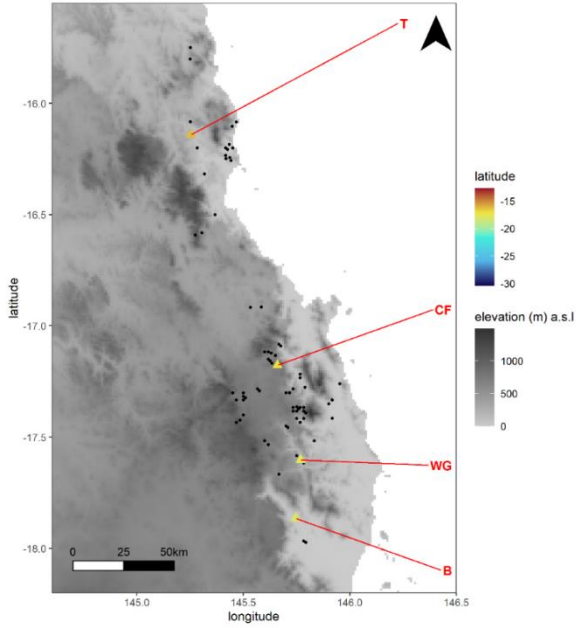
<i>Elaeocarpus johnsonii</i>	✓	✗	✗	✗	✓	
<i>Elaeocarpus grandis</i>	✗	✓	✓	✗	✓	
<i>Endiandra discolor</i>	✗	✗	✓	✓	✗	✗
<i>Pleioluma queenslandica</i>	✗	✗	✗	✓	✗	✗
<i>Elaeocarpus reticulatus</i>	✗	✗	✗	✗	✗	

Large Fruit with Known History of Indigenous Use

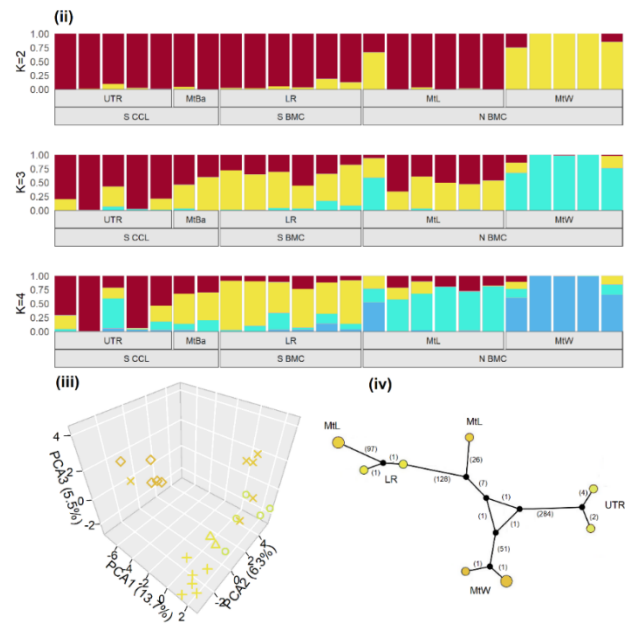
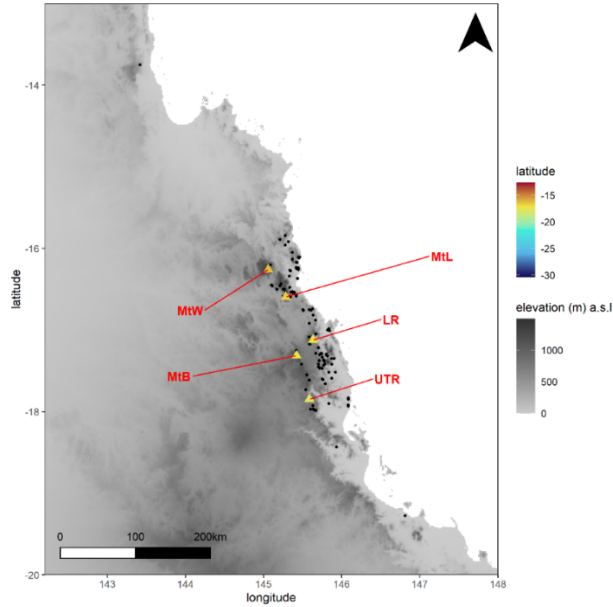
We assessed the northern and southern ranges of *Castanospermum australe* separately, due to the large geographic and genetic disjunction between the two regions. In the northern range, *C. australe* showed only one signal of dispersal (Table 3). We found low-moderate pairwise F_{st} values and a Mantel correlate consistent with IBD expected of non-anthropogenic dispersal (Table 2). The best supported sNMF models ($K=2-3$) revealed divergence across the BMC and no outliers that may indicate LDD (Figure S1; Figure 3a(ii)). The PCA ordination was most concordant with $K=3$, and both models suggest putative admixture or ILS across the BMC at sites ToS and CT (Signal 2; Figure 3a(iii)).



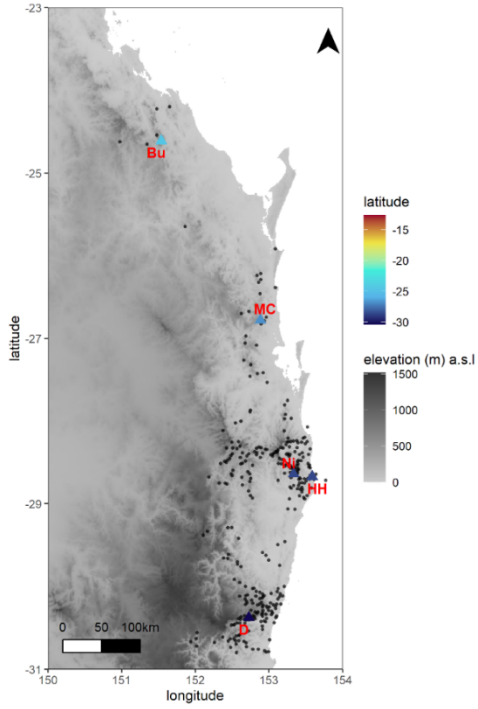
3b(i) *Endiandra insignis*



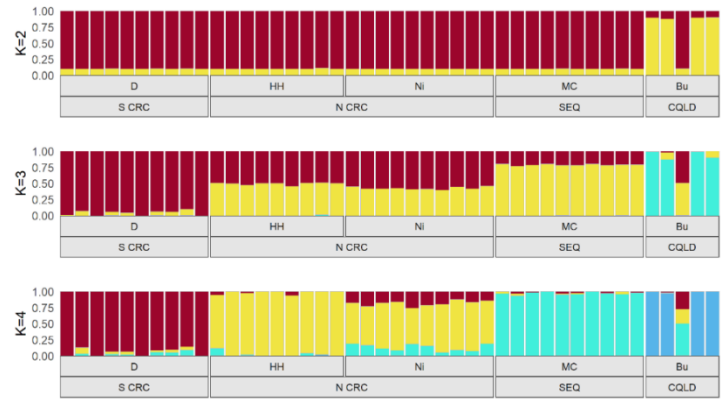
3c(i) *Beilschmiedia bancroftii*



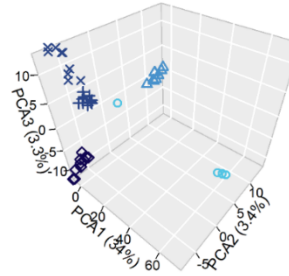
3d(i) *Planchonella australis*



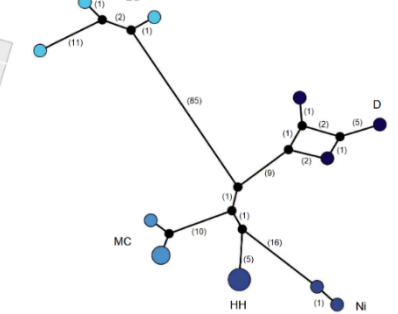
(ii)



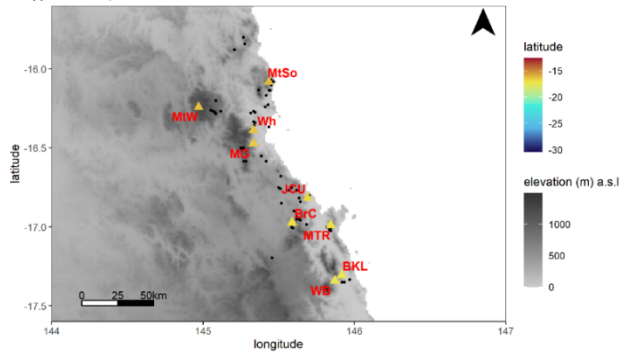
(iii)



(iv)



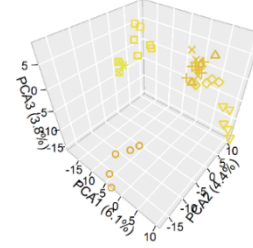
3e(i) *Elaeocarpus bancroftii*



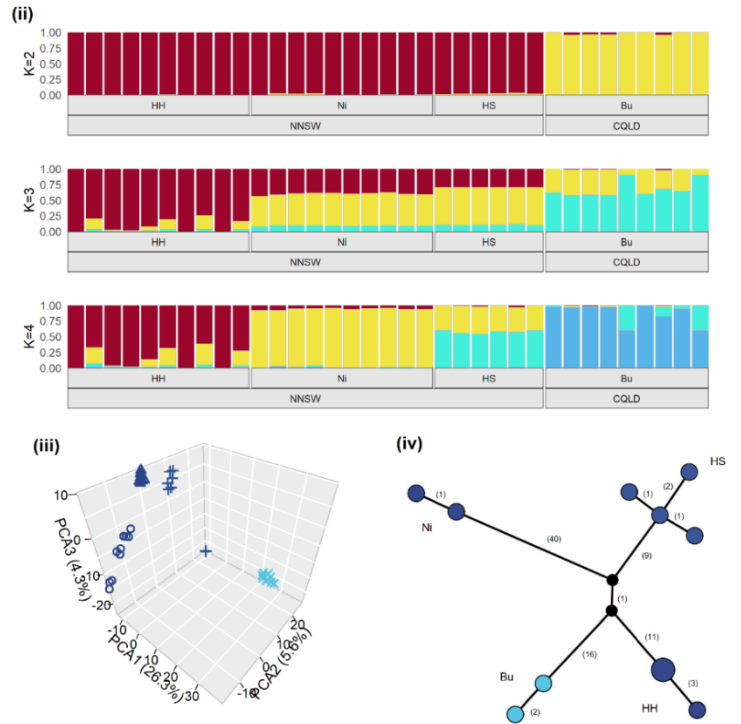
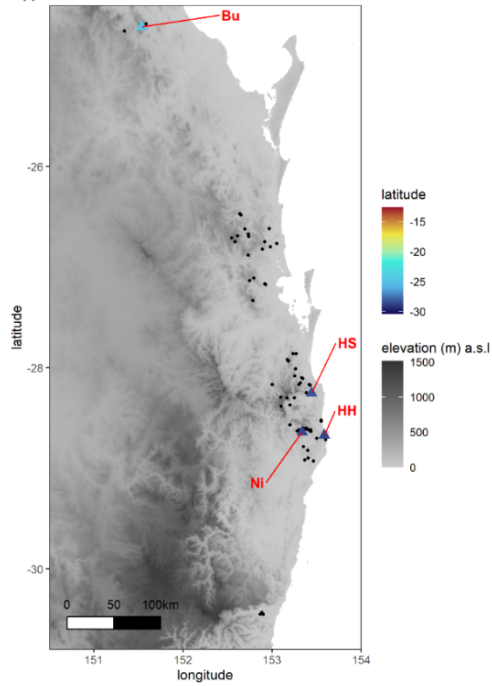
(ii)



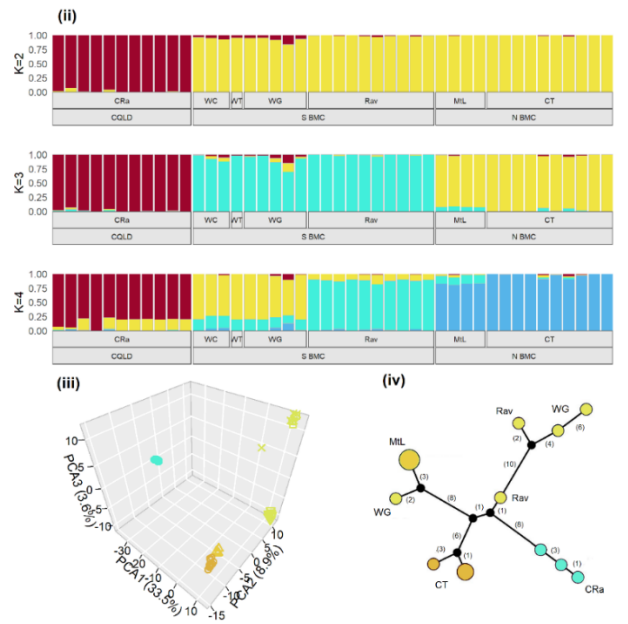
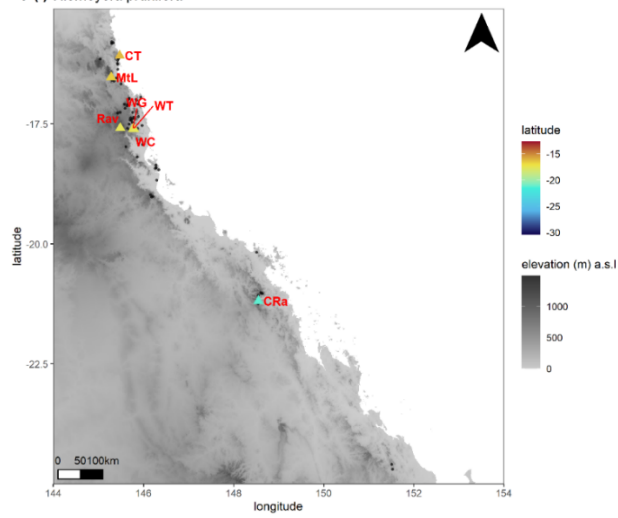
(iii)



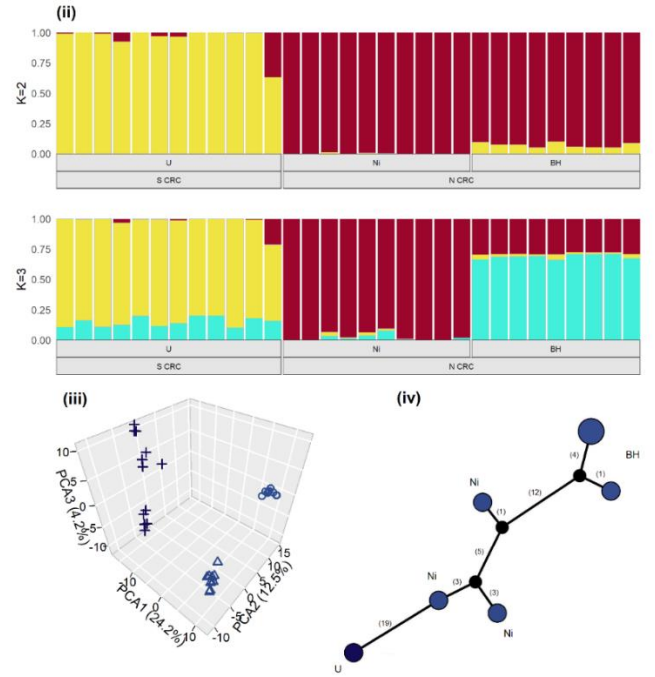
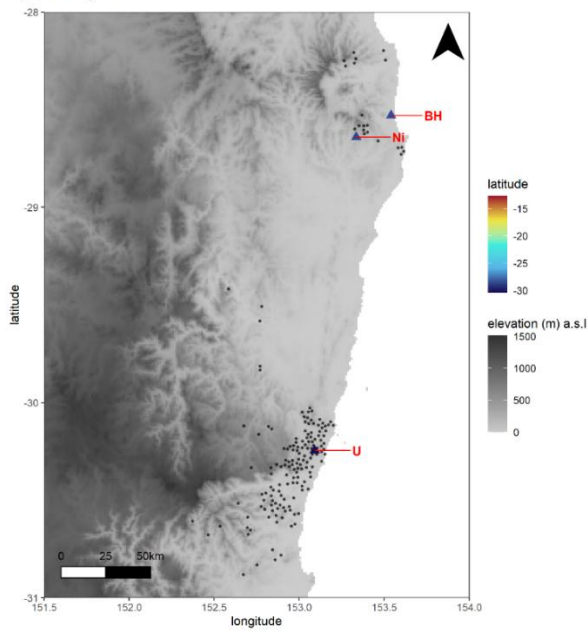
3h(i) *Endiandra pubens*



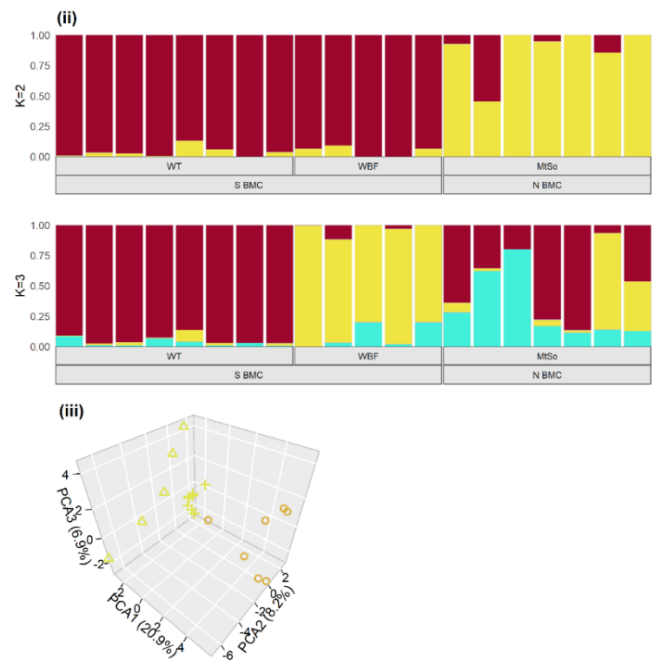
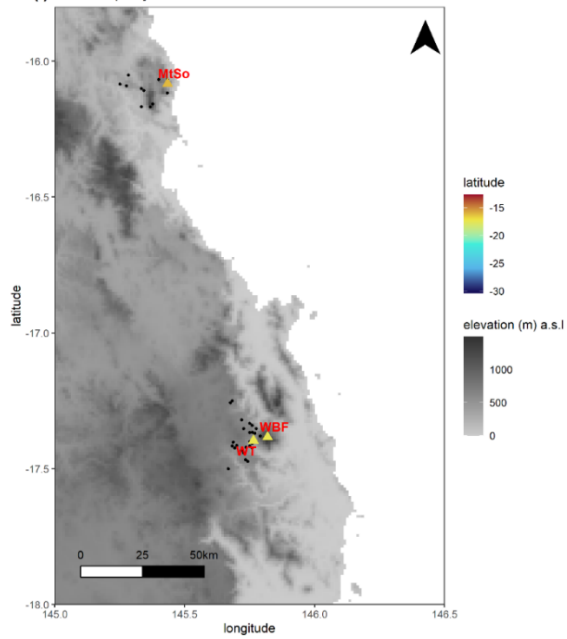
3i(i) *Niemeyera prunifera*



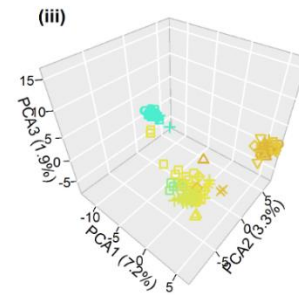
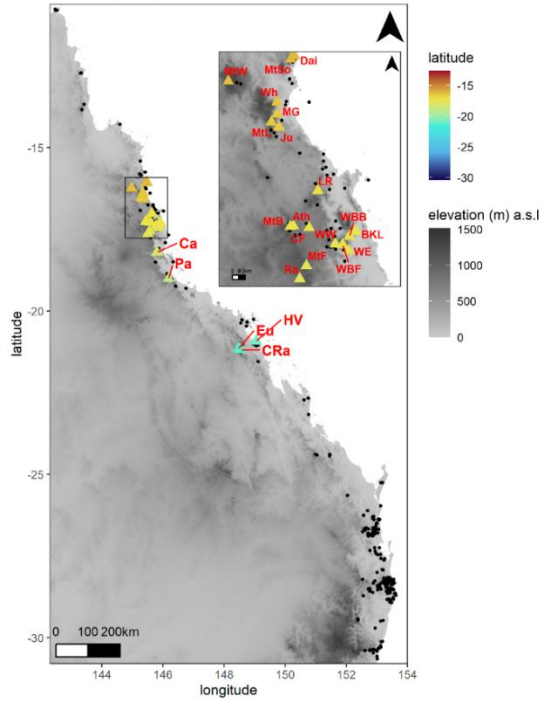
3j(i) *Niemeyera whitei*



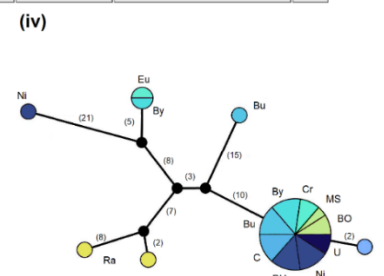
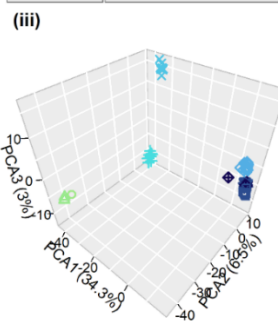
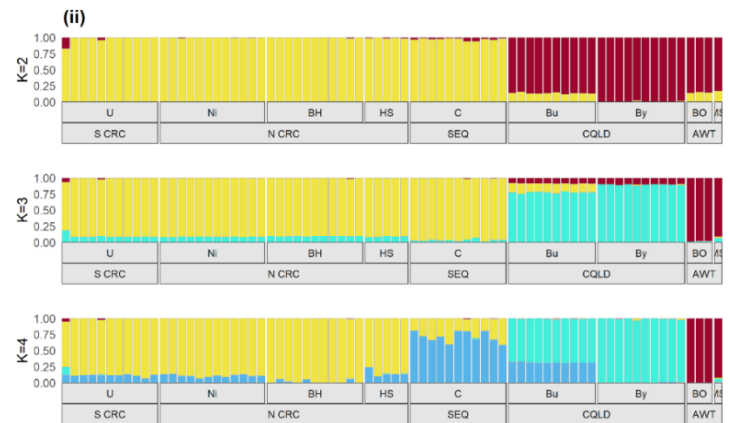
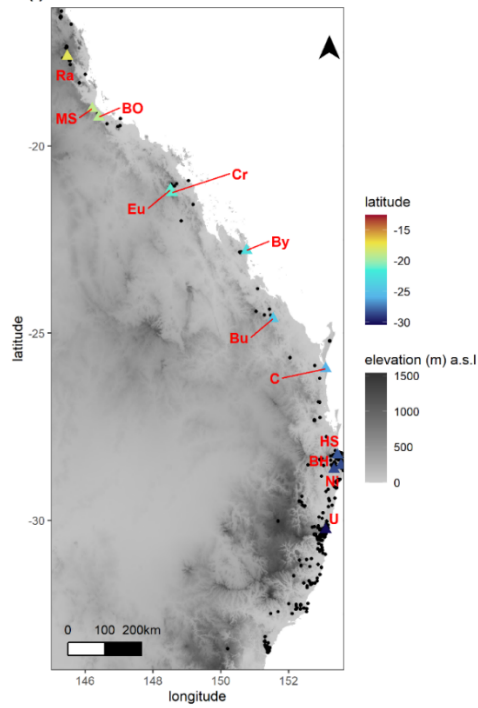
3k(i) *Elaeocarpus johnsonii*



3l(i) *Elaeocarpus grandis*



3m(i) *Endiandra discolor*



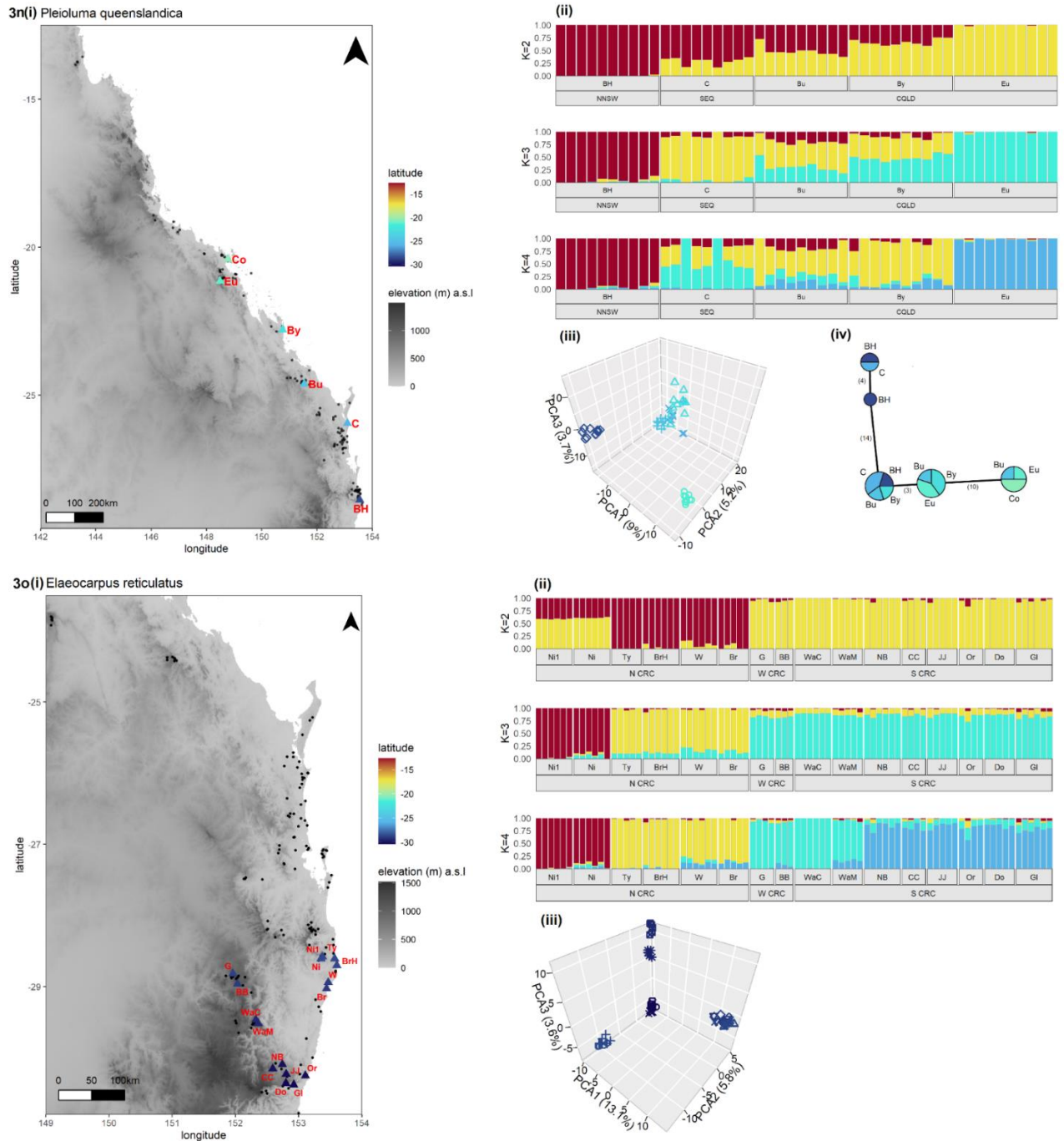


Figure 3. (a–o) The 15 study species evaluated for genomic signals of dispersal. For each species, (i) the distribution of the species in the study area is indicated by the black circles and the sample sites are coloured according to a latitudinal gradient defined by the extent of the study area. (ii) Genotype assignment proportions identified by sNMF, assuming $K = 2-4$. The sample site and geographic region (or position in relation to a barrier) are indicated by the bottom panel. (iii) Principal components analysis of nDNA genomic variance between samples, ordinated by first three primary axes of variation. Samples are coloured according to latitude and shape indicates sample site. (iv) Median-joining network of chloroplast haplotypes (epsilon = 0). Circles are proportional to the number of samples per haplotype and coloured by the latitude of the sample site. The number of mutations between haplotypes are in brackets, and the length of nodes are indicative but not directly proportional to number of mutations.

In the southern range, *C. australe* displayed two signals of dispersal that may be attributed to post-megafauna dispersal and presents a good candidate for further study (Table 3). First, we found low pairwise F_{st} values and a low Mantel correlate that suggests an absence of IBD consistent with recent or rapid migration (Signal 1; Table 2). The best-supported sNMF models assumed $K=2-4$, though $K=4$ was most consistent with the PCA ordination (Figure S1; Figure 3a(iv-v)). Both models show support for Signal 2, in which lowland sites (MP and Raz) have genomic profiles “admixed” between populations south of the CRC and upland sites north of the CRC. We did not find evidence of Signal 4 and the species shows unexpectedly strong structure between upland and lowland sites north of the CRC. This contrasts with the cpDNA results reported by [32], which indicates widespread haplotype sharing in NNSW. The greater structure in the nDNA data may suggest that connectivity between sites has been lost in more recent generations.

Endiandra insignis met one genomic signal of dispersal consistent with post-megafauna dispersal, though we identified it as a candidate for further study (Table 3). We did not find support for Signal 1, and *E. insignis* showed high F_{st} values, and a Mantel correlate consistent with IBD and limited faunal dispersal (Table 2). We did not find evidence of admixture between sites (Signal 2) and the best supported sNMF models ($K=1-2$; Figure S1) revealed divergence across the CCL (Figure 3b(ii)). The PCA showed variation across the CCL and BMC (Figure 3b(iii)). We found evidence of LDD in the cpDNA data (Signal 4) that contrasts with the nDNA patterns. The haplotype network suggests dispersal across the CCL with a shared haplotype at sites B and CF that is highly differentiated from the other samples at those sites (Figure 3b(iv)). This pattern is more consistent with recent migration between the two sites rather than an ancestral haplotype. The lack of nDNA evidence for LDD may suggest dispersal has ceased in more recent generations, allowing for nDNA diversity to accumulate between sites.

Beilschmiedia bancroftii showed genomic patterns consistent with three putative signals of post-megafauna dispersal, making the species a good candidate for further study (Table 3). First, we found support for Signal 1 with a combination of low F_{st} values and Mantel correlate, that suggests an absence of IBD and recent or rapid migration (Table 2). The best supported sNMF models assume $K=1-2$ (Figure S1) and together with the PCA reveal *B. bancroftii* is the only large-fruited species to show homogeneity among all sites excluding MtW (Figure 3c(ii-iii)). The PCA and sNMF also show one MtL sample clusters with MtW, potentially the outcome of LDD (Signal 3). The cpDNA data shows putative haplotype LDD (Signal 4) with one haplotype at MtL that is highly diverged from all others and may be a migrant from an unsampled population (Figure 3c(iv)). Alternatively, it may be a hybrid. Finally, the cpDNA network shows low variation within sites and high diversity between sites that suggests a long history of population isolation

and bottlenecks. This is the opposite pattern to the nDNA data, suggesting that gene flow has shifted over time.

Planchonella australis met only one signal of dispersal (Table 3) and is not considered a candidate for further study. We found low pairwise F_{st} values and a Mantel score that corresponds with IBD, consistent with long-term faunal connectivity (Table 2). The best supported sNMF model ($K=2$; Figure S1) and the PCA show the primary source of variation is across the Wide Bay-Burnett (CQLD), and there is low variation albeit latitudinal structure between populations south of the barrier (Figure 3d(ii-iii)). One sample from CQLD has a genotype that clusters with the populations south of the Wide-Bay Burnett, suggesting past or recent LDD (Signal 3). The cpDNA network shows high variation consistent with vicariance across the Wide Bay-Burnett and moderate haplotype diversity within and between the southern populations (Figure 3d(iv)). These patterns match that of the nDNA data and together suggest long-term population stability and periodic isolation rather than rapid migration and range expansion that we would expect of extensive Holocene faunal or anthropogenic dispersal. There is no cpDNA available for the CQLD sample that showed southern ancestry in the nDNA data, so it is unclear if the sample is a recent migrant.

Elaeocarpus bancroftii showed genomic patterns consistent with two signals of post-megafuna dispersal, and we considered it a candidate for further studies (Figure 1). We found support for Signal 1 with a combination of low pairwise F_{st} values and the absence of IBD, suggesting rapid migration (Table 3). The best supported sNMF model assumes $K=1$ (Figure S1), and there is weak population structure in the PCA, primarily across the CCL (Figure 3e(ii-iii)). The $K=3$ sNMF model is most concordant with the PCA and shows mixed genotypes that suggest admixture or ILS between sites within and north of the BMC (Signal 2). We did not have cpDNA data for this species, and so could not test for Signal 4.

Large fruit with unknown Indigenous use

We assessed *Endiandra globosa* in the AWT and NSW separately, due to the large geographic and genetic disjunction between the two regions. In the AWT, the genomic patterns in *E. globosa* were consistent with only one signal of dispersal (Figure 1). We found high pairwise F_{st} values over short distances that correspond with IBD, suggesting long-term isolation (Table 3). The best supported sNMF model ($K=3$; Figure S1) and PCA revealed structure across the CCL, and outlier genotypes in WT potentially indicative of LDD (Signal 3; Figure 3f(ii-iii)). The cpDNA data is mostly concordant with the nDNA patterns and shows haplotype divergence across the CCL and haplotype-sharing between neighboring sites (Figure 3f(iv)).

As there were only two *E. globosa* sites sampled in NNSW, we could not perform the Mantel or sNMF analyses for this region. We found *E. globosa* in NNSW matched one signal of dispersal and we did not consider it a candidate for further study (Figure 1). According to the PCA, most variation is between sites though there are outlier samples in HS, suggesting LDD (Signal 3; Figure 3f(iii)). The cpDNA shows the opposite trend to the nDNA data, with greater haplotype variation within BH and low variation between sites (Figure 3f(iv)). However, we did not find evidence of haplotype dispersal (Signal 4).

Endiandra compressa did not show any genomic patterns consistent with dispersal and was not considered for further study (Table 3). We found high F_{st} values, and a high Mantel correlate consistent with limited faunal dispersal (Table S1; Table 3). The primary source of variation was across the BMC according to the best supported sNMF model ($K=2$; Figure S1) and PCA ordination, though there is some structure across the CCL (Figure 3g(iii)). The cpDNA network contrasts with the nDNA patterns and shows greater divergence between geographically proximate sites south of CCL while differentiation across the BMC is comparatively low (Figure 3g(iv)).

The genomic patterns in *Endiandra pubens* did not match any signals of dispersal and was not considered for further study (Figure 1). The populations in NNSW have moderate pairwise F_{st} values and a Mantel score consistent with IBD rather than rapid migration (Table 2). The best-supported sNMF model ($K=2$; Figure S1) and PCA reveal divergence between NNSW and CQLD (Figure 3h(ii-iii)). The PCA shows one outlier sample from NNSW, that may indicate LDD, however this is not evident in the sNMF models. The cpDNA network conflicts with the nDNA data and shows greater variation within NNSW than between regions (Figure 3h(iv)).

We found only one genomic signal of dispersal in *Niemeyera prunifera* though we regard it as a candidate for investigation of Indigenous dispersal (Table 3). We did not find support for Signal 1 and *N. prunifera* has moderate pairwise F_{st} values and a high Mantel correlate that suggests IBD. The best supported sNMF model ($K=3$; Figure S1) and PCA show differentiation between CQLD and the AWT and across the BMC, though no evidence of outliers or admixture (Figure 3i(ii-iii)). The cpDNA network displays high diversity within populations and only moderate differentiation between populations (Figure 3i(iv)). The relationships between some haplotypes are not geographically concordant and are consistent with LDD (Signal 4), including across the BMC. There is weaker population structure in the cpDNA compared with the nDNA data and may suggest past rapid migration followed by a decrease in dispersal over time.

Niemeyera whitei did not correspond with any signals and we did not consider it a candidate for further study (Table 3). We found high pairwise F_{st} values that correspond moderately with IBD, consistent with limited faunal dispersal (Figure S1; Table 2). The best supported sNMF model ($K=3$; Figure S1) shows admixture or ILS, though this is not evident in the PCA clusters (Figure 3j(ii-iii)). The cpDNA network is concordant with the nDNA structure across the CRC, and the high variation suggests it is a long-term barrier (Figure 3j(iv)).

We found one signal of dispersal within *Elaeocarpus johnsonii* and did not consider it for further study (Table 3). The species has low-moderate F_{st} values, and a Mantel result consistent with IBD and long-term faunal dispersal (Table 2). The best-supported sNMF model ($K=2$; Figure S1) and PCA ordination show most variation is across the BMC and within sites (Figure 3k(ii-iii)). Both models indicate one MtSo sample has a mixed genotype that clusters with populations both sides of the BMC suggesting past LDD across the barrier (Signal 3). We did not have cpDNA data available to test for Signal 4.

Small fruit with known history of Indigenous use

Elaeocarpus grandis has genomic patterns that match two signals of dispersal, though we do not consider it a candidate for further study as we could not eliminate the influence of faunal vectors (Table 3). We performed separate Mantel tests for north and south of the BMC. To the south, we found low F_{st} values, and a low Mantel correlate consistent with rapid migration (Signal 1). North of the BMC, low F_{st} values combined with a moderate Mantel score consistent with IBD driven by widespread faunal dispersal (Table S1; Table 2). The best supported sNMF model ($K=3$; Figure S1) is concordant with the PCA (Figure 3l(ii-iii)). Both analyses identified three relatively homogeneous population clusters separated by the BMC and a 2° latitudinal disjunction to the south, consistent with extensive regional faunal dispersal. The models also show four samples from north of the BMC cluster with populations south of the barrier, potentially indicating LDD (Signal 3).

Small fruit with unknown Indigenous use

The genomic patterns in *Endiandra discolor* align with two signals of dispersal, however the species was not considered a candidate for further study as it showed patterns more consistent with widespread faunal dispersal (Table 3). We performed a Mantel test in NSW only, as the other sites were too disjunct for a meaningful analysis. We found low pairwise F_{st} values and a very low Mantel score that suggests rapid migration consistent with Signal 1, though this is likely facilitated by widespread faunal dispersal (Table S1; Table 2). Each of the sNMF models are equally supported and $K=4$ shows admixed profiles between NSW-SEQ and SEQ-CQLD, consistent with Signal 2 (Figure S1; Figure 3m(ii)). However, given SEQ and

CQLD cluster separately in the PCA (Figure 3m(iii)), incomplete lineage sorting is more plausible than admixture. In the chloroplast haplotype network, *E. discolor* has one widespread haplotype distributed from the AWT to NNSW and some unique northern haplotypes differentiated along a latitudinal gradient (Figure 3m(iv)). This pattern is consistent with the nDNA data and suggests periods of isolation across latitudinal barriers and subsequent widespread re-connectivity.

The patterns we found in *Pleioluma queenslandica* were consistent with long-term faunal dispersal and the species was not considered a candidate for further study (Table 3). We found low pairwise F_{st} values across more than 7° of latitude (Table S1), though we had insufficient samples to test IBD within regions. The best-supported sNMF models ($K=1-2$; Figure S1) and PCA ordination show clinal variation in CQLD consistent with admixture or ILS between a northern and southern genotype (Signal 2; Figure 3m(ii-iii)). The cpDNA network shows range-wide haplotype sharing with moderate variation between haplotypes (Figure 3g). This is consistent with the nDNA data and suggests a stable history of gene flow rather than LDD.

We did not find any genomic signals in *Elaeocarpus reticulatus* and it was not considered for further investigation of Indigenous dispersal (Table 3). We found high pairwise F_{st} values that moderately correlate with IBD (Table 2). The best supported sNMF model ($K=3$; Figure S1) and the PCA ordination show the primary variation is across the CRC (Figure 3o(ii-iii)). There is also variation between coastal and upland sites north of the barrier and between the sites west and south of the barrier.

Discussion

Reconstructing the demographic history of non-domesticated species with coalescent models can be a costly and challenging endeavor that requires extensive sampling and/or deep sequencing. Therefore, we sought to develop a simple and cost-effective screening strategy that can be used to screen out species with genomic patterns consistent with long-term widespread faunal dispersal and identify “candidate” species that show dispersal signals that warrant further investigation. The genomic signals we found in *Castanospermum australe* confirm the utility of our workflow, in which extensive Indigenous dispersal has already been demonstrated [32]. Our findings demonstrate that fast and widely used population genomic analyses can be employed to identify candidate species from opportunistically collected and somewhat sparse sample sets. Another advantage of our approach is that the genomic tests did not require any assumptions about the biogeographic history of the study species, making it a good first step. Our approach can be replicated in other study systems that have undergone a megafauna extinction and where Indigenous dispersal has been recorded.

We identified five candidates out of 15 species that show interesting dispersal patterns of putative Indigenous influence. Neither of the large-fruited study species displayed signals of ongoing or widespread dispersal. This raises the hypothesis that prior to putative Indigenous dispersal events within the candidate species, there was a considerable period of isolation driven by the megafauna extinction. As a next step, coalescent analyses can be used to estimate the antiquity of dispersal events. Based on the genomic patterns we found, we have suggested some hypothetical scenarios of past Indigenous dispersal to explore for each candidate (Table 4). Candidates can be co-analysed with ecologically similar and co-distributed species to contrast the influence of Indigenous versus faunal dispersal.

Table 4. Candidate species that warrant investigation of historical Indigenous dispersal and suggested follow up studies. Species were identified as candidates if they displayed at least one of five genomic signals of dispersal that can be tested as anthropogenic vs non-anthropogenic in future studies, and generated hypotheses on Indigenous dispersal scenarios. We considered species as weak candidates if they displayed genomic patterns from which putative Indigenous dispersal could not be differentiated from widespread faunal dispersal or if they showed an absence of dispersal events. NSW=northern New South Wales, QLD=central Queensland. BMC=Black Mountain Corridor. LDD=long distance dispersal, IBD=isolation by distance, ILS=incomplete lineage sorting.

Species	Dispersal hypotheses	Follow up studies
<i>Castanospermum australe</i>	a) During the Holocene, <i>C. australe</i> was introduced to NSW from a single northern lineage by humans or oceanic currents, and/or humans rapidly expanded its range in the region. b) Extensive human-dispersal pathways in NSW disrupted natural patterns of IBD evident in the north. c) Upland populations in NSW were established by humans. Founder effects and/or a subsequent lack of gene flow into these populations has led to drift.	a) Sample upland sites and multiple lowland sites in multiple catchments across the species' distribution, including QLD. b) Whole-genome sequencing for phased dataset that can be used to identify the geographic distribution of identity-by-descent blocks and recent coalescent events. Select population samples within each region to date the arrival of <i>C. australe</i> in NSW and test for recent co-ancestry with northern genotypes. c) Employ directional migration models between catchments to verify non-water modes of dispersal and test putative human dispersal pathways inferred from ethnographic sources. d) Employ directional migration models within catchments to verify that connectivity has been lost at upland sites.
<i>Endiandra insignis</i>	a) Mid-late Holocene human-mediated dispersal between two previously isolated sites, B and CF. b) Holocene propagation along ancient walking routes between Atherton Tableland and the coast. c) A subsequent decline or loss of dispersal has led to drift between populations.	a) Sample additional populations at Atherton where there is archaeological evidence of <i>E. insignis</i> seed processing, and east along ancient walking routes between the Atherton Tableland and the coast. b) To investigate dispersal across the BMC and between isolated upland sites, sample additional sites north of the BMC and at southern part of the range near the most differentiated population at site B. c) Coalescent isolation with migration model to test for pre-Holocene vicariance between Bolinda and Curtain Fig, followed by Holocene-era LDD.
<i>Bielschmiedia bancroftii</i>	a) Following megafauna decline, a long history of isolation has driven extreme haplotype differentiation between sites. Bottlenecks have reduced nDNA diversity and overall differentiation between sites.	a) Additional cp-sequencing per population to identify further evidence of dispersal events. b) Isolation with migration coalescent models to test hypothesis of long-term vicariance followed by recent Indigenous-facilitated migration between sites.

	b) Reinforcement - Holocene-era Indigenous dispersal facilitated limited migration between sites.	
<i>Elaeocarpus bancroftii</i>	a) Rapid dispersal along cultural rather than geographic pathways. b) Reinforcement - Holocene-era Indigenous dispersal facilitated limited migration and admixture across the BMC.	a) Cp-sequencing to better infer dispersal between sites. b) Coalescent model to evaluate ILS versus admixture between populations across the BMC.
<i>Niemeyera prunifera</i>	a) Mid-late Holocene human-mediated LDD explains the disjunct distribution of <i>N. prunifera</i> in the AWT and CQLD and the migration of cp-haplotypes between geographically distant sites. b) A subsequent decline or loss of dispersal has led to drift and strong nDNA structure.	a) Sample additional populations in southern AWT to investigate the likelihood of vicariance versus LDD as the cause of disjunct distribution between AWT and CQLD. b) Coalescent analysis to date divergence between AWT and CQLD. Divergence < 10 kya is likely human LDD, ≥ 21 kya is likely climate-driven vicariance. c) Test for founder effects in CQLD, as support for LDD.

An important underpinning of our screening strategy was to eliminate faunal vectors (or other non-anthropogenic vectors) as the sole mode of dispersal within candidate species. To test the efficacy of our approach, we compared simulated and real genomic datasets of large and small-fruited species with edible fruit. Most of the candidates we identified are large-fruited species with a known history of Indigenous use and carry signals of dispersal that are distinctive from widespread faunal dispersal. Likewise, the results of our simulation study demonstrate that long-term range-wide faunal dispersal scenarios expected of small-fruited species yield patterns of population differentiation that are clearly distinct from species with a history of post-megafauna isolation followed by Indigenous dispersal.

Our findings confirm that dispersal-limited plants are more likely to carry genomic signatures that are suitable for investigating past Indigenous dispersal. First, we used pairwise genetic distance estimates to demonstrate that the large-fruited study species are more dispersal-limited than the small-fruited and wind-dispersed species. Then in the screening process, we found that the barrier effects evident in large-fruited species made distinctive signals of dispersal more apparent, particularly putative signals of LDD (Signal 3-4). Interestingly, we did not detect an overall trend of greater gene flow in the AWT (where a larger cohort of faunal dispersers still survives) compared with NNSW. This was corroborated by the *Castanospermum australe* results, which displayed greater dispersal in NNSW compared with AWT, suggesting that dispersal by cassowaries or other large fauna has not confounded the dispersal signals detected in AWT.

By the same token, we found that small-fruit species are generally less suitable for investigating Indigenous dispersal. While some species such as *Pleioluma queenslandica* and *Endiandra discolor* have cpDNA patterns consistent with faunal-mediated post-glacial recolonisation, the results are less clear-cut in other species. For instance, *Elaeocarpus grandis* and *Planchonella australis* continue to be well-utilised by various Aboriginal groups and show nDNA signals of LDD. However, *P. australis* shows CpDNA structure more consistent with long-term isolation than extensive faunal or Indigenous mediated dispersal. Given their small fruit size in general, it is difficult to differentiate the relative influence of humans from volant frugivores or other natural dispersal vectors. In the case of *E. grandis*, rainforest restoration activities over the past few decades may also confound dispersal signals.

Out of all the candidates, *Niemeyera prunifera* is the only species for which we could not find any literature or verbal reports of use by Indigenous groups. The patterns we found for this species highlights the utility of genomic tests to investigate historical Indigenous dispersal, even in the absence of strong ethnographic evidence. On the other hand, we identified *Endiandra globosa* as a poor candidate for Indigenous dispersal studies, despite archaeological evidence that the seed of morphologically similar and closely-related Laurels were processed and consumed during the late Holocene [71,72]. It is worth noting that seed biology may prohibit successful attempts at long-distance dispersal of some food trees, as the seed of many Australian rainforest species do not store well and would not survive long journeys[84].

Conclusions

Overall, the workflow we have presented enabled us to identify genomic signals of dispersal that may be attributed to the past influence of Indigenous peoples and can be differentiated from widespread faunal dispersal. This includes species with edible fruit that lack published ethnographic evidence of Indigenous use. We found that the utilisation of both nDNA and cpDNA data was important for detecting putative dispersal signals, and its absence from the *Elaeocarpus* datasets made it more difficult to assess these species. We also found that three cpDNA samples per site was not always sufficient to identify dispersal events, and more samples would have aided interpretation where evidence of LDD was found in the nDNA. Therefore, we recommend that future screening studies utilise cpDNA sequence data for all samples.

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Appendix A: Simulation study to compare the genomic signals of hypothetical Indigenous versus faunal-mediated dispersal scenarios.

Materials & Methods

We used fastsimcoal 2.7 (Excoffier et al. 2013, 2021) to simulate 9 hypothetical dispersal scenarios for species with a history of long-term isolation (1 model), long-term faunal mediated dispersal (2 models), or Indigenous dispersal following long-term isolation (6 models). To compare the genomic impact of dispersal traits on population differentiation, we constructed models that varied only in the timing and pattern of historical migration events (see Table A1 for model parameters and figure captions for interpretation). The migration rate (Nm) specified at each historical event are outlined in Table A2. Each model was simulated with 100 replicates.

The demographic models assume a 110 ky cycle of habitat suitability that approximates the climatic history of the Australian continent. We simulated high migration rates and population growth during warm-wet periods (110 kya and 5-9 kya), moderate migration rates and population growth during interglacial periods (9-18 kya, 40-60 kya, 70-110 kya), and no migration with a population bottleneck during glacial periods (60-70 kya and 18-25 kya). All models consist of 6 demes with an effective population size (N_e) of 400 with population growth = 0, and we sampled 20 diploid individuals per deme. This excludes the models that simulate mid-Holocene range expansion, in which deme0 has $N_e=200$ and originates from deme1.

To simulate independent unlinked SNP loci analogous to DArTseq, we followed the procedure recommended by Excoffier et al. (2021) to generate short DNA sequences over a large number of chromosomes that are only mutate via transitions (transition rate = 1). Under a finite-site mutation model, genes were simulated across 240 chromosomes that each contain 200 DNA sequence linkage blocks (100 bp). We fixed the recombination rate to $1.0e-9$ and the mutation rate to $2.0e-8$. We selected these values to ensure there were no recombination events and a maximum of one mutation per loci. For each scenario, we simulated historical events assuming a 20-year and 40-year generation time ($t=absolute\ time/generation\ time$). We calculated pairwise F_{st} values (Slatkin's distance) from the output of each simulation with 100 permutations ($p=0.05$) in Arlequin 3.5.2.2 (Excoffier and Lischer 2010).

Table Appendix 1 Historical events that determine coalescence under 9 dispersal scenarios. The first three columns indicate the time of historical events in years or generations before present assuming a 20 year and 40 year generation time (“gen20” and “gen40”). Fission between demes was used to simulate rapid range expansion events. Going backwards in time, the “source” is the deme from which genes originate, “sink” is the deme to which they go, and “m” indicates the percentage of genes in the sink that originate from the source (1=all genes). Ne is re-scaled by “size” at each historical event and by the “growth rate” per generation until the next event (negative values imply population expansion backwards in time). The migration matrix at each historical event is indicated for each dispersal scenario. fd=post-glacial faunal dispersal, fd+exp=post-glacial faunal dispersal and range expansion, nd=post-megafauna isolation, hd1-6=post-megafauna Indigenous dispersal scenarios.

years	gen20	gen40	source	sink	m	size	growth rate	Migration matrix according to dispersal scenarios								
								fd	fd+exp	nd	hd1	hd2	hd3	hd4	hd5	hd6
0	0	0	0	0	0	1	0	0	0	2	2	2	2	2	2	2
200	10	5	0	0	0	1	-0.02	-	-	-	6	6	-	-	7	-
3999	199	99	0	0	0	1	-0.02	-	-	-	-	-	6	-	-	-
4000	200	100	0	0	0	1	-0.02	-	-	-	-	-	-	-	-	7
4999	249	124	0	1	1	1	-0.02	-	-	-	-	6	2	2	-	-
5000	250	125	0	0	0	1	-0.02	1	1	2	2	2	2	2	2	2
6000	300	150	0	1	1	1	-0.02	-	1	-	-	-	-	-	-	-
9000	450	225	0	0	0	1	-0.005	0	0	2	2	2	2	2	2	2
18000	900	450	0	0	0	0.5	0.02	2	2	2	2	2	2	2	2	2
25000	1250	625	0	0	0	1	0.005	3	3	2	2	2	2	2	2	2
40000	2000	1000	0	0	0	1	-0.005	0	0	2	2	2	2	2	2	2
60000	3000	1500	0	0	0	0.5	0.02	2	2	-	2	2	2	2	2	2
70000	3500	1750	0	0	0	1	-0.005	0	0	4	4	4	4	4	4	4
110000	5500	2750	0	0	0	1	-0.02	1	1	5	5	5	5	5	5	5

Table Appendix 2 Migration matrices employed in simulation models.

Matrix	Migration	Nm	Dispersal vector
0	Symmetric distance-weighted migration with barrier between deme2 and deme3	0.0005, 0.0002, 0.0000	Volant fauna
1	High symmetric distance-weighted migration with no barrier	0.0200, 0.0100, 0.0050, 0.0025, 0.0012	Volant fauna
2	No migration	0.0000	NA
3	Low symmetric distance-weighted migration with barrier between deme2 and deme3	0.0025, 0.0012, 0.0000	Volant fauna
4	Symmetric stepping-stone with barrier between deme2 and deme3	0.0050, 0.0000	Megafauna
5	High symmetric stepping-stone migration with no barrier	0.0200, 0.0000	Megafauna
6	Low island migration model	0.0025	Human
7	Low asymmetric stepping-stone migration	0.0025	Human

Results

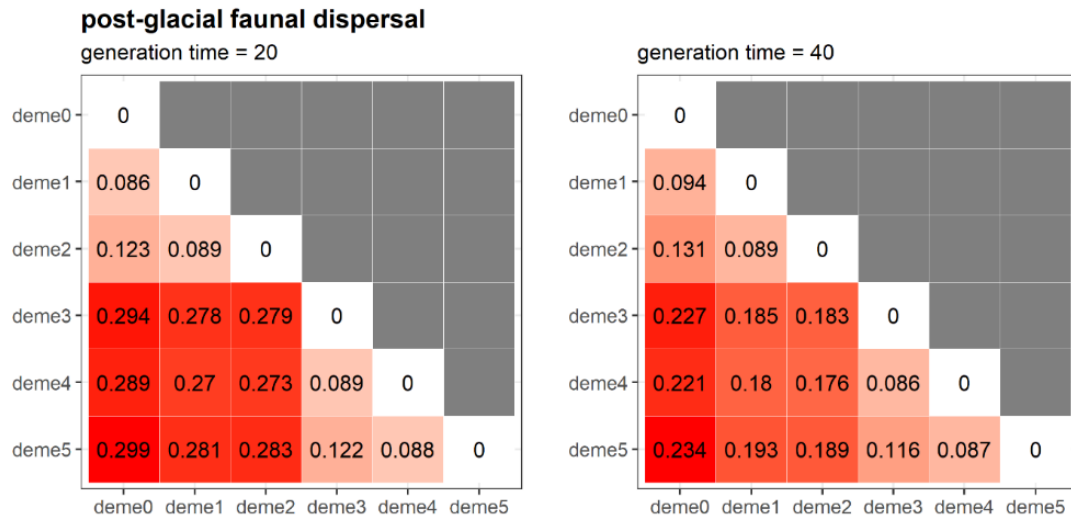


Figure Appendix 1 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-glacial faunal-mediated dispersal scenario ("fd" in Table A1). This scenario of faunal dispersal assumes a symmetric distance-weighted migration matrix.

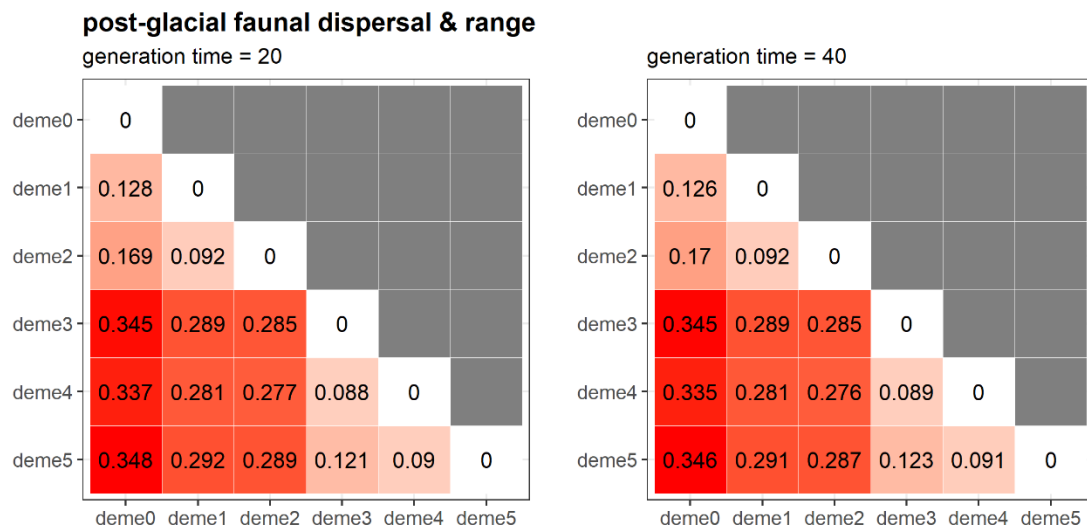


Figure Appendix 2 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-glacial faunal-mediated dispersal scenario ("fd+exp" in Table A1). This scenario of faunal dispersal assumes that deme0 was established by propagules from deme1 6kya, and a symmetric distance-weighted migration matrix.

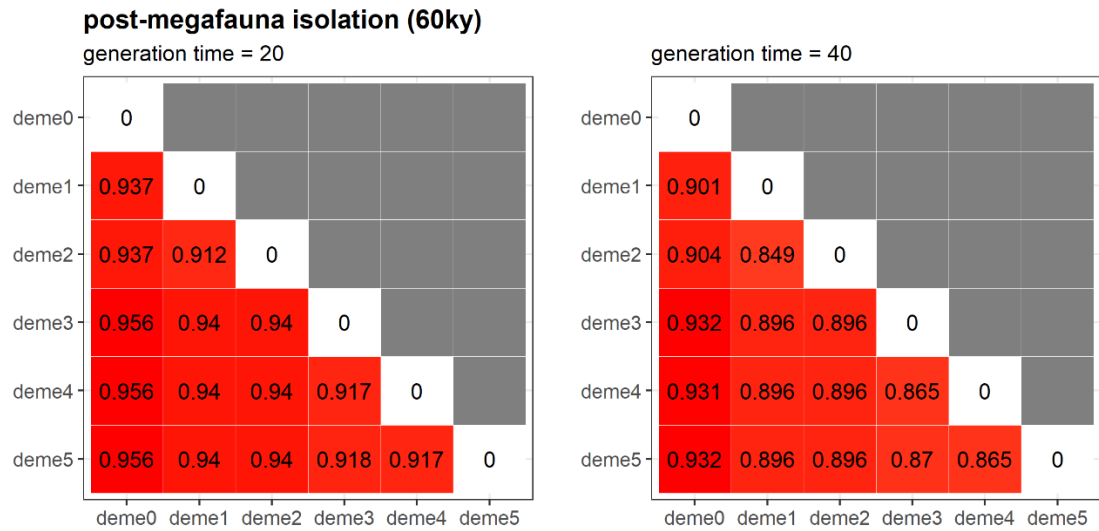


Figure Appendix 3 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-megafauna dispersal scenario ("nd" in Table A1). This dispersal scenario assumes that there has been no migration for 60,000 years (3500 or 1750 generations).

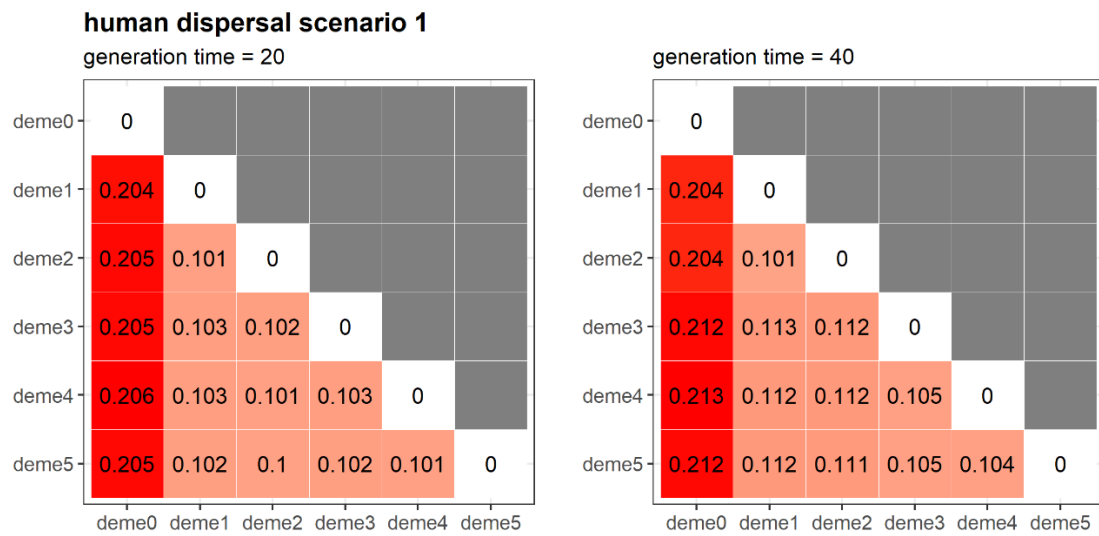


Figure Appendix 4 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-megafauna Indigenous-mediated dispersal scenario ("hd1" in Table A1). This scenario of Indigenous dispersal assumes a symmetric island model of migration between all demes from 5000-200 years ago.

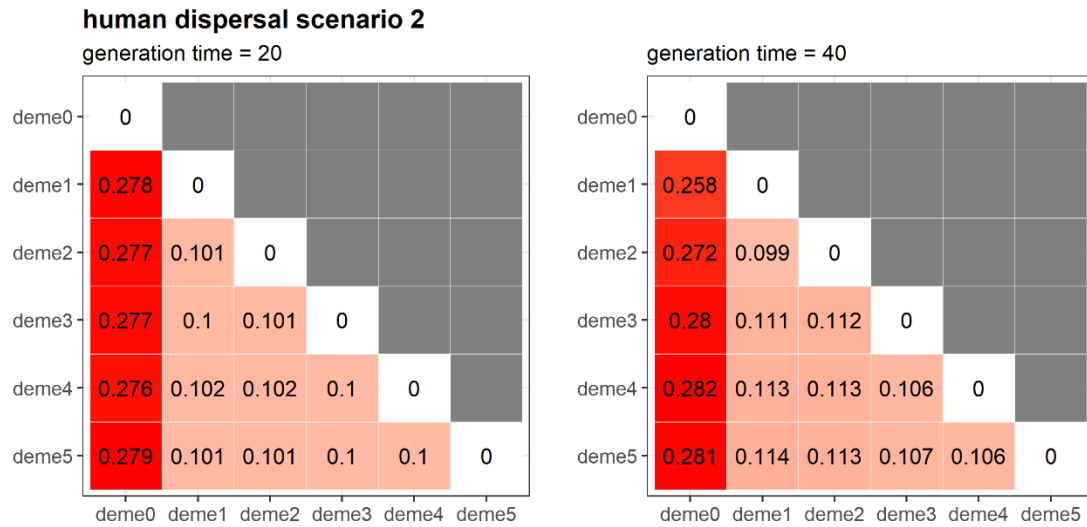


Figure Appendix 5 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-megafauna Indigenous-mediated dispersal scenario ("hd2" in Table A1). This scenario of Indigenous dispersal assumes that deme0 was established by propagules from deme1 5kya, followed by a symmetric island model of migration between all demes between 5000-200 years ago.

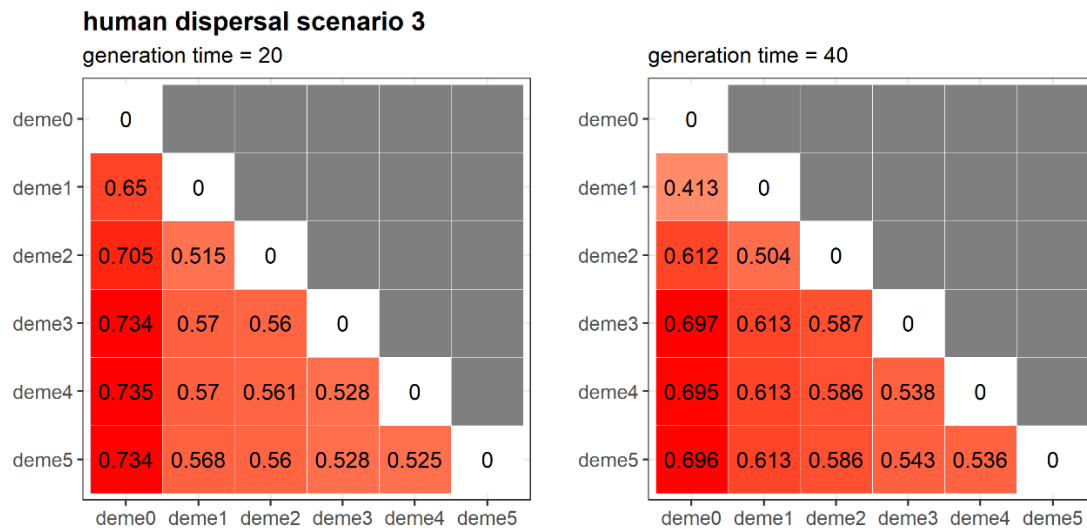


Figure Appendix 6 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-megafauna Indigenous-mediated dispersal scenario ("hd3" in Table A1). This scenario of Indigenous dispersal assumes that deme0 was established by propagules from deme1 5kya, followed by a symmetric island model of migration between all demes between 5000-4000 years ago.

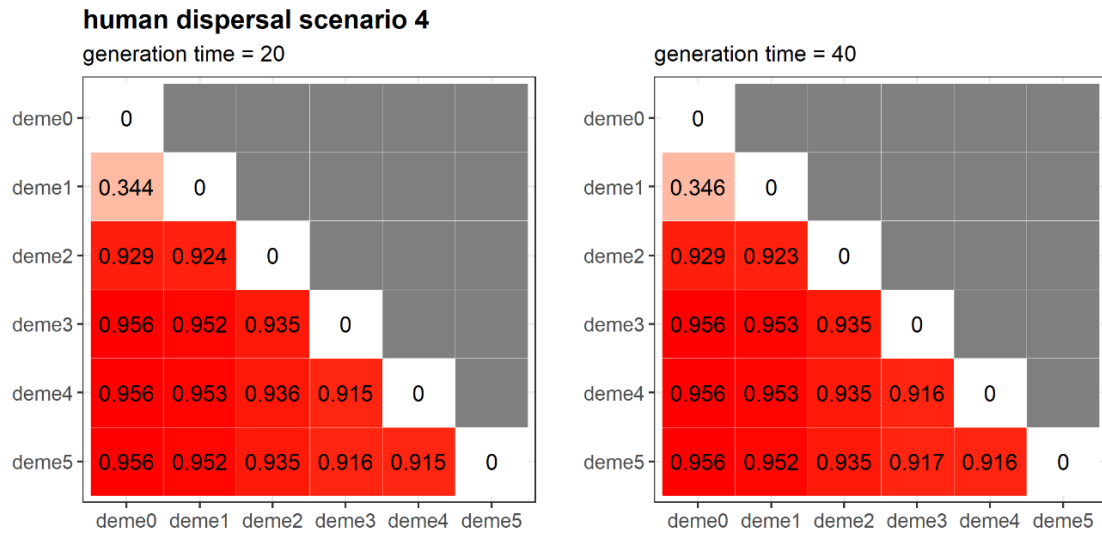


Figure Appendix 7 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-megafauna Indigenous-mediated dispersal scenario ("hd4" in Table A1). This scenario of Indigenous dispersal assumes that deme0 was established by propagules from deme1 5kya, with no further migration.

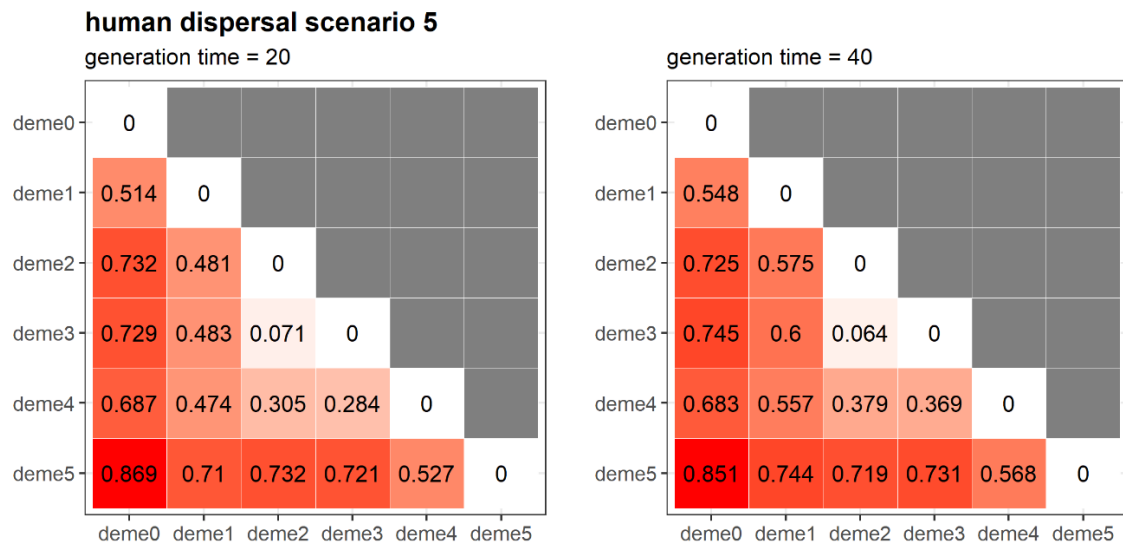


Figure Appendix 8 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-glacial faunal-mediated dispersal scenario ("hd5" in Table A1). This scenario of Indigenous dispersal assumes an asymmetric stepping-stone model of migration between 5000-200 years ago.

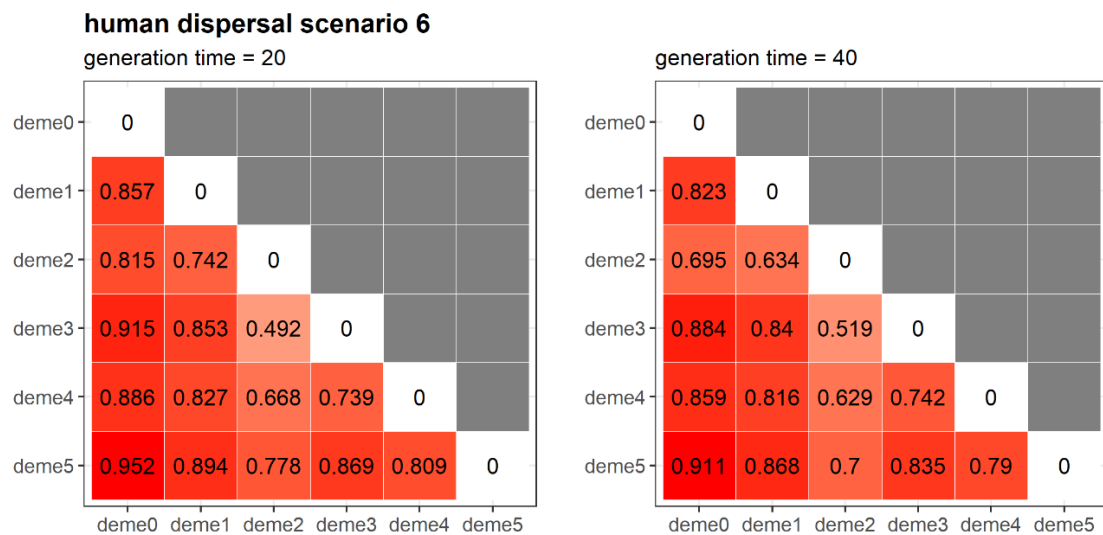


Figure Appendix 9 The mean pairwise F_{st} values calculated across 100 replicate simulations of a post-glacial faunal-mediated dispersal scenario ("hd6" in Table A1). This scenario of Indigenous dispersal assumes an asymmetric stepping-stone model of migration between 5000-4000 years ago.

References

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- Excoffier, L., Dupanloup, I., Huerta-Sánchez, E., and M. Foll (2013) Robust demographic inference from genomic and SNP data. *PLOS Genetics*. **2013**, *9*(10), e1003905.
- Excoffier, L., Marchi, N., Marques, D.A., Matthey-Doret, R., Gouy, A., Sousa, V.C. fastsimcoal2: demographic inference under complex evolutionary scenarios. *Bioinformatics*. **2021**, *37*(24), 4882–4885, doi: <https://doi.org/10.1093/bioinformatics/btab468>.

Supplementary Materials

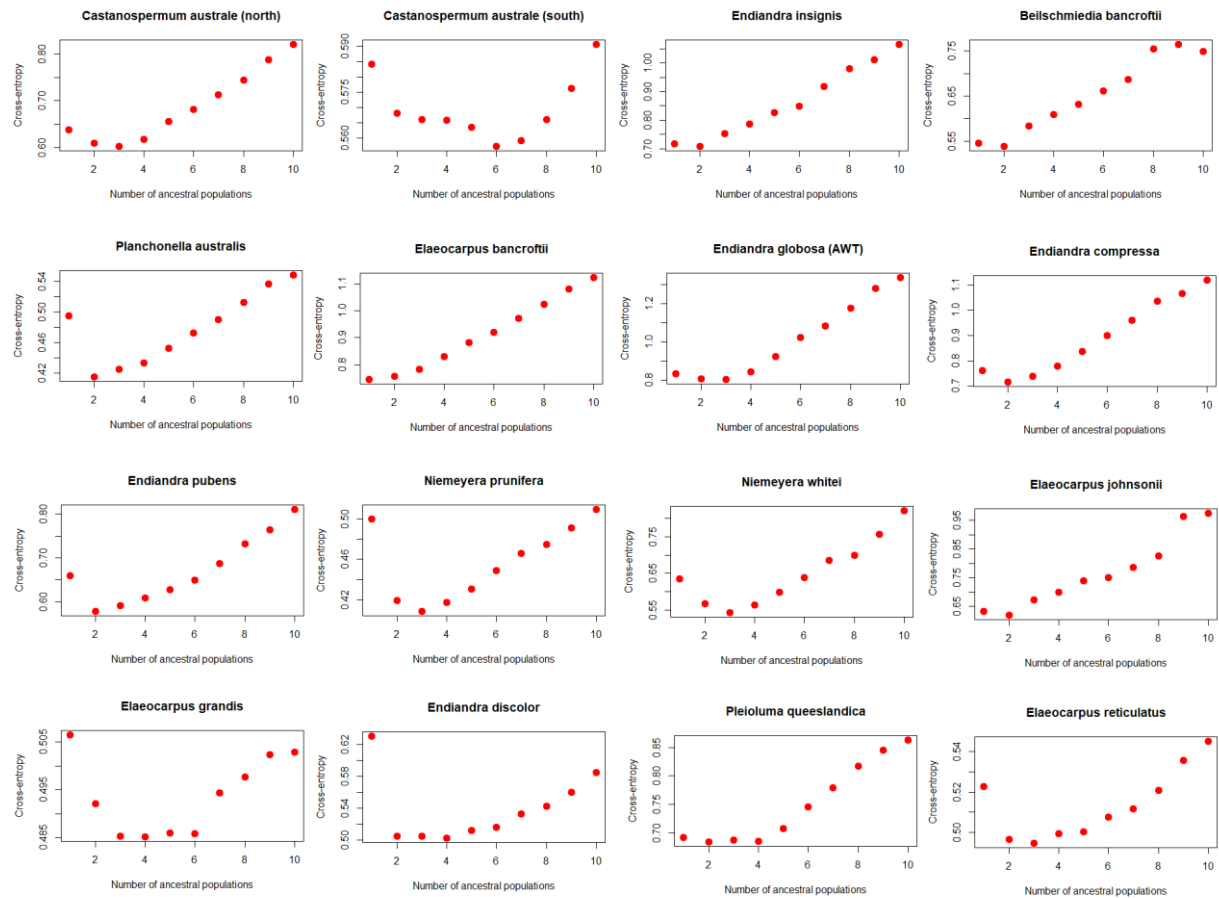


Figure S1: Cross-entropy criterion plotted against the number of ancestral gene pools (K) used to construct sNMF models. The smallest criterion was used to help assess the model that best described the genomic variance within each species.

Table S1. Pairwise genetic and geographic distance values used to calculate each species' Mantel score and construct violin plots of average pairwise F_{st} estimates amongst species grouped by fruit traits.

Fruit trait (mm)	Family	Species	Site1	Site2	distance (km)	F_{st}
edible >30	Elaeocarpaceae	<i>Elaeocarpus bancroftii</i>	Malbon Thompson Range	Mt Sorrow	110	0.118
edible >30	Elaeocarpaceae	<i>E. johnsonii</i>	WooroonooranBF	Mt Sorrow	151	0.220
edible >30	Elaeocarpaceae	<i>E. johnsonii</i>	Mt Sorrow	WooroonooranW	150	0.230
edible >30	Elaeocarpaceae	<i>E. johnsonii</i>	WooroonooranBF	WooroonooranW	6	0.072
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Dorrigo D	209	0.253
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Dorrigo D	206	0.150
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Dorrigo D	203	0.156
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Dorrigo D	201	0.236
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Junuy Jurum	196	0.265

edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Junuy Jurum	192	0.162
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Junuy Jurum	188	0.168
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Junuy Jurum	188	0.249
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Nymboi-Binderay	184	0.251
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Nymboi-Binderay	179	0.147
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Nymboi-Binderay	177	0.234
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Nymboi-Binderay	176	0.154
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Dorrigo D	171	0.266
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broadwater	Dorrigo D	161	0.224
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Junuy Jurum	157	0.276
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Washpool M	155	0.235
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Washpool C	155	0.278
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Washpool C	152	0.264
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Washpool M	151	0.224
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broadwater	Junuy Jurum	147	0.236
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Nymboi-Binderay	146	0.262
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Washpool M	144	0.146
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Washpool C	143	0.179
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Washpool M	140	0.150
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Washpool C	139	0.185
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broadwater	Nymboi-Binderay	137	0.223
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Washpool C	126	0.291
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Washpool M	125	0.245
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broadwater	Washpool C	119	0.251
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broadwater	Washpool M	118	0.211
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool C	Dorrigo D	109	0.104
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool M	Dorrigo D	103	0.078
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool C	Junuy Jurum	96	0.113
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool M	Junuy Jurum	90	0.088
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool C	Nymboi-Binderay	80	0.107
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool M	Nymboi-Binderay	74	0.088
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Broadwater	50	0.211
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Broadwater	49	0.129
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Broadwater	48	0.221

edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Wardell	41	0.245
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Broadwater	40	0.120
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Wardell	39	0.255
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Wardell	39	0.153
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Broken Head	Wardell	30	0.137
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nymboi-Binderay	Dorrigo D	30	0.039
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap	Broken Head	26	0.222
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Broken Head	26	0.209
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Nightcap	21	0.240
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Tyagarah	19	0.224
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nymboi-Binderay	Junuy Jurum	16	0.038
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Junuy Jurum	Dorrigo D	14	0.048
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Tyagarah	Broken Head	11	0.074
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Wardell	Broadwater	10	0.124
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Washpool C	Washpool M	6	0.062
edible <30	Elaeocarpaceae	<i>E. reticulatus</i>	Nightcap1	Nightcap	4	0.031
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Bridle Creek	Mt Sorrow	101	0.114
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Malbon Thompson Range	Whyanbeel	86	0.114
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	JCU	Mt Sorrow	86	0.099
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Bridle Creek	Whyanbeel	71	0.073
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	JCU	Whyanbeel	61	0.062
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Mt Windsor	Mt Sorrow	53	0.100
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Mossman Gorge	Mt Sorrow	45	0.098
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Whyanbeel	Mt Sorrow	36	0.073
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Malbon Thompson Range	Bridle Creek	27	0.147
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Malbon Thompson Range	JCU	25	0.115
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Bridle Creek	JCU	21	0.077
edible >30	Elaeocarpaceae	<i>E.bancroftii</i>	Mossman Gorge	Whyanbeel	9	0.060
edible >30	Fabaceae	<i>Castanospermum australe</i>	Iron Range NP	Gooligan Creek	605	0.233
edible >30	Fabaceae	<i>C. australe</i>	Iron Range NP	South Tolga Scrub	544	0.250
edible >30	Fabaceae	<i>C. australe</i>	Iron Range NP	Cape Tribulation	440	0.237
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Orara	334	0.139
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Victoria Park III	242	0.210
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Big Scrub	211	0.173
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Moore Park	185	0.117
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Razorback	184	0.123

edible >30	Fabaceae	<i>C. australe</i>	Hogans Scrub	Orara	179	0.159
edible >30	Fabaceae	<i>C. australe</i>	Cape Tribulation	Gooligan Creek	174	0.193
edible >30	Fabaceae	<i>C. australe</i>	Mary Cairncross	Hogans Scrub	174	0.138
edible >30	Fabaceae	<i>C. australe</i>	Razorback	Orara	152	0.119
edible >30	Fabaceae	<i>C. australe</i>	Moore Park	Orara	149	0.125
edible >30	Fabaceae	<i>C. australe</i>	Big Scrub	Orara	136	0.188
edible >30	Fabaceae	<i>C. australe</i>	Victoria Park III	Orara	112	0.218
edible >30	Fabaceae	<i>C. australe</i>	Cape Tribulation	South Tolga Scrub	110	0.205
edible >30	Fabaceae	<i>C. australe</i>	Moore Park	Victoria Park III	73	0.190
edible >30	Fabaceae	<i>C. australe</i>	Hogans Scrub	Victoria Park III	72	0.123
edible >30	Fabaceae	<i>C. australe</i>	Razorback	Victoria Park III	66	0.180
edible >30	Fabaceae	<i>C. australe</i>	South Tolga Scrub	Gooligan Creek	64	0.094
edible >30	Fabaceae	<i>C. australe</i>	Hogans Scrub	Moore Park	59	0.119
edible >30	Fabaceae	<i>C. australe</i>	Moore Park	Big Scrub	50	0.155
edible >30	Fabaceae	<i>C. australe</i>	Hogans Scrub	Razorback	48	0.116
edible >30	Fabaceae	<i>C. australe</i>	Hogans Scrub	Big Scrub	43	0.088
edible >30	Fabaceae	<i>C. australe</i>	Razorback	Big Scrub	41	0.148
edible >30	Fabaceae	<i>C. australe</i>	Big Scrub	Victoria Park III	31	0.118
edible >30	Fabaceae	<i>C. australe</i>	Razorback	Moore Park	12	0.045
edible >30	Lauraceae	<i>Beilschmiedia bancroftii</i>	Upper Tully Range	Mt Windsor	175	0.191
edible >30	Lauraceae	<i>B. bancroftii</i>	Upper Tully Range	Mt Lewis	131	0.047
edible >30	Lauraceae	<i>B. bancroftii</i>	Lamb Range	Mt Windsor	114	0.169
edible >30	Lauraceae	<i>B. bancroftii</i>	Upper Tully Range	Lamb Range	71	0.062
edible >30	Lauraceae	<i>B. bancroftii</i>	Lamb Range	Mt Lewis	68	0.047
edible >30	Lauraceae	<i>B. bancroftii</i>	Mt Lewis	Mt Windsor	46	0.159
edible >30	Lauraceae	<i>B. tooram</i>	Upper Tully Range	Lamb Range	64	0.056
edible >30	Lauraceae	<i>B. volckii</i>	Wooroonooran C	Tulip	147	0.350
edible <30	Lauraceae	<i>Cryptocaria glaucesens</i>	Nightcap	Never Never	204	0.179
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap S	Never Never	200	0.169
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Mt Hyland	198	0.196
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap	Mt Hyland	195	0.186
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap S	Mt Hyland	191	0.177
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Hortons Creek	173	0.157
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap	Hortons Creek	170	0.148
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap S	Hortons Creek	166	0.140
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Washpool C	143	0.190

edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap	Washpool C	141	0.180
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap S	Washpool C	138	0.171
edible <30	Lauraceae	<i>C. glaucesens</i>	Washpool C	Never Never	107	0.053
edible <30	Lauraceae	<i>C. glaucesens</i>	Washpool C	Mt Hyland	78	0.062
edible <30	Lauraceae	<i>C. glaucesens</i>	Hortons Creek	Never Never	41	0.093
edible <30	Lauraceae	<i>C. glaucesens</i>	Mt Hyland	Never Never	36	0.047
edible <30	Lauraceae	<i>C. glaucesens</i>	Hortons Creek	Mt Hyland	27	0.106
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Nightcap S	10	0.034
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Nightcap	7	0.039
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap	Nightcap S	4	0.031
edible <30	Lauraceae	<i>C. glaucesens</i>	Nightcap N	Never Never	209	0.187
edible >30	Lauraceae	<i>Endiandra compressa</i>	Tulip	Wooroonooran South	172	0.301
edible >30	Lauraceae	<i>E. compressa</i>	Tulip	Bellenden Ker Lowlands	142	0.358
edible >30	Lauraceae	<i>E. compressa</i>	Bellenden Ker Lowlands	Wooroonooran South	42	0.125
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Ulidarra	862	0.515
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Nightcap	701	0.506
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Brunswick Heads	697	0.523
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Hogan's Scrub	665	0.505
edible <30	Lauraceae	<i>E. discolor</i>	Bulburin	Ulidarra	646	0.397
edible <30	Lauraceae	<i>E. discolor</i>	Bulburin	Nightcap	483	0.387
edible <30	Lauraceae	<i>E. discolor</i>	Bulburin	Brunswick Heads	479	0.408
edible <30	Lauraceae	<i>E. discolor</i>	Cooloola	Ulidarra	478	0.088
edible <30	Lauraceae	<i>E. discolor</i>	Bulburin	Hogan's Scrub	448	0.377
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Cooloola	424	0.504
edible <30	Lauraceae	<i>E. discolor</i>	Cooloola	Nightcap	301	0.079
edible <30	Lauraceae	<i>E. discolor</i>	Cooloola	Brunswick Heads	291	0.108
edible <30	Lauraceae	<i>E. discolor</i>	Cooloola	Hogan's Scrub	259	0.101
edible <30	Lauraceae	<i>E. discolor</i>	Hogan's Scrub	Ulidarra	224	0.069
edible <30	Lauraceae	<i>E. discolor</i>	Byfield	Bulburin	218	0.134
edible <30	Lauraceae	<i>E. discolor</i>	Bulburin	Cooloola	216	0.385
edible <30	Lauraceae	<i>E. discolor</i>	Brunswick Heads	Ulidarra	196	0.061
edible <30	Lauraceae	<i>E. discolor</i>	Nightcap	Ulidarra	180	0.031
edible <30	Lauraceae	<i>E. discolor</i>	Hogan's Scrub	Nightcap	44	0.057
edible <30	Lauraceae	<i>E. discolor</i>	Hogan's Scrub	Brunswick Heads	32	0.091
edible <30	Lauraceae	<i>E. discolor</i>	Brunswick Heads	Nightcap	23	0.047
edible >30	Lauraceae	<i>E. globosa</i>	Tchupala	Bellenden Ker Lowlands	42	0.232

edible >30	Lauraceae	<i>E. globosa</i>	Crawfords	Bellenden Ker Lowlands	41	0.250
edible >30	Lauraceae	<i>E. globosa</i>	Barong	Bellenden Ker Lowlands	32	0.254
edible >30	Lauraceae	<i>E. globosa</i>	Brunswick Heads	Hogans Scrub	31	0.095
edible >30	Lauraceae	<i>E. globosa</i>	Tchupala	Barong	11	0.107
edible >30	Lauraceae	<i>E. globosa</i>	Crawfords	Barong	10	0.126
edible >30	Lauraceae	<i>E. globosa</i>	Tchupala	Crawfords	3	0.078
edible <30	Lauraceae	<i>Elaeocarpus grandis</i>	Hidden Valley	Mt Windsor	676	0.281
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Mt Windsor	668	0.217
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Daintree	661	0.258
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Mt Windsor	659	0.201
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Daintree	657	0.205
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Daintree	649	0.188
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Mt Lewis	630	0.261
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Julatten	623	0.269
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Mt Lewis	622	0.197
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Julatten	615	0.211
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Mt Lewis	613	0.183
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Julatten	607	0.198
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Mt Baldy	557	0.251
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Mt Baldy	546	0.181
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Mt Baldy	537	0.168
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Ravenshoe S	522	0.211
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Bartle Frere	519	0.235
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Bartle Frere	510	0.164
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Ravenshoe S	508	0.145
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Bartle Frere	502	0.150
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Ravenshoe S	499	0.135
edible <30	Lauraceae	<i>E. grandis</i>	Hidden Valley	Paluma	368	0.224
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Paluma	347	0.150
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Paluma	338	0.137
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Daintree	338	0.111
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Mt Windsor	334	0.115
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Mt Lewis	292	0.102
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Julatten	286	0.119
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Mt Baldy	209	0.087
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Bartle Frere	184	0.060

edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Daintree	176	0.084
edible <30	Lauraceae	<i>E. grandis</i>	Paluma	Ravenshoe S	168	0.051
edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Mt Windsor	166	0.087
edible <30	Lauraceae	<i>E. grandis</i>	Bartle Frere	Mt Windsor	158	0.088
edible <30	Lauraceae	<i>E. grandis</i>	Bartle Frere	Daintree	154	0.078
edible <30	Lauraceae	<i>E. grandis</i>	Mt Baldy	Daintree	135	0.113
edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Mt Lewis	126	0.074
edible <30	Lauraceae	<i>E. grandis</i>	Mt Baldy	Mt Windsor	125	0.113
edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Julatten	121	0.090
edible <30	Lauraceae	<i>E. grandis</i>	Bartle Frere	Mt Lewis	112	0.068
edible <30	Lauraceae	<i>E. grandis</i>	Bartle Frere	Julatten	106	0.087
edible <30	Lauraceae	<i>E. grandis</i>	Mt Baldy	Mt Lewis	84	0.099
edible <30	Lauraceae	<i>E. grandis</i>	Mt Baldy	Julatten	79	0.116
edible <30	Lauraceae	<i>E. grandis</i>	Eungella	Hidden Valley	64	0.153
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Hidden Valley	59	0.168
edible <30	Lauraceae	<i>E. grandis</i>	Julatten	Daintree	58	0.058
edible <30	Lauraceae	<i>E. grandis</i>	Mt Windsor	Daintree	56	0.057
edible <30	Lauraceae	<i>E. grandis</i>	Mt Lewis	Daintree	56	0.040
edible <30	Lauraceae	<i>E. grandis</i>	Julatten	Mt Windsor	54	0.071
edible <30	Lauraceae	<i>E. grandis</i>	Mt Lewis	Mt Windsor	47	0.049
edible <30	Lauraceae	<i>E. grandis</i>	Bartle Frere	Mt Baldy	44	0.064
edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Bartle Frere	43	0.033
edible <30	Lauraceae	<i>E. grandis</i>	Ravenshoe S	Mt Baldy	42	0.059
edible <30	Lauraceae	<i>E. grandis</i>	Clarke Range	Eungella	9	0.025
edible <30	Lauraceae	<i>E. grandis</i>	Julatten	Mt Lewis	7	0.041
edible >30	Lauraceae	<i>Endiandra insignis</i>	Bolinda	Curtain Fig	77	0.255
edible >30	Lauraceae	<i>E. insignis</i>	Wooroonooran S	Curtain Fig	49	0.198
edible >30	Lauraceae	<i>E. insignis</i>	Bolinda	Wooroonooran S	29	0.147
edible >30	Lauraceae	<i>E. introrsa</i>	Dorrigo	Nightcap	210	0.242
edible >30	Lauraceae	<i>E. pubens</i>	Brunswick Heads	Bulburin	496	0.421
edible >30	Lauraceae	<i>E. pubens</i>	Nightcap	Bulburin	483	0.402
edible >30	Lauraceae	<i>E. pubens</i>	Hogan's Scrub	Bulburin	448	0.426
edible >30	Lauraceae	<i>E. pubens</i>	Brunswick Heads	Hogan's Scrub	49	0.108
edible >30	Lauraceae	<i>E. pubens</i>	Nightcap	Hogan's Scrub	44	0.076
edible >30	Lauraceae	<i>E. pubens</i>	Brunswick Heads	Nightcap	25	0.071
edible <30	Lauraceae	<i>Neolitsea dealbata</i>	Mt Warning	Junuy Juluum	236	0.224
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Junuy Juluum	231	0.283

edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Glennifer	226	0.210
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Glennifer	224	0.278
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Junuy Juluum	220	0.247
edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Junuy Juluum	220	0.212
edible <30	Lauraceae	<i>N. dealbata</i>	Broken Head	Junuy Juluum	215	0.265
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Glennifer	212	0.236
edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Glennifer	210	0.208
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Bruxner Park	207	0.218
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Bruxner Park	207	0.273
edible <30	Lauraceae	<i>N. dealbata</i>	Killen Falls	Junuy Juluum	205	0.251
edible <30	Lauraceae	<i>N. dealbata</i>	Broken Head	Glennifer	203	0.242
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Nymboi-binderay	202	0.249
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Nymboi-binderay	197	0.316
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Bruxner Park	194	0.246
edible <30	Lauraceae	<i>N. dealbata</i>	Killen Falls	Glennifer	193	0.234
edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Bruxner Park	189	0.210
edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Nymboi-binderay	186	0.246
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Nymboi-binderay	186	0.280
edible <30	Lauraceae	<i>N. dealbata</i>	Broken Head	Nymboi-binderay	182	0.288
edible <30	Lauraceae	<i>N. dealbata</i>	Broken Head	Bruxner Park	179	0.252
edible <30	Lauraceae	<i>N. dealbata</i>	Killen Falls	Nymboi-binderay	172	0.282
edible <30	Lauraceae	<i>N. dealbata</i>	Killen Falls	Bruxner Park	170	0.248
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Broken Head	64	0.206
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Killen Falls	62	0.188
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Broken Head	53	0.165
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Killen Falls	49	0.147
edible <30	Lauraceae	<i>N. dealbata</i>	Bruxner Park	Junuy Juluum	49	0.060
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Killen Falls	48	0.113
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Broken Head	47	0.130
edible <30	Lauraceae	<i>N. dealbata</i>	Nymboi-binderay	Bruxner Park	40	0.098
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Nightcap	34	0.094
edible <30	Lauraceae	<i>N. dealbata</i>	Nymboi-binderay	Junuy Juluum	34	0.060
edible <30	Lauraceae	<i>N. dealbata</i>	Bruxner Park	Glennifer	32	0.043
edible <30	Lauraceae	<i>N. dealbata</i>	Nymboi-binderay	Glennifer	30	0.066
edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Broken Head	30	0.111

edible <30	Lauraceae	<i>N. dealbata</i>	Nightcap	Killen Falls	28	0.081
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges 1	Nightcap	24	0.075
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Border Ranges	22	0.076
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Border Ranges 1	20	0.062
edible <30	Lauraceae	<i>N. dealbata</i>	Mt Warning	Nightcap	20	0.051
edible <30	Lauraceae	<i>N. dealbata</i>	Glennifer	Junuy Juluum	17	0.035
edible <30	Lauraceae	<i>N. dealbata</i>	Border Ranges	Border Ranges 1	14	0.038
edible <30	Lauraceae	<i>N. dealbata</i>	Broken Head	Killen Falls	11	0.081
wind <30	Myrtaceae	<i>Tristaniopsis collina</i>	Nightcap	Darkwood	217	0.189
wind <30	Myrtaceae	<i>T. collina</i>	Border Ranges	Dorrigo	211	0.158
wind <30	Myrtaceae	<i>T. collina</i>	Border Ranges	Moonpar	200	0.171
wind <30	Myrtaceae	<i>T. collina</i>	Border Ranges	Orara West	200	0.198
wind <30	Myrtaceae	<i>T. collina</i>	Nightcap	Dorrigo	199	0.141
wind <30	Myrtaceae	<i>T. collina</i>	Nightcap	Moonpar	188	0.147
wind <30	Myrtaceae	<i>T. collina</i>	Nightcap	Orara West	185	0.180
wind <30	Myrtaceae	<i>T. collina</i>	Orara West	Darkwood	39	0.140
wind <30	Myrtaceae	<i>T. collina</i>	Moonpar	Darkwood	29	0.105
wind <30	Myrtaceae	<i>T. collina</i>	Border Ranges	Nightcap	27	0.160
wind <30	Myrtaceae	<i>T. collina</i>	Moonpar	Orara West	26	0.096
wind <30	Myrtaceae	<i>T. collina</i>	Orara West	Dorrigo	21	0.085
wind <30	Myrtaceae	<i>T. collina</i>	Dorrigo	Darkwood	19	0.101
wind <30	Myrtaceae	<i>T. collina</i>	Moonpar	Dorrigo	15	0.051
wind <30	Myrtaceae	<i>T. collina</i>	Border Ranges	Darkwood	228	0.210
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Bellinger	231	0.134
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Bellinger	228	0.129
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Bonville	226	0.185
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Bonville	225	0.186
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Glennifer	221	0.130
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Glennifer	221	0.123
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Bellinger	218	0.107
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Bonville	214	0.160
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Bellinger	210	0.106
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Glennifer	209	0.106
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Bobo	204	0.133
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Bellinger	203	0.137
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Bobo	203	0.121
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Bonville	203	0.156

wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Glennifer	199	0.100
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Bucca	199	0.142
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Nymboida	198	0.143
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Bucca	196	0.146
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Nymboida	194	0.125
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Bonville	192	0.190
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Bobo	192	0.107
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Glennifer	190	0.135
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Bucca	186	0.121
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Nymboida	184	0.108
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Bobo	183	0.105
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Nymboida	177	0.111
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Bobo	175	0.136
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Bucca	174	0.120
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Nymboida	171	0.144
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Bucca	163	0.147
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	Cangai	145	0.143
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Cangai	132	0.129
wind <30	Myrtaceae	<i>T. laurina</i>	KillenFalls	Cangai	131	0.143
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	Cangai	128	0.113
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	Cangai	126	0.108
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Bonville	119	0.151
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Glennifer	109	0.093
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Bellinger	108	0.089
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Bucca	101	0.110
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Bobo	90	0.082
wind <30	Myrtaceae	<i>T. laurina</i>	Cangai	Nymboida	76	0.079
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	KillenFalls	63	0.128
wind <30	Myrtaceae	<i>T. laurina</i>	Bucca	Bellinger	50	0.093
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	KillenFalls	48	0.104
wind <30	Myrtaceae	<i>T. laurina</i>	Nymboida	Bonville	45	0.146
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	KillenFalls	41	0.127
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	NightcapLRC	40	0.098
wind <30	Myrtaceae	<i>T. laurina</i>	Nymboida	Bucca	39	0.105
wind <30	Myrtaceae	<i>T. laurina</i>	Nymboida	Bellinger	34	0.087
wind <30	Myrtaceae	<i>T. laurina</i>	Nymboida	Glennifer	33	0.086
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	Tweed	31	0.118

wind <30	Myrtaceae	<i>T. laurina</i>	Bucca	Glennifer	30	0.082
wind <30	Myrtaceae	<i>T. laurina</i>	Bobo	Bonville	29	0.137
wind <30	Myrtaceae	<i>T. laurina</i>	Bucca	Bonville	29	0.140
wind <30	Myrtaceae	<i>T. laurina</i>	Bobo	Bellinger	28	0.074
wind <30	Myrtaceae	<i>T. laurina</i>	Bucca	Bobo	27	0.093
wind <30	Myrtaceae	<i>T. laurina</i>	BarkersVale	NightcapLRC	25	0.072
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	BarkersVale	24	0.091
wind <30	Myrtaceae	<i>T. laurina</i>	NightcapLRC	KillenFalls	23	0.101
wind <30	Myrtaceae	<i>T. laurina</i>	Tweed	NightcapLRC	22	0.091
wind <30	Myrtaceae	<i>T. laurina</i>	Bobo	Glennifer	19	0.071
wind <30	Myrtaceae	<i>T. laurina</i>	Nymboida	Bobo	16	0.059
wind <30	Myrtaceae	<i>T. laurina</i>	Border Ranges	BarkersVale	15	0.092
edible <30	Sapindaceae	<i>Doryphora australis</i>	Mt Warning	Orara	206	0.203
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Clouds SF	205	0.211
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Clouds SF	202	0.220
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Clouds SF	200	0.201
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Orara	200	0.205
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Clouds SF	196	0.214
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Orara	196	0.207
edible <30	Sapindaceae	<i>D. australis</i>	Hayters Hill	Clouds SF	190	0.269
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap N	Clouds SF	189	0.217
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap N	Orara	188	0.205
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap S	Clouds SF	183	0.221
edible <30	Sapindaceae	<i>D. australis</i>	Hayters Hill	Orara	182	0.251
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap S	Orara	180	0.209
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Washpool	141	0.131
edible <30	Sapindaceae	<i>D. australis</i>	Hayters Hill	Washpool	136	0.181
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Washpool	132	0.114
edible <30	Sapindaceae	<i>D. australis</i>	Washpool	Orara	126	0.227
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap N	Washpool	123	0.114
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Washpool	120	0.091
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Washpool	120	0.101
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap S	Washpool	118	0.138
edible <30	Sapindaceae	<i>D. australis</i>	Washpool	Clouds SF	96	0.236
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Hayters Hill	60	0.100
edible <30	Sapindaceae	<i>D. australis</i>	Clouds SF	Orara	50	0.068
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Brunswick Heads	50	0.043

edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Hayters Hill	49	0.113
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Hayters Hill	43	0.122
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Brunswick Heads	40	0.060
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Nightcap S	39	0.058
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Nightcap N	34	0.017
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Brunswick Heads	30	0.058
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Nightcap S	28	0.064
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Nightcap S	27	0.066
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap N	Hayters Hill	26	0.118
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap S	Hayters Hill	25	0.103
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Nightcap S	24	0.054
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Nightcap N	23	0.021
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Mt Warning	21	0.032
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Nightcap N	21	0.056
edible <30	Sapindaceae	<i>D. australis</i>	Mt Warning	Nightcap N	20	0.039
edible <30	Sapindaceae	<i>D. australis</i>	Brunswick Heads	Hayters Hill	16	0.087
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges 1	Mt Warning	14	0.042
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Border Ranges 1	11	0.024
edible <30	Sapindaceae	<i>D. australis</i>	Nightcap N	Nightcap S	7	0.064
edible <30	Sapindaceae	<i>D. australis</i>	Border Ranges	Orara	206	0.191
edible >30	Sapotaceae	<i>Niemeyera prunifera</i>	Clarke Range	Robinson Creek	514	0.554
edible >30	Sapotaceae	<i>N. prunifera</i>	Clarke Range	Gooligans Creek	495	0.578
edible >30	Sapotaceae	<i>N. prunifera</i>	Clarke Range	Crawfords Lookout	492	0.595
edible >30	Sapotaceae	<i>N. prunifera</i>	Crawfords Lookout	Cape Tribulation	174	0.281
edible >30	Sapotaceae	<i>N. prunifera</i>	Gooligans Creek	Cape Tribulation	173	0.279
edible >30	Sapotaceae	<i>N. prunifera</i>	Robinson Creek	Cape Tribulation	168	0.239
edible >30	Sapotaceae	<i>N. prunifera</i>	Crawfords Lookout	Robinson Creek	33	0.146
edible >30	Sapotaceae	<i>N. prunifera</i>	Gooligans Creek	Robinson Creek	30	0.148
edible >30	Sapotaceae	<i>N. prunifera</i>	Crawfords Lookout	Gooligans Creek	4	0.099
edible >30	Sapotaceae	<i>N. prunifera</i>	Clarke Range	Cape Tribulation	655	0.584
edible >30	Sapotaceae	<i>N. whitei</i>	Brunswick Heads	Ulidarra	196	0.309
edible >30	Sapotaceae	<i>N. whitei</i>	Nightcap	Ulidarra	180	0.331
edible >30	Sapotaceae	<i>N. whitei</i>	Nightcap	Brunswick Heads	23	0.302
edible >30, small seed	Sapotaceae	<i>Planchonella australis</i>	Dorrigo	Nightcap	202	0.068
edible >30, small seed	Sapotaceae	<i>P. australis</i>	Dorrigo	Mary	401	0.092
edible >30, small seed	Sapotaceae	<i>P. australis</i>	Hayters Hill	Nightcap	25	0.067

edible >30, small seed	Sapotaceae	<i>P. australis</i>	Hayters Hill	Mary Cairncross	222	0.097
edible >30, small seed	Sapotaceae	<i>P. australis</i>	Nightcap	Mary Cairncross	212	0.076
edible >30, small seed	Sapotaceae	<i>P. australis</i>	Dorrigo	Hayters	207	0.092
edible <30	Sapotaceae	<i>Pleioluma queenslandica</i>	Brunswick Heads	Eungella	967	0.220
edible <30	Sapotaceae	<i>P. queenslandica</i>	Cooloolah	Eungella	711	0.166
edible <30	Sapotaceae	<i>P. queenslandica</i>	Brunswick Heads	Byfield	697	0.146
edible <30	Sapotaceae	<i>P. queenslandica</i>	Bulburin	Eungella	497	0.113
edible <30	Sapotaceae	<i>P. queenslandica</i>	Brunswick Heads	Bulburin	479	0.115
edible <30	Sapotaceae	<i>P. queenslandica</i>	Cooloolah	Byfield	424	0.091
edible <30	Sapotaceae	<i>P. queenslandica</i>	Byfield	Eungella	297	0.098
edible <30	Sapotaceae	<i>P. queenslandica</i>	Brunswick Heads	Cooloolah	291	0.135
edible <30	Sapotaceae	<i>P. queenslandica</i>	Bulburin	Byfield	218	0.056
edible <30	Sapotaceae	<i>P. queenslandica</i>	Cooloolah	Bulburin	216	0.069

Chapter 4. *Araucaria bidwillii* (Araucariaceae) genomics suggest Indigenous Peoples adapted plant translocation practices under settler-colonialism

Abstract

Retracing the past anthropogenic dispersal of culturally important taxa offers insights to the biogeographic history of species, as well as the history of the people who interacted with them. Bunya Pine (*Araucaria bidwillii* Hook.) is a culturally and spiritually significant conifer tree for several Indigenous groups in eastern Australia. Sharing the edible nuts and attending Bunya gatherings is an important way for these groups to maintain their cultural connections and it has been hypothesized that prior to European colonisation, Indigenous Peoples facilitated the dispersal of Bunya Pine as part of these ancient traditions. We utilised ethnohistorical information on the use of Bunya Pine by Indigenous Peoples and European settlers to interpret genomic patterns within and between disjunct distributions of Bunya Pine. We found signatures of long-term isolation within the Australian Wet Tropics (AWT) and extensive geneflow within southeast Queensland (SEQ) that does not fit geographically structured models of faunal or passive dispersal. These findings are consistent with recently documented ethnographic data that indicates custodianship of Bunya Pine by Indigenous Peoples in SEQ, that was not practiced in AWT. Within SEQ, we found greater population structure amongst sites known to pre-date European colonization, than when colonial-era planted sites were included in our analyses, suggesting that pre-colonial translocation was sporadic or localized rather than systematic and widespread. Increased Indigenous translocations in conjunction with plantings by European settlers appears to have erased the natural pre-colonial population structure of SEQ Bunya Pine. Our stairway plot models suggest sharp population decline of SEQ Bunya Pine in the early and late Pleistocene, though we did not find evidence that anthropogenic dispersal facilitated effective population size growth of the species in the Holocene. We conclude that pre-colonial translocation of SEQ Bunya Pine was restricted by kinship-based custodial rights, and that translocation intensified to maintain cultural connectivity when Indigenous Peoples were displaced by European settlers.

Policy implications

Our findings help us understand the demographic impacts of translocations and can be used to shape a biocultural conservation strategy for Bunya Pine that addresses biological and cultural values.

Introduction

There is growing recognition that Indigenous Peoples around the world have influenced the biogeography of some non-crop plant species (1, 2). In recent years, an academic debate has emerged over whether the Indigenous Peoples of Australia practiced early forms of agriculture prior to European colonization in 1788 (3–5). This debate is set against an international discussion of what defines agriculture, and various scholars have sought to broaden the scope by describing Indigenous lifeways that sit between agriculture and hunter-gathering (6–9). In Australia, this includes “domiculture” whereby the accumulation of discarded fruit seeds has led to the incidental growth of edible species near traditional campsites (10, 11). A handful of colonial sources also indicate that some Indigenous Peoples practiced intentional plant translocations in disparate parts of the Australian continent (12–14), while other reports remark on the apparent absence of propagation by Indigenous Peoples (15, 16). However, colonial observations are not always a reliable source to make inferences about the ancient past, as cultural practices are liable to change with time (9). Genomic researchers are presented with the opportunity to contribute to this debate as highly informative ‘genotyping by sequencing’ data becomes increasingly accessible for the study of non-crop species. With mixed success, a small number of studies have utilized genetic techniques in attempt to retrace the historical dispersal of non-crop plants by Indigenous Peoples (14, 17–20). Importantly, retracing the movement of culturally significant species can also tell us about human histories and cultural practices (21–24), including that of Indigenous people (19).

Araucaria bidwillii (Bunya Pine) is a long-lived, coniferous tree that is culturally and spiritually significant for many Indigenous groups in eastern Australia. It has a disjunct distribution with fragmented populations in Southeast QLD (SEQ) and over 1400 km north in two small adjacent pockets within the Australian Wet Tropics (AWT; Figure 1). Bunya Pine cones are amongst the largest of coniferous trees, at over 300 mm in length and up to 10 kg in weight (25). The cones contain large, highly nutritious and palatable nuts over 30 mm wide that mature between December and March each year, usually with a ‘bumper crop’ every third year, depending on location (26). Mature cones fall from the tree intact, and their heavy weight enables passive down-slope dispersal [25]. No extant fauna can facilitate long-distance dispersal of Bunya Pine propagules (see Materials and Methods), hence questions about anthropogenic dispersal have risen to explain the disjunct distribution of the species. The fossil record appears to suggest that the widest distribution of *Araucaria* Section Bunya (*A. bidwillii* and *A. hunsteinii*) peaked

sometime during the Mesozoic (65-245 Mya) and its range has been contracting since (25). Hence, an alternative hypothesis of the disjunct populations could be vicariance.

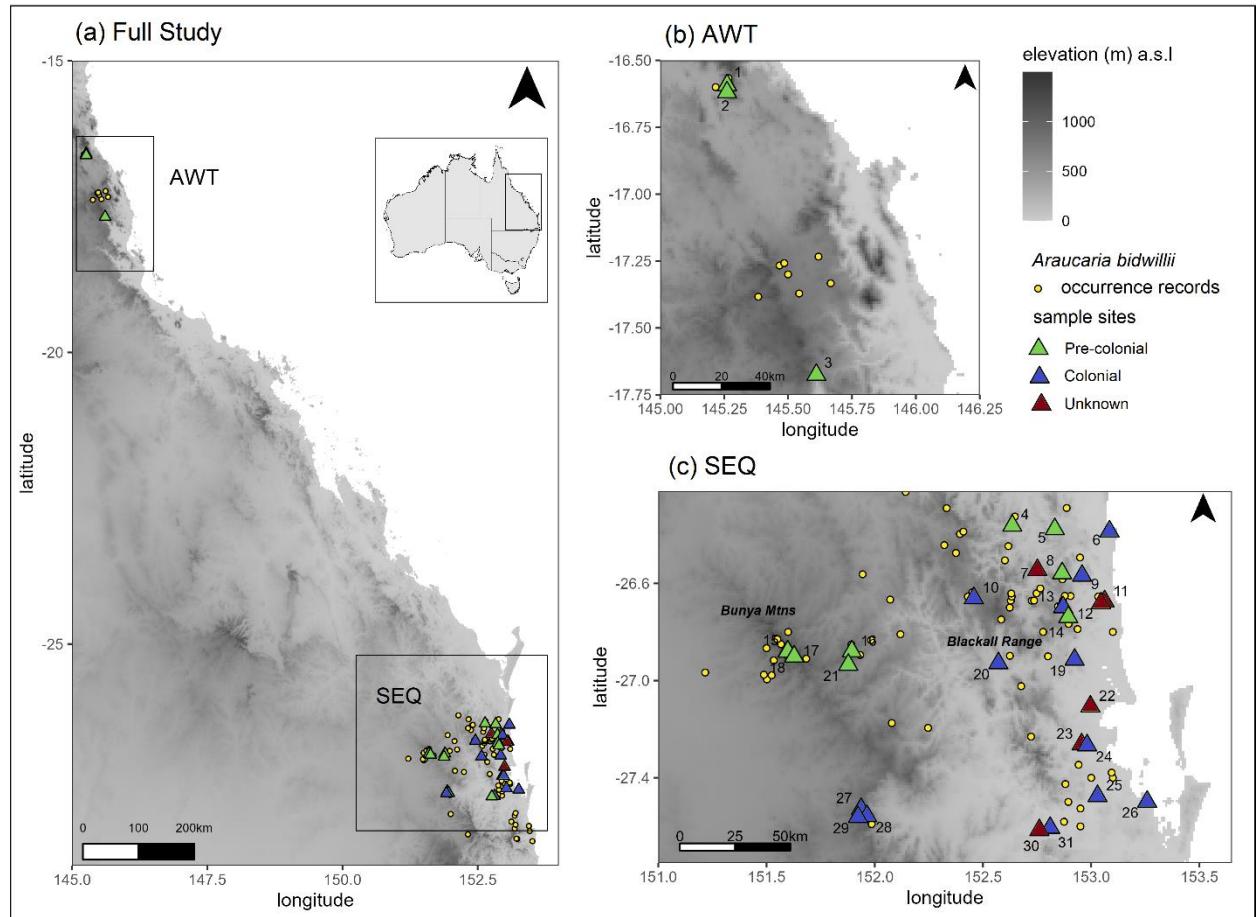


Figure 1. Distribution of Bunya Pine (*Araucaria bidwillii*) in the study area. Sample sites are indicated by the numbered triangles, and colour-coded to indicate the time of origin inferred from ethnohistoric data in Supplementary Table 1. The corresponding site information is outlined in Table 1. Unsourced occurrence records of Bunya Pine are indicated by yellow circles.

In favour of the hypothesis that pre-colonial Indigenous Peoples intentionally propagated and dispersed food plants, oral traditions by Indigenous groups in SEQ describe Bunya Pine translocation and storage, although it is unclear whether this was a widespread practice ((27); Kerkhove, unpublished data). Ancient propagation of Bunya Pine has been speculated by European settlers since the 19th Century (28, 29). Living Indigenous Biocultural Knowledge (IBK) and colonial historic accounts indicate that Indigenous Peoples of SEQ maintained Bunya Pine groves through laws that inhibited damage and overexploitation of the trees (26, 30–32), and pruned back Bunya Pine branches to encourage nut production (33). It was also widespread practice to store Bunya Pine kernels in various types of mudholes

(30, 34–37), often with the intention to let the kernels germinate and produce cotyledons, as this improved their taste and nutritional value (38, 39).

Whether intentional or incidental, pre-colonial Bunya Pine translocation is likely to be associated with the “Bunya treks”, the traditional pathways taken to attend Bunya feasts. Prior to European settlement, many Indigenous tribes and clans would travel up to hundreds of kilometres from their respective lands to attend tri-annual gatherings during the Bunya Pine fruiting season (31, 32, 40–42). People would store and consume Bunya Pine nuts and seedlings as part of their return journey (30, 32). The major gatherings held in the Bunya Mountains (Darling Downs) and the Blackall Range (Figure 1) ceased in the 1880s due to the intensification of logging activities, though was reportedly still practiced at Hawkwood Station on the northwestern edge of the SEQ Bunya Pine in the 1930s (43). Connection to this tradition is kept alive by the contemporary Indigenous diaspora whose ancestors were forcibly removed from their homelands by European settlers and planted Bunya Pine in various Aboriginal reserves run by Christian missionaries across southeast Australia (27). However, other historical accounts claim that there were Indigenous prohibitions on planting Bunya Pine in other locations (44). This may indicate that Bunya Pine propagation was historically governed by kinship or place-based lore, and/or that intentional propagation arose in response to the impacts of colonisation.

An earlier study that utilised RAPD markers found high diversity within Bunya Pine populations and greater differentiation between proximate sites within the Bunya Mountains than with an eastern population near the Blackall Range, potentially indicating past translocation along the SEQ Bunya treks (45). In contrast, IBK of Bunya Pine use and dispersal appears to be lacking amongst Indigenous groups in the AWT (27). It is unclear whether European colonisation disrupted IBK related to Bunya Pine in the AWT, or whether it was never a major part of the diet or cosmology amongst Indigenous groups in the region.

In this study, we combined ethnohistoric data and SNPs obtained via genotyping by sequencing (DArTseq (46)), with the aim of detecting the genomic signal of either ancient or more recent anthropogenic movement of Bunya Pine propagules. We compared genomic patterns between Bunya Pine in the AWT and SEQ to test three lines of enquiry: (1) Does Bunya Pine in SEQ show greater admixture and/or lower population structure than in the AWT, consistent with ethnographic evidence of dispersal by Indigenous Peoples? (2) Can we exclude genomic patterns expected of faunal-mediated

dispersal in SEQ, such as isolation-by-distance or serial founder range expansion? and (3) Can we find evidence of population size expansion in SEQ consistent with recent anthropogenic influence?

Materials and Methods

Study species and study area

Bunya Pine is a dry rainforest emergent tree (up to 50 m tall) that forms dense groves on basalt or other igneous derived soils on elevations between 150-1000 m and within 160 km from the coast (47). These areas receive annual rainfall of 900 mm or greater and mean maximum temperatures of 28-32°C and a mean minimum of 5-10°C (48). The species belongs to the clade (Araucaria Sect. Bunya and Sect. Araucaria) with the largest seed (49) and seed cones of any extant conifer (50), potentially as part of a faunal-mediated dispersal syndrome (50, 51). The emergence of large seed cones in Araucariaceae coincided with the diversification of sauropod dinosaurs in the Jurassic, which were putative dispersal vectors (52). Currently there is no evidence that suggests Bunya Pine was dispersed by extinct megafauna. Observations of extant fauna indicate that bush rats (*Rattus fuscipes*) can cache Bunya seed short distances uphill (47) and sulphur-crested cockatoos (*Cacatua galerita*) can move the seed at least 153 m (53). However, the absence of large dispersal vectors likely accounts for the highly restricted distribution of Bunya Pine, despite the species' potential to grow outside the conditions that characterise its contemporary range (47).

Alternatively, the large, carbohydrate rich seeds may have been an adaptation that facilitated the colonization of ancient volcanic ash-disturbed environments (54, 55) rather than to attract faunal dispersers. Upon imbibition, Bunya Pine seeds develop an underground tuber that can remain dormant until conditions are suitable for seedling survival (56). However, only a percentage of a given cohort will germinate immediately when conditions are optimal, and the rest will germinate sporadically over a two-year period (56). The staggered germination rate and a below-ground bud reserve that facilitates seedling resprouting is likely to confer some ability for Bunya Pine to regenerate after fire and drought (56). These recruitment traits may have provided a competitive advantage over rainforest angiosperms during dryer glacial periods. The 230 Kyo palynological record at Lynch's Crater (AWT) shows that Araucarian dry rainforest expanded in glacial periods and was replaced by wetter rainforest during inter-glacials (57). However, gymnosperms were gradually outcompeted by modern dry adapted flora, and Araucaria underwent a sharp decline c. 45 Kya with the onset of seasonally low winter rainfall and a more intense fire regime (58). Today, the AWT has a tropical monsoonal climate with an average annual rainfall of 1420 mm, that primarily falls over the summer. Consequently, Bunya Pine is restricted to three high elevation sites that maintain moist conditions throughout the year (59). Reportedly, native Bunya Pine

was not logged in the region (59), although plantations sourced from SEQ stock were established nearby in the Atherton Tableland (43).

SEQ has a cooler, subtropical climate that receives less annual rainfall than the AWT, though more consistently throughout the year. Bunya Pine of presumably pre-colonial origin can be found in locally abundant though fragmented stands across five upland areas (Figure 1). At the time of European colonization, Bunya Pine dominated the Blackall Range (60), and occupied dense patches or occurred as scattered forest emergents along several lowland rivers north of Brisbane (33, 47, 61, 62), including at old campsites where it was customary for Indigenous Kabi Kabi people to leave seeds of edible plants (63). Early colonial accounts record the species along the Bunya treks heading north-west to the Darling Downs via Petrie (62), Neurum (64) and Woodford (61); and heading north on the coastal plain to the Blackall Range via Beerwah (30), Caboolture (65) and Nambour (62). However, extensive, illegal logging in the 1860s through the early twentieth century led to the near eradication of Bunya Pine in these locations (41, 66).

Sampling scheme

We took Bunya Pine leaf DNA samples from sites known to have been planted in the 19th Century on European-colonial settlements but often with an unknown provenance, in addition to “pre-colonial” sites that either represent the natural distribution of Bunya Pine or potentially established by pre-colonial Indigenous Peoples. Where available, historic evidence for anthropogenic establishment of Bunya Pine at SEQ sites is described in Supplementary Table 1, with consideration of Indigenous and European settler influence. Historical evidence was obtained from archival newspaper articles, herbarium records, European settler journals and correspondence, and landscape surveys via TROVE (<https://trove.nla.gov.au/>) or cultural heritage reports. Evaluation of the historic data was also used to designate the sample sites as either “pre-colonial”, “colonial” or “unknown” for genomic analyses (Supplementary Table 1). Depending on the accessibility and number of trees at each site, we sampled between 1-12 individuals (Table 1).

Table 1. Sample scheme and diversity statistics calculated for *Araucaria bidwillii* sites sub-sampled to n=5, across 5894 SNPs. Sites with less than 5 samples (n) were excluded from the correlation test. Statistics are not available for sites with n<2. Dataset (D): 1=all samples, 2=all SEQ samples, 3= natural or pre-colonial SEQ samples. Site type: P=pre-colonial, C=colonial, U=unknown. ar=allelic richness per locus, Ho=observed heterozygosity per locus, uHe=unweighted expected heterozygosity per locus, fis=inbreeding coefficient, pa=private alleles.

Site	Locality	Lat, long	n	D	Type	ar	Ho	uHe	fis	pa	%p
AWT											
1	Mt Lewis, Leichhardt Creek	-16.593, 145.26	12	1	P	1.24	0.07	0.12	0.26	211	25.7
2	Mt Lewis, Station Creek	-16.619, 145.26	9	1	P	1.15	0.05	0.09	0.36	174	18.3
3	Cannabullen	-17.675, 145.61	10	1	P	1.11	0.05	0.07	0.20	301	14.8
SEQ											
4	Amamoor	-26.362, 152.64	12	1-2	C	1.35	0.10	0.22	0.42	42	27.4
5	Tuchekoi National Park	-26.377, 152.83	1	1-2	U	NA	NA	NA	NA	NA	NA
6	Noosa National Park	-26.386, 153.08	5	1-2	C	1.42	0.13	0.22	0.27	22	30.6
7	Moy Pocket	-26.545, 152.75	6	1-2	U	1.38	0.12	0.21	0.36	52	27.9
8	Mapleton State Forest	-26.558, 152.87	7	1-3	P	1.27	0.09	0.18	0.33	34	23.5
9	Koongalba House	-26.568, 152.96	10	1,2	C	1.35	0.08	0.21	0.46	53	26.5
10	Jimna	-26.661, 152.46	1	1-2	C	NA	NA	NA	NA	NA	NA
11	Buderim Farm	-26.676, 153.06	5	1-2	U	1.35	0.10	0.17	0.25	39	24.8
12	Buderim	-26.682, 153.04	3	1-2	U	1.25	0.14	0.21	0.14	7	21.9
13	Baroon Dam	-26.698, 152.87	3	1-2	C	1.04	0.10	0.16	0.14	45	17.1
14	Dilkusha	-26.739, 152.89	6	1-3	P	1.39	0.10	0.19	0.39	53	27.4
15	Yarraman State Forest	-26.879, 151.89	6	1-3	P	1.43	0.11	0.22	0.37	89	31.2
16	Bunya Mountains National Park, M	-26.881, 151.60	8	1-3	P	1.30	0.08	0.21	0.49	52	25.9
17	Bunya Mountains National Park, D	-26.879, 151.60	9	1-3	P	1.28	0.07	0.19	0.49	38	25.4
18	Bunya Mountains National Park, MC	-26.901, 151.63	7	1-3	P	1.38	0.10	0.21	0.39	19	26.8
19	Bankfoot House	-26.914, 152.92	2	1-2	C	1.01	0.09	0.12	-0.17	15	8.8
20	Kilcoy Homestead	-26.928, 152.57	4	1-2	C	1.18	0.12	0.18	0.17	13	23.5
21	The Palms National Park	-26.935, 151.88	5	1-3	P	1.20	0.05	0.17	0.56	66	20.8
22	Morayfields	-27.107, 152.99	6	1-2	U	1.22	0.08	0.19	0.45	66	23.1
23	Rollo Petrie	-27.262, 152.96	5	1-2	U	1.45	0.14	0.22	0.21	19	31.4
24	Petrie School	-27.266, 152.98	4	1-2	C	1.16	0.13	0.19	0.09	22	23.7
25	Brisbane Botanic Gardens	-27.475, 153.03	6	1-2	C	1.43	0.12	0.22	0.31	36	29.7
26	Ormiston House	-27.498, 153.26	6	1-2	C	1.39	0.10	0.22	0.39	57	28.6
27	Toowoomba BH	-27.528, 151.94	3	1-2	C	1.14	0.11	0.18	0.17	11	20.9
28	Toowoomba QP	-27.559, 151.96	6	1-2	C	1.29	0.11	0.21	0.36	44	26.9
29	Toowoomba	-27.562, 151.92	3	1-2	C	1.12	0.09	0.16	0.10	19	21.9
30	Ipswich TAFE	-27.606, 152.81	1	1-2	U	NA	NA	NA	NA	NA	NA
31	Ipswich QP	-27.615, 152.76	1	1-2	C	NA	NA	NA	NA	NA	NA

Generation of genomic data and filtering

For all samples, nDNA extraction from leaf samples and SNP genotyping using DArTseq technology (Sansaloni et al., 2011) was undertaken at Diversity Arrays Technology Pty Ltd (Canberra, Australia). We filtered markers according to reproducibility average (proportion of technical replicates for which the marker score is consistent) and call rate (proportion of individuals with non-missing scores). We selected markers with a reproducibility average of at least 0.8 and a minimum call rate of 0.7 and retained only one SNP per CloneID using a random filter. To explore regional hypotheses of dispersal, we subset the data for separate analyses of the full study area, the AWT, SEQ and SEQ pre-colonial samples. Only sites identified as “pre-colonial” were analysed in the SEQ pre-colonial group, while all sample sites including those designated as “unknown” were analysed in the SEQ group. For the calculation of unbiased F_{st} and diversity-based statistics, we removed sites with less than 5 samples and subset sites to have a maximum of 6 samples.

Analysis of population structure and genomic diversity

To assess whether Bunya Pine in SEQ showed greater admixture and/or lower population structure than in the AWT, we used the R package *adagenet* 2.1.5 (67) to perform a Principal Components Analysis (PCA) across the full study area and separately for the AWT, SEQ and SEQ pre-colonial sites. In addition, we employed the *sNMF* function in the R package *LEA* (68) to calculate the individual ancestry coefficients of samples across the full study, and separately for SEQ and SEQ pre-colonial. We compared models that assume $K=1-4$, with 10 replicates per model, and assessed the model that best-fit the data with the cross-entropy criterion.

Finally, we used the R-package *BEDASSLE* 1.6 (69) to calculate the pairwise F_{st} values between all sites across the full study area. We used the full study dataset and R packages “*poppr*” (70, 71) to calculate the number of private alleles and “*diveRsity*” (72) to estimate allelic richness (confidence interval = 0.05, 999 bootstraps), observed heterozygosity, expected heterozygosity, proportion of polymorphic loci, and inbreeding coefficient for each site. To assess whether geography or colonial planting impacts genomic diversity of Bunya Pine populations, we performed a Pearson’s correlation analysis between all diversity estimates and latitude, longitude and colonial heritage.

Tests for faunal-mediated dispersal

For our second hypothesis, we sought to investigate whether we could eliminate faunal-mediated dispersal as a primary driver of gene-flow in SEQ. First, we tested for a pattern of isolation by distance (IBD), which is expected of stable and long-term faunal-mediated dispersal. We expected human-

mediated dispersal would be more likely to correspond with cultural factors than IBD. We used the R-package *vegan* 2.5.7 (73) to perform a Mantel test between pairwise F_{st} values and geographic distance between sites ($p=0.05$, 999 permutations). Second, we tested for a stepping-stone range expansion model consistent with faunal-mediated habitat expansion from a single deme. Here we used an approach that tests whether drift under population expansion can explain the observed genetic structure (74). This approach infers the strength of founder effects associated with spatial expansion and the most likely expansion origin, and tests significance against a null model of equilibrium IBD (74, 75). The effective founder distance (d) is calculated as the deme size (in km) for which N_e is reduced by 1% in a founder event. Based on results from an *Arabidopsis thaliana* dataset (75), we consider $d < 5$ km to indicate strong founder effects and $d > 25$ km to indicate weak founder effects. The model detects weak or non-significant d if range expansion was gradual, the species underwent long periods of post-expansion drift, or the species had multiple reticulate expansions per lineage. We assumed that recent and/or rapid anthropogenic dispersal could yield founder effects, but that it is not likely to have followed a stepping-stone model of expansion. Therefore, we anticipated moderate to strong though non-significant d in SEQ [70].

Inference of population size over time

To test our third hypothesis, we employed Stairway plot 2.1.1 (76, 77) to compare the demographic history of Bunya Pine populations in the AWT and SEQ. Stairway plot uses a flexible multi-epoch coalescent model to estimate N_e of a population through time, by calculating the expected composite likelihood of a given one-dimensional SNP frequency spectrum (SFS). We anticipated that the SEQ population would show an ancient bottleneck associated with habitat decline, followed by a human-assisted population expansion. On the other hand, we expected an ancient population decline followed by stationarity in the AWT.

To meet the assumption that samples are drawn from a panmictic population, we pooled the Mt Lewis sites to represent the AWT and all southern sites to represent SEQ. We used a customized script following (78) to sample the folded SFS from the minimum sample size across all SNPs for each population. First, we used the R package *dartR* (79) to filter out loci with a read depth less than 9, and loci with a linkage threshold greater than $R^2=0.5$ and 0.8 . We ran multiple stairway plots for each population to determine the impact of the number of SNPs, linkage filtering and sample size. We found that the size and timing of ancient N_e shifts were consistent between datasets, though more recent N_e estimates varied with sample size. Therefore, we settled on three final datasets ($R^2=0.5$) that maximized the number of samples and SNPs: 5789 SNPs across 16 AWT samples, 5102 SNPs across 87 SEQ samples and 5687 SNPs across 27 SEQ pre-colonial

samples. As the program does not account for overlapping generations, we set the generation time to 20 years (indicating recruitment within a maternal line every 20 years) and trialed two mutation rates: 2.0×10^{-8} and 7.71×10^{-10} . The latter rate is the average silent site divergence rate estimated from 31 conifer species across 42 single copy nuclear genes (80). In addition, we used the program Ne-estimator (81) via dartR to estimate contemporary Ne for each population.

Results

Population structure & genomic diversity

The pairwise F_{st} estimates (Supplementary Figure 1) indicate high variation within the AWT (mean=0.476) and moderate to low variation within SEQ (mean=0.137). Genomic differentiation between the Mt Lewis sites and Cannabullen is equivalent to variation between AWT and SEQ sites. The best-supported sNMF model according to the cross-entropy criterion suggests $K=3$ ancestral clusters, that correspond with one SEQ population, and two populations in the AWT (Mt Lewis and Cannabullen) that are separated by the Black Mountain Corridor (Figure 2a). The PCA identified three population clusters that are concordant with sNMF (Figure 2b).

For the separate SEQ analyses, both the PCA and sNMF showed there was greater population structure in the pre-colonial dataset than when all samples were included (Figure 2). The sNMF genotype assignment plots suggested SEQ was one homogenous population when all samples were included (Figure 2c), however when only pre-colonial sites were included, Mapleton had a genotype distinct from all other sites assuming $K>2$ (Figure 2e). However, the best-fit model for both the SEQ and SEQ pre-colonial datasets assumed $K=1$, which suggests only one ancestral population in the region. When all sites were included, the PCA showed Mapleton, Buderim Farm and Toowoomba were marginally distinct from the rest of the population (Figure 2d). The pre-colonial dataset showed greater PC loadings and Mapleton and Dilkusha clustered discrete from the remaining sites. In contrast, we found considerable variation within and between AWT sites in the PCA ordination (Supplementary Figure 2). The primary variation was across the Black Mountain Corridor biogeographic barrier, though there was considerable differentiation between the two Mt Lewis sites that suggested long-term isolation.

We found greater genetic diversity within SEQ than the AWT (Table 1), with a significant negative correlation between latitude and A_r , H_o , uHe and $\%p$ when calculated across the full study area (Supplementary Table 2). However, we found the opposite trend with pA , which was much greater in AWT sites compared with SEQ. Estimates of F_{is} did not have a significant correlation with any geographic variable. When calculated amongst SEQ sites only, we found a significant and strong negative

correlation between %p and latitude (Supplementary Table 2). We did not find any significant differences between diversity estimates of the pre-colonial and colonial sites (Supplementary Table 3).

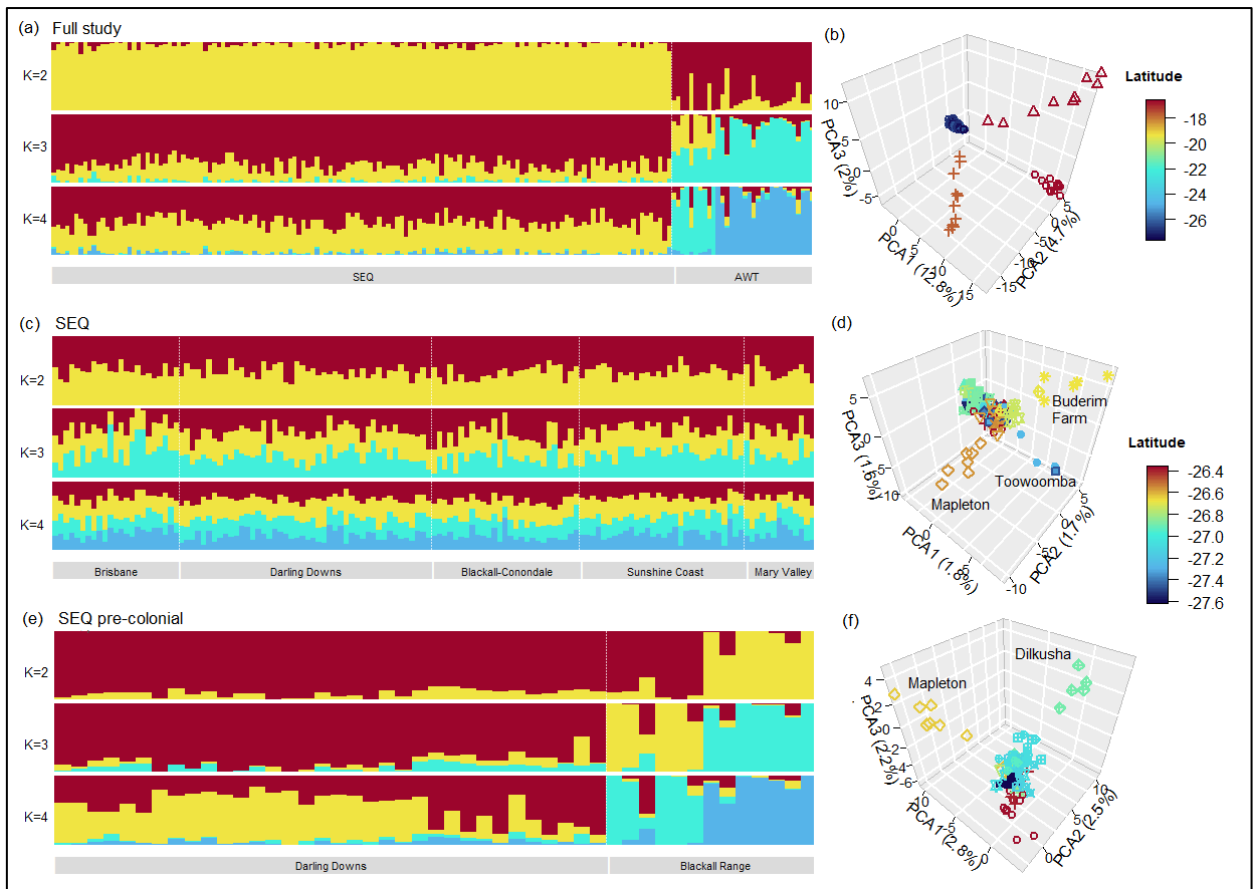


Figure 2. Population structure of Bunya Pine (*Araucaria bidwillii*) samples. The figures on the left (a,c,e) display genotype assignment proportions assuming $K=2$ to 4 ancestral genotypes. The figures on the right (b,d,f) display a Principal Components Analysis of genomic variance among samples, ordinated by the three primary axes of variation. Samples are coloured by latitude. The top panel represents 171 samples from the full study area, the middle panel displays 139 samples from SEQ (Southeast Queensland), and the bottom panel shows 47 samples of precolonial sites in SEQ.

Tests for IBD and range expansion in SEQ

We found a low correlation between genomic and geographic distance amongst both the SEQ pre-colonial ($r^2 < 0.00$, $P = 0.46$) and full SEQ ($r^2 = -0.09$, $P = 0.78$) datasets, indicating that gene-flow did not follow a pattern of isolation-by-distance (Supplementary Figure 3). We also found weak support for a serial-founder expansion model. The strongest founder effect (q) was estimated from the full SEQ dataset, however the low and poorly supported correlation efficient ($Rsq = 0.049$, $P = 54.08$) indicated the model failed to identify the origin of range expansion (Supplementary Table 4). The overall poor support suggested that the dispersal history of Bunya Pine violated one or more of the assumptions of the Slatkin

range expansion model and may indicate expansion from multiple demes and/or that subsequent high rates of gene flow have obscured the initial founder effect.

Inference of population size over time

The stairway plots indicated that the northern and southern Bunya Pine had contrasting demographic histories, though did not support our hypothesis of a recent anthropogenic-driven population expansion in SEQ. The stairway plot for AWT showed a gradual N_e decline and relative stability for the past 2 million years (Figure 3a). This pattern is consistent with population decline following a loss of suitable habitat and dispersal vectors in AWT. The SEQ stairway plot indicated a severe bottleneck event 2 million years ago, followed by a period of N_e recovery, and a second sharp N_e decline 50,000 years ago (Figure 3b).

The N_e -estimator results indicated that contemporary N_e in the AWT is 1-2 orders of magnitude smaller than the SEQ pre-colonial and colonial populations (Table 4). Within SEQ, the colonial sites collectively had a greater N_e than the pre-colonial sites. Singletons made a large contribution to the estimated N_e in the colonial population, consistent with recent population expansion.

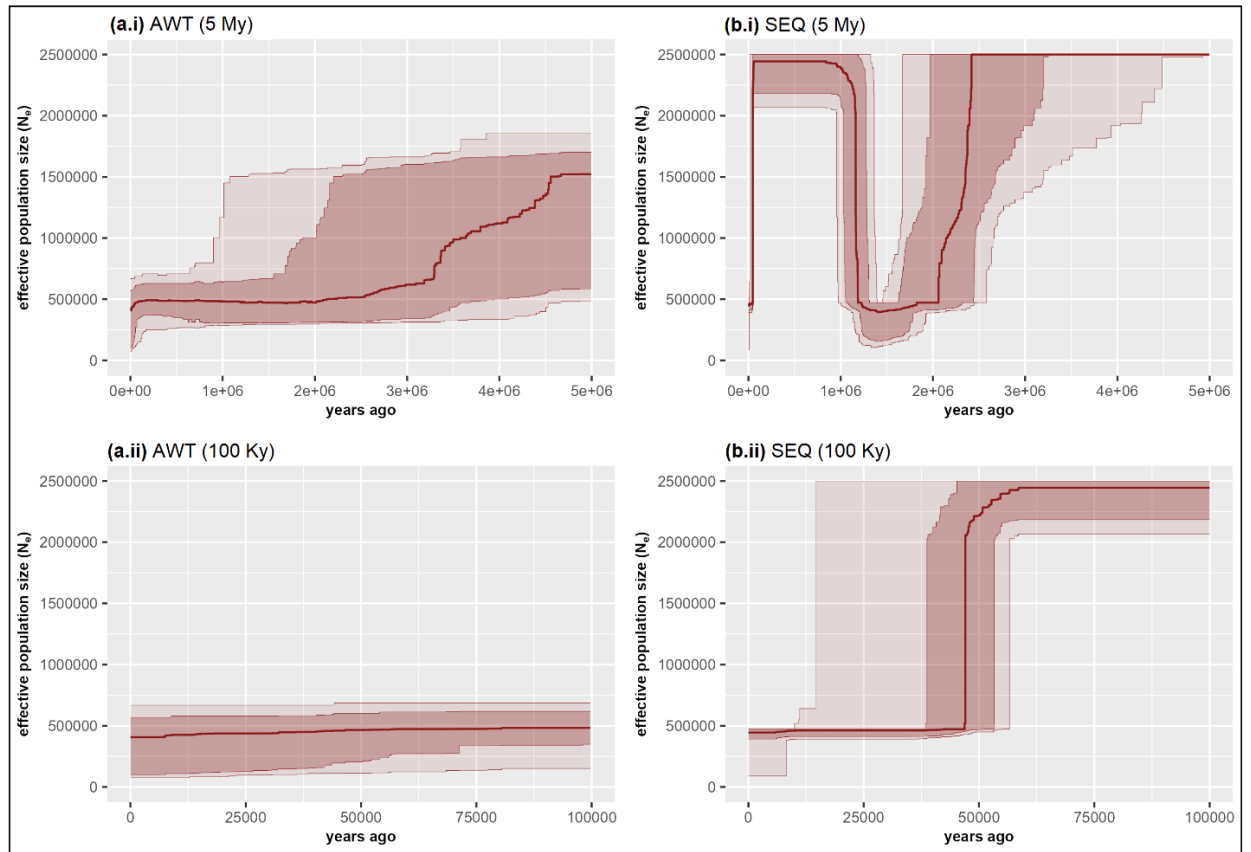


Figure 3. Stairway Plot 2 inference of Bunya Pine (*Araucaria bidwillii*) effective population size through time, with folded SFSs and masking singletons. Red line: median of 200 inferences based on subsampling. Dark red band: 87% confidence interval of the inference. Light red band: 97.5% confidence interval of the inference. (a) AWT = Australian Wet Tropics, with samples from Mt Lewis only. (b) SEQ = Southeast Queensland. (i) Inference for the past 5 million years. (ii) Inference for the past 100 thousand years.

Discussion

We compared genomic patterns within and between two disjunct regions of Bunya Pine and found signatures of long-term isolation within the AWT and extensive dispersal across all sites in SEQ. We found support for our first two hypotheses of low geographic structure in SEQ that does not follow expected models of faunal dispersal, though we did not find evidence of a recent population expansion. In most cases, evidence from the historic data was insufficient to identify anthropogenic sites as exclusively Indigenous or European settler in origin. For instance, several sites (9, 22, 24-25, 27) were planted by Indigenous workers on the properties of European settlers (Supplementary Table 1).

Regional variation in Bunya Pine dispersal is consistent with IBK

In line with our first hypothesis, we found low geographic structure and genetic variation in the southern range of Bunya Pine, consistent with previously identified putative signals of Indigenous-mediated dispersal (18, 82). For instance, the low F_{st} values and an absence of IBD in SEQ suggests recent and/or

rapid dispersal. By contrast, we found elevated pA (private alleles) though lower N_e and allelic diversity in the AWT, along with greater variation between sites. This suggests long-term isolation and drift has led to fixation between sites. In addition, we observed barrier effects across the historically dry Black Mountain Corridor (82–87), which can be expected if human influence has been minimal, since faunal-mediated and passive dispersal is inhibited by habitat barriers. These regional differences in dispersal cannot be attributed to different faunal assemblages, since there are fewer extant vertebrates in SEQ than the AWT (88), and local dispersal by sulphur-crested cockatoos has been observed in both regions (53). In addition, we did not find evidence of serial founder effects in SEQ that can be expected of rapid faunal-mediated range expansion in response to increased habitat availability. While wind-pollination would facilitate some gene flow between sites, it is not likely to account for the greater gene flow in SEQ. It has been previously demonstrated that effective pollen flow in *Araucaria* follows a pattern of IBD (89), and given the large size of *Araucaria* pollen grains (90), dispersion capacity is limited within dense forests (89, 91, 92).

The contrasting dispersal signals that we observed between AWT and SEQ support the conclusion that regional differences in culture and resource availability rather than colonial disruption can explain the limited IBK of Bunya Pine in the AWT (27). Given the high divergence between proximate sites in Mt Lewis and the signal of an ancient population size decline, it is highly plausible that Bunya Pine had already retreated as a significant landscape feature by the time humans began to permanently settle the rainforest areas of the AWT in the mid-Holocene (93, 94). So, although ethnohistorical evidence indicates that Indigenous Peoples in the AWT utilised tree nuts to support large inter-regional gatherings (95) – perhaps similar to the Bunya gatherings in SEQ – it appears that Bunya Pine was not a major feature here. Archaeobotanical investigations have uncovered ancient nut processing from a suite of other rainforest trees in the region (93–98), and it is speculated that the diversity of species with nutritious and palatable nuts may account for the limited significance of Bunya Pine in the tropics (27). Similarly, a comparative study of edible and non-edible tuberous Platysace in South-Western Australia found that the edible *P. trachymeniodes* displayed regional variation in cpDNA evidence of anthropogenic dispersal (14). Research suggested that dispersal patterns corresponded with Noongar cultural boundaries and resource availability, and postulated that as a less palatable food source, *P. trachymeniodes* was primarily exploited in a region where other edible Platysace were absent. It is postulated that the minimal food resources in the region required people to move around more than neighbouring regions, which may have involved the transplantation of *P. trachymeniodes* (14). Together, these findings highlight that phylogeographic and genomic studies of culturally significant species have great potential to offer insights to ancient or Indigenous human histories.

We investigated the possibility of ancient dispersal between the AWT and SEQ, as anthropogenic mediated long-distance dispersal and range expansion has been postulated for several culturally significant species throughout the Australian continent. For instance, human introductions are postulated to explain the disjunct distribution of *Castanospermum australe* on the east coast (17) and *Capparis mitchellii* in South Australia (99). However, we found high genomic divergence that suggests a process of vicariance between the northern and southern Australian populations of Bunya Pine. This is consistent with the previous RAPD study of Bunya Pine (45), and the information given by knowledge holders, who did not suggest dispersal between regions (27), despite other evidence of ancient trade and cultural connections (100).

Local anthropogenic dispersal rather than range expansion

We did not find support for our hypothesis of anthropogenically induced population size expansion in Bunya Pine. Although we inferred an elevated N_e and ancient bottleneck recovery in SEQ that was not evident in AWT, these shifts appear to pre-date plausible human activity. Nor did we find evidence of incipient domestication in the form of reduced diversity at sites of putative anthropogenic origin. These patterns contrast with the evidence of founder effects and high F_{is} observed in the southern Brazilian groves of *Araucaria angustifolia*, (101–104), which appears to have been planted as part of Indigenous territorial expansions 1-2 Kya (18, 105). The weak signal of population growth suggests that Bunya Pine translocation may have entailed a small number of kernels from a mix of locations or seasons, rather than mass plantings from only a handful of individuals or cones. Such a practice would promote genetic diversity within populations, rather than a signature of founder effects and selection. This may have been a consequence of protocols that restricted who was permitted to plant Bunya Pine and where. Custodial rights and obligations amongst Indigenous Peoples were built up through generations of interaction with the Bunya Pine forests (44) to the extent that one colonial report stated that ‘every tree was said to belong to some particular family’ (106). Another theory is that the small stands of Bunya Pine adjacent to creeks and campsites that were historically along the Bunya treks (33, 47, 61, 62) had regenerated from mud-stores that gathering attendees made on their return journeys, suggesting incidental Indigenous dispersal. Sample sites 7, 9, 22-23 and a handful of unsampled (including now cleared) sites are candidates of Bunya seed-store regeneration, however some of these putative seed stores may be colonial in origin (Supplementary Table 1).

We found subtle differences between the colonial and pre-colonial sites in SEQ that raises the possibility that Indigenous translocations of Bunya Pine changed through time. When the analyses only included

sites believed to have pre-dated European colonisation, some genetic structure was evident between the two areas of the traditional Bunya gatherings in the Blackall Range and the Western Downs. Although historical records indicate that there was some overlap in the tribes that attended (31), it is not clear whether the events were connected (40). The genomic patterns we detected may be the legacy of two distinct eastern and western Bunya treks associated with the gatherings. When all sites were included in our analyses, the genotype assignment plots suggested SEQ is one population, which may indicate that colonial plantings were sourced from across the region and thereby obscured the putative pre-colonial east-west structure. This interpretation of the data would suggest that Indigenous movement of Bunya Pine intensified following European colonisation. Indigenous Peoples have adopted plant translocations to maintain connection with sacred sites or inaccessible parts of country in Central Australia (107, 108) and northwestern Australia (109). Colonial displacement and migration reportedly prompted other Indigenous Peoples to uptake long-distance plant dispersals in North America (110, 111) and Aotearoa (New Zealand) (112). Greater sampling of pre-colonial sites in the Blackall Range may enable us to retrace the source of colonial Bunya Pine plantings. We could also use the additional samples to build and evaluate two models of pre-colonial migration: one that assumes an eastern and western dispersal pathway, or a single dispersal pathway that links both areas.

Pleistocene decline of Bunya Pine

Our findings are consistent with the Pleistocene decline of *Araucaria* in the palynological record (57), and supports an earlier hypothesis that the onset of rainfall seasonality led *Araucaria* to become restricted to moist highland refugia in its northern range and areas like SEQ that receive winter rain (58). It is noteworthy that we found divergence across the Black Mountain Corridor (BMC) within AWT to be equivalent to that between SEQ and AWT. This suggests a very ancient process of habitat fragmentation for Bunya Pine in AWT and is consistent with barrier effects detected in several other mesic taxa (82–87), with some BMC divergences dating back to the late Tertiary (113).

The stairway plot and evidence from the fossil record indicated a more ancient decline in the northern Bunya Pine than can be attributed to the Holocene megafauna extinction, although it does not preclude the possibility that localized pre-Holocene faunal extinctions played a role in Bunya Pine's range contraction. For instance, the Mid-Brunhes Climatic Event was a major climatic reorganization that led to increased aridity in northern Australia and a turnover from mesic to dry-adapted species, including the local extinction of megafauna from Mt Etna in central eastern QLD between 280-205 Kya (88). These climate shifts may have led to the extirpation of Bunya Pine in the region spanning between AWT and SEQ, and a range reduction within AWT. The lower rainfall received by SEQ may cause greater

sensitivity to climate shifts in the southern Bunya Pine and potentially explains the dramatic bottlenecks observed for this population. Additionally, the recent population crash inferred for SEQ suggests that the megafauna extinction and/or inter-glacial warming are plausible drivers of population decline in the region. Long-read sequence data is required to accurately date the population decline and regional divergences. These estimates could be calibrated with various records of faunal extinction events and climatic shifts to infer whether megafauna extinctions played a role in the decline of Bunya Pine.

Conclusions

In this study, we have presented genomic data that suggests pre-colonial dispersal of Bunya Pine by Indigenous Peoples in SEQ was either locally limited or obscured by subsequent colonial translocations; whilst anthropogenic dispersal did not occur in AWT. Our findings are concordant with evidence given by Indigenous knowledge holders (27), and we draw three general conclusions: (1) Variation in the contemporary IBK of Bunya Pine can be attributed to cultural differences between AWT and SEQ, rather than the geographically uneven loss of knowledge. (2) Ancient Indigenous Peoples did not facilitate long-distance dispersal of Bunya Pine between the AWT and SEQ. (3) Indigenous Peoples in SEQ appear to have altered their Bunya Pine translocation practices through time. Under settler colonialism, Indigenous Peoples translocated Bunya Pine long distances to maintain their cultural connectivity in new or altered homelands. However, we speculate that precolonial anthropogenic dispersal of Bunya Pine was more locally restricted. Whilst genomic studies have previously been employed to uncover Indigenous-mediated dispersal of culturally significant non-crop species, here we have demonstrated that plant genomics can also be deployed to uncover or clarify aspects of human history and the impacts of colonization on Indigenous translocation practices.

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Supporting Information

Supplementary Table 1. Bunya Pine (*Araucaria bidwillii*) stands in Southeast Queensland and historical information on the Indigenous and European-settler connections that may explain how the trees were planted or established at each site. Numbers correspond to the site number to indicate location on Figure 1 or NS indicates site not sampled. Site types assigned based on the weight of evidence: **P**=pre-colonial, **C**=colonial, **U**=unknown.

	Site (type)	Indigenous connection	European-settler connection
4	Amamoor State Forest (U)	Oral legend that there are a small number of ancient Bunyas near the plantation (Luke Barrowcliffe, <i>pers. comm.</i> to M. Fahey, March 2021).	Major state forest, though provenance unknown.
6	Munna Point, Noosaville (C)	Munna Point, a few hundred meters from the sample site, was once the main assembly site and large camp for northern groups en-route to the Blackall Ranges Bunya gatherings. Observers witnessed a lot of dancing and feasting on oysters (1).	Bunya Pine at Site 6 appear juvenile (either natural regeneration or recently planted).
7	Moy Pocket (U)	Property owners claim that the trees pre-date the previous two owners, and it is possible the trees regenerated from a Bunya store (<i>pers. comm.</i> to M. Fahey, March 2021).	May have been planted by the first European settlers that bought the property.
8	Mapleton State Forest (P)	Two Bunya Pines at least 150 years old and possibly planted just prior to or at the early stages of European settlement - they are located away from the natural Bunya Pine groves, though close to a traditional pathway, camp, and water source (2).	
9	Koongalba House, Yandina (C)	Koongalba House dates to 1894. Before that, the site (a ridge above the river) was a major Indigenous camp and corroboree ground, which is mentioned in accounts since the 1860s. There was a potential Bunya store at a spring once part of the property, and an apparent ceremonial arrangement. The Blythe/Low family owners claim that Indigenous Peoples planted and lived by the Bunya Pine trees (Audienne Blyth <i>pers. comm.</i> R. Kerhove and M. Fahey April 2021). A written account describes Susan (Kabi Kabi woman) planting a row of Bunya trees along Gympie Road and Wharf Street Yandina with property owner Christina Low c. 1895-1910. The kerosene can buckets used in the plantings are kept at Koongalba House (3).	Christina Low planted these together with the Kabi woman, hence this seems a colonial-era event (3).

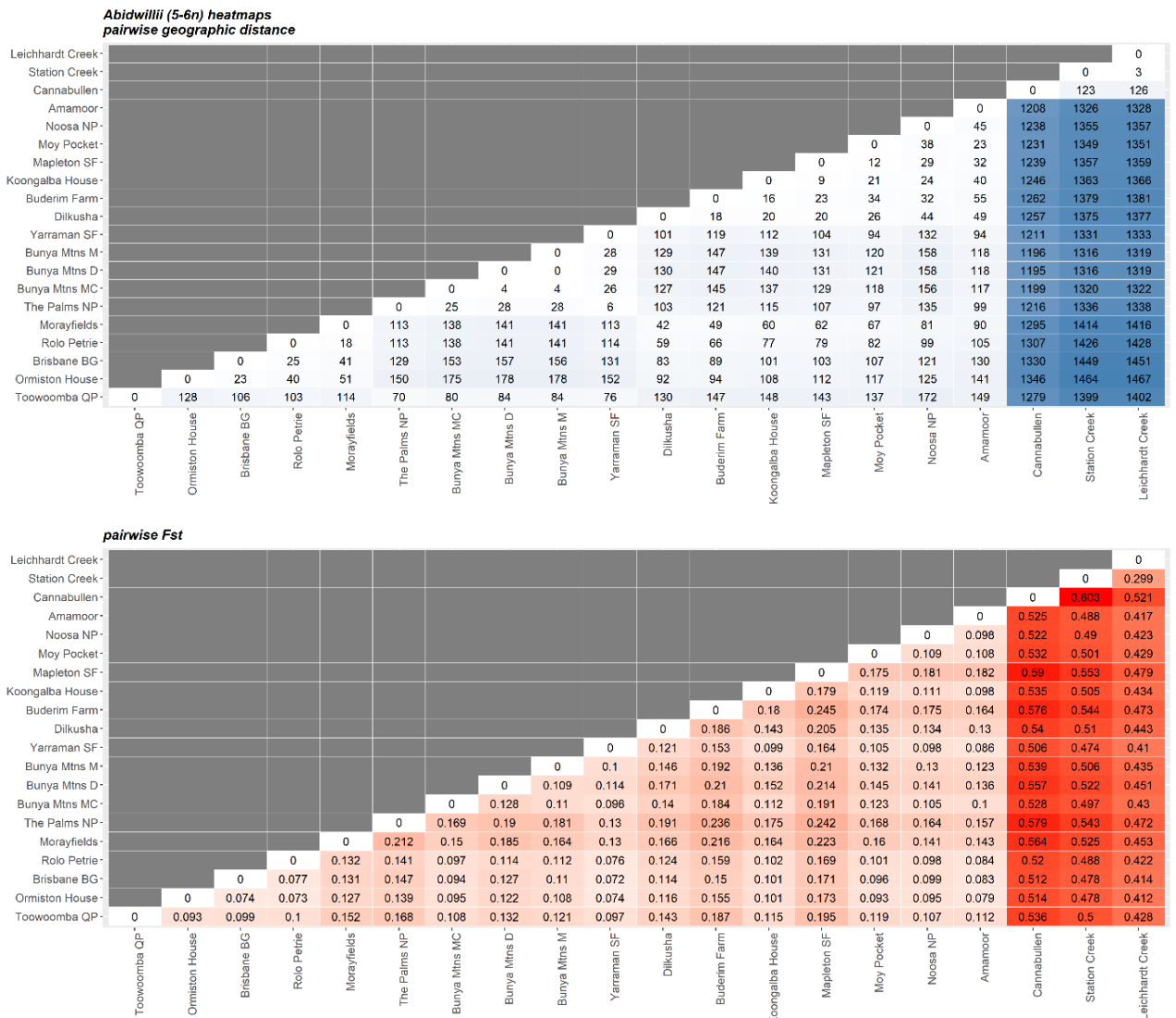
10	Jimna State Forest (C)	One of the main 'toor' (inter-tribal meeting) locations during the Bunya festival (4).	Major state forest, though provenance of plantation unknown.
11	Buderim Farm, Orme Rd (U)	Wise family claim the trees pre-date the farm, which was established in 1901. (Meredith Walker and Heather Johnson, <i>pers. comm.</i> to R. Kerkhove, March 2021). Artefacts at Wises Road indicate a small pre-colonial encampment near this location (5).	Two Buderim historians suggest that the European settler Gustav Reibe planted Bunya Pine(s) on Orme Road in 1880 (Weir via Meredith Walker email to R. Kerkhove 16 March 2021) or c. 1895 (Bill Lavarack <i>pers. comm.</i> to R. Kerkhove, 2012).
12	Buderim Forest Bushland Reserve (U)	Buderim was at a crossroads between Bunya treks, a signalling point and a campsite for groups to fish along the coast to the east. Artefacts at Orme Road indicates a small pre-colonial encampment at this location (6). It is where many European settlers learnt of the Bunya gatherings. "Some of the aboriginals who came for the nuts had their camp at Buderim, and on returning to their camp told Mr. Dixon, who lived at Buderim at that time that they had gathered them at Dulong" (7). NB: Dulong is approx. 15 km north-west of Buderim.	Timber getter William Pettigrew spoke of planting Bunya Pines in Buderim in the 1870s (8).
13	Baroon Dam, Maleny (C)	Main location of the traditional Blackall Ranges Bunya gatherings (4, 9).	Area was intensively logged and oral legend that Bunyas in the area are purported to be more recently planted (R. Kerkhove).
14	Dilkusha Nature Refuge (P)	Very large old Bunyas inhabited the property when it was bought in 1984, and the property owners believe the remnant rainforest on site pre-dates European settlement (Hillary Pearl, email to M. Fahey, 2022).	
15	Yarraman State Forest (P)	Isolated population that pre-dates European settlement (10).	
NS	Jimbour House, Jimbour East	Large old Bunya Pine in historic photographs of the gardens surrounding the house. The ridge beyond the shearing sheds was a major pre-Colonial camp. Meston noted in 1890 "a camp of about 14 blacks within 300 yards of the head station" and Ray Humphreys described the "Jimbour blacks" as "Bunya blacks" who trekked from that point up for bunya nuts (11). Indigenous Peoples occupied on the abandoned property in the 1910s, until driven off.	Possible mixed settler-Indigenous plantings of seedlings obtained from the Bunya Mountains: In 19 th century, the Bell family (Jimbour owners) would support and even assist the nut-gathering from the mountains on the property. "Jimbour Station was always receptive to the declining tribal people and many from there made their trek to the mountains for bunya nuts.... Preservation of the native culture was also a policy of the property, and it was one of the last areas in southern Queensland

			where genuine corroborees were held" (11).
16-17	Mowbullen, Bunya Mountains National Park (P)	Mowbullen was the principal dance ground and bora of the Bunya gatherings (4).	
18	Munro's Camp, Bunya Mountains National Park (P)	An important camp close to natural groves of Bunya Pine: 'the Burnett aborigines camped on the top of the range in a nice, sheltered pocket of scrub, known as Munro's camp' (12).	Logger's camp from 1880s (13).
19	Bankfoot House, Glasshouse Mountains (C)	Plausible Bunya trek campsite: "the next day they started for the Glasshouse Mountains... camped at the foot of Beerwah Mountain... on the way to these (Bunya) feasts the blacks in those days would often catch emus in the vicinity of the Glass House Mountains"(14). Bankfoot House camp was 2 kms east of Mt Beerwah summit and Old Gympie Road was the only route. Kabi Kabi people assisted with timber work here 1860s-1890s and there are Indigenous graves on the site (15). Kabi Kabi oral tradition that the large twin Bunya Pines were planted here to honour slain twin children of one of the workers (Bev Hand <i>pers comm.</i> to R. Kerkhove, March 2021).	Bankfoot House Museum claims that the Bunyas were planted from seed collected from a natural population near the property (<i>pers. comm.</i> to M. Fahey, 2021). No photographic evidence of Bunya trees in 1870s-1890s, although large Bunya trees evident in 1910s-1930s photographs at the museum.
20	Kilcoy Homestead (C)	Area historically abundant with natural Bunya Pine (16).	Trees are adjacent to a Homestead property established in the 1840s and likely planted by resident European settlers.
21	The Palms National Park (P)	Remnant subtropical rainforest in a spring-fed gully with various culturally significant species: piccabeen palm (<i>Archontophoenix cunninghamiana</i>), Black Bean (<i>Castanospermum australe</i>) and Bunya. Ancient Indigenous campsite and hunting area and stop-over en-route to the Bunya mountains (interpretative sign at The Palms National Park, Queensland Parks Wildlife Services).	
22	Moray Fields, North Shore Heritage Park, Morayfield (U)	According to Moreton Council official signage, this is a traditional Bunya patch and camp along the Bunya trek, and the Bunyas were planted by Indigenous people. There was also a patch of 'natural' Bunya close to the river near this site, that may have regenerated from a seed store.	The main Bunya patch is very close to ruins of former Moray Fields Homestead and appears planted. Indigenous Peoples worked at the cotton plantation at Moray Fields between 1861-1870 and may have planted Bunya Pines at this time.

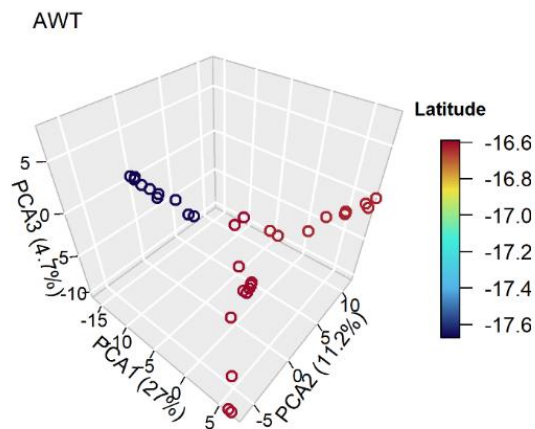
		Cultural heritage survey of Eve Fesl (Kabi Kabi elder) also confirmed the existence of a 'natural' Bunya patch here (17). Also see references for the nearby Caboolture Creek bridge, indicating pre-colonial presence of Bunya Pine.	
NS	Caboolture Creek bridge, Caboolture	Petrie (1904) noted this was a camp along the Bunya trek: 'The third night they camped at Caboolture....' (14). The surveyor Robert Dixon noted 'bunya scrub' at Caboolture on a map of Moreton Bay in 1842, that pre-dates settlement in the region (18). Lagoon Creek north-east of here was a major Aboriginal camp and resource area into the 1890s. 1873 photograph shows tall bunya growing in natural forest next to the bridge (19).	Trees appear young (either naturally regenerated or recently planted).
23	Rollo Petrie Forest, Sideling Creek, Petrie (U)	Major Indigenous camp of Petrie area, that continued as late as 1910s and one of the 'Bunya trek' stops (20, 21). Although the trees appear less than 70 years old, they may have regenerated from a Bunya seed store beside the creek. The surveyor Robert Dixon noted 'bunya scrub' and 'camp' at Petrie (or possibly further north-west) in 1842, pre-dating European settlement in the region (18).	The Bunya Pine here were likely planted as part of the development of 'Old Petrie Town' precinct revegetation in 1980s-1990s.
24	Our Lady of the Way School, Petrie (C)	Bunya trek camp: "this time it happened to be the Pine..."; site of bora and former Petrie homestead (Murrumba) which was built with local (Pine Rivers) Aboriginal men and was the frequent "drop in" for Aboriginal people, especially Dalaipi, a renowned headman. He planted 'Dalaipi Forest' which still stands here. Another camp was on the Australian Paper Mill site near Yebri Creek, Petrie (14, 22-24).	The Petries had great interest in the commercial potential of Bunya trees and planted the surrounds of Murrumba Homestead with Bunya Pine as early as 1850s-1860s, reportedly obtained from local Indigenous people. The staff (and builders) of Murrumba were all from the local Kabi Pine Rivers clan, headed by Dalaipi – meaning the planters were likely the local Kabi Kabi people (14, 24).
25	Brisbane City Botanic Gardens (C)	The Bunya Pine saplings were planted c. 170 years ago when Indigenous Peoples were populous and occupied the Brisbane area. Dalaipi (Kabi Kabi headman) planted Bunyas at Petrie's Murrumba Homestead (Site 24) and was associated with Walter Hill and accompanied his scientific expedition to the Mackay region. Therefore, Dalaipi	Bunya Pines derive from saplings purportedly gifted to Walter Hill (resident botanist) by Tom Petrie in 1855.

		was likely involved with locating and planting the Bunya Pine here (24).	
26	Ormiston House, Brisbane (C)	Newspaper report on the estate describes “a forest” of figs and “Bunya Bunyas” – suggesting a natural or Indigenous patch that pre-dates Ormiston House (25). Originally there was a campground near Ormiston House. Contemporary Quandamooka people have an oral tradition that describes a connection to Ormiston’s Bunyas: “Every year the monastery has two trailer loads of cones delivered to the Quandamooka people... sustaining their ancient cultural connection...” (26).	Louis Hope may have obtained Bunya Pine seedlings from botanist Walter Hill (Dr Jessica Stoja (Ormiston House), email to M. Fahey, 27 March 2021), and Jerry Coleby-Williams (26) believed Bunya Pines were planted by Louis Hope (no source given). Newspaper reports from 1919 and 1933 describe the “row of Bunya pines”, suggesting they were planted (27, 28).
NS	Grinstead Park, Enoggera; and Burwood Road crossing of Kedron Brook, Mitchelton	A large Bunya Pine tree by a water source (a small creek adjoining Kedron Brook) and a traditional Bunya trek camp: ‘They camped the first night at Ba-yu-ba... now known as Enoggera...’ (14). The water supported an area of extensive camps and corroboree grounds. The trees are roughly 200 m from former camp sites (now Mt Maria College, Alderley Station and Grinstead Park) (29–31).	By appearance, the tree is only 70–100 years old, thus possibly planted when the park was developed.
27	Baille-Henderson Hospital, Toowoomba (C)	There was formerly a camp at the bottom of the hospital site, by the creek below Nicoll Avenue. An oral tradition that Indigenous Peoples were in some manner involved in the Bunya tree planting (Adrian Beattie, Western Wakka Wakka custodian, <i>pers. comm.</i> to R. Kerkhove, May 2021).	Psychiatric Hospital built 1888-1919 and the trees are mostly in avenues. Some are known to have been established c. 1910 (32).
28	Queens Park, Toowoomba (C)	Identified as Indigenous planted by contemporary Traditional Owners. Possibly connected with a camp at the bottom of the park between Ruthven Street North and Bridge Street and/or connected to the dance ground at Toowoomba TAFE across the road. The camp was occupied by Indigenous Peoples up till 1880s – some coming in large numbers for ‘blanket days’ (33, 34).	Bunya possibly planted on ‘Abor Day’ - a common school activity late 19th- early 20th century to encourage tree planting (Prof Maurice French, <i>pers. comm.</i> 21 September 2021). There were similar plantings at Glenvale and Geham State Schools near Toowoomba in 1896 and 1932 (35, 36).
29	Hursley Road & Greenwattle Street, Toowoomba (C)	Possible colonial or pre-colonial signalling spot. This site consists of a couple of large ‘landmark’ trees on a high spot, by colonial-era house, with clear views to other Bunya Pine stands (<i>pers. obs.</i>).	Ian Menkins: “the few surviving ones... the really big ones got felled when that housing estate went in” – suggesting that contemporary trees are not pre-colonial. Menkin does not believe any Bunya trees were planted by Aboriginal people (Ian Menkins,

			<i>pers. comm.</i> to R. Kerkhove, 6 March 2021).
30	Ipswich TAFE (U)	Possible marker tree that sits above a large former Indigenous camp: "The pine sits on the site of the former Kruger sawmill site...the base of the rise was bulldozed." The former owners seem to believe the tree had special significance: "Ted Kruger insisted that this tree always be preserved. There was once a large fig tree near this pine tree" (37).	Likely planted in historic times and kept for nostalgic reasons: "under it the locals would play games of cricket"; "Historical associations with the Kruger sawmill site" (37).
31	Queens Park, Ipswich (C)	Major campsite, bora grounds (traditional meeting place), chalcedony mine and tournament site until 1890s. "Queens Park as camping... confirmed by local oral tradition.... (had) a spring in the vicinity." This may have been a Bunya Pine seed store (37). The oldest Bunya Pine grows by a known Indigenous lookout and near a sacred limestone ridge and mine. This is just above the spring and putative seed store.	Queens Park was surveyed in 1842 and was a central feature of Ipswich CBD by 1862. It contains many old, planted trees and once had a resident botanist who grew exotic seedlings including Bunya Pine.
NS	RSL Hall Nicholas Street, Ipswich	No Bunya Pine present, however there were originally a set of springs between Nicholas, South, Ellenborough and Limestone Streets. Possible former seed store: "Camping place...significant because it was a place where people assembled...on their way to bunya festivals...The presence of a spring is confirmed by historical accounts" (37).	
NS	Nielson Park, Tarlington Street, Toowoomba	John Swarbruck (botanist) identified Bunya Pine saplings as 'natural' remnant regrowth (park was never cleared) that may have regenerated from an old seed store. The site is near a formerly important resource area, in a waterhole at the termination of East Creek (near MacKenzie St). (John Swarbrick, <i>pers. comm.</i> to R. Kerkhove, 3 October 2021).	Botanist and explorer Allan Cunningham did not note the presence of Bunya Pine at Toowoomba on his expedition from Brisbane to the Darling Downs in 1827, suggesting the species did not extend further south



Supplementary Figure 1. Pairwise Fst values estimated from dataset “5-6n”, demonstrating genomic differentiation across the full distribution of Bunya Pine (*Araucaria bidwillii*).



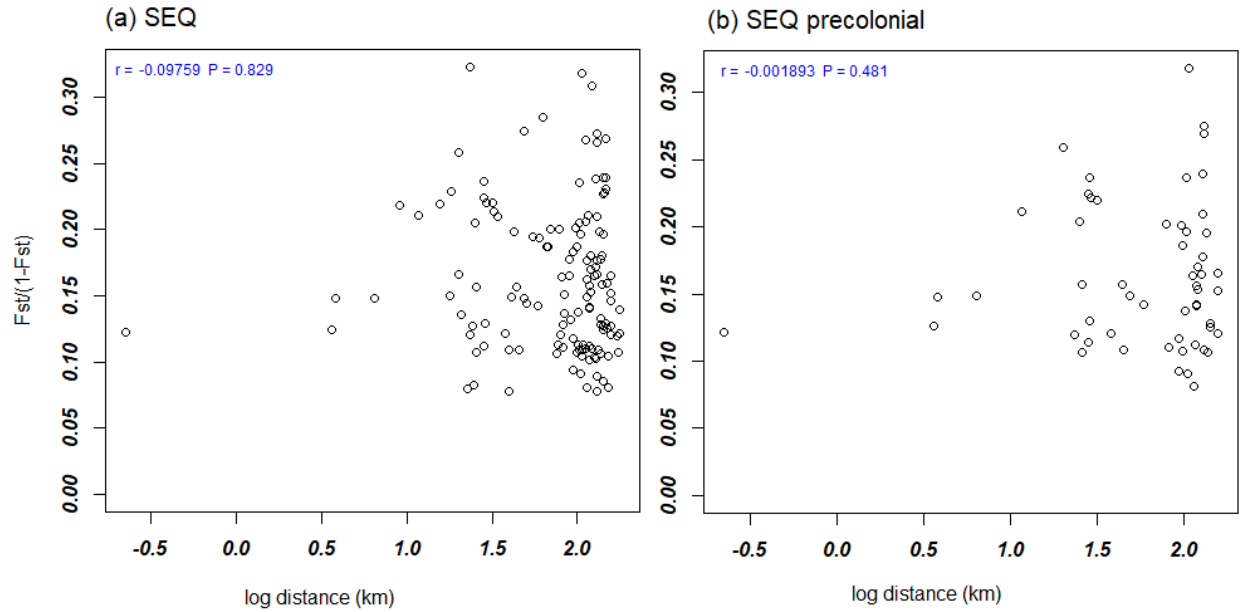
Supplementary Figure 2. The primary three axes of variation in a Principal Components Analysis of genomic variance amongst Bunya Pine (*Araucaria bidwillii*) samples in the Australian Wet Tropics.

Supplementary Table 2. Pearson's correlation between estimates of Bunya Pine (*Araucaria bidwillii*) genetic diversity and geographic variables at each site. Diversity was calculated from 5 individuals across 5894 SNPs per site. Ar=allelic richness per locus, Ho=observed heterozygosity per locus, uHe=unweighted expected heterozygosity per locus, fis=inbreeding coefficient, pA=private alleles. Values marked with * are significant (p=0.01).

Full Study	Ar	Ho	uHe	fis	pA	%p
var*latitude	-0.65*	-0.61*	-0.91*	-0.38	0.90*	-0.63*
SEQ						
var*longitude	0.33	0.45	0.06	-0.52	-0.15	0.23
var*latitude	-0.02	-0.15	-0.24	0.07	-0.08	-0.72*

Supplementary Table 3. t-Test (two-Sample assuming unequal variances) to determine a significant difference in Bunya Pine (*Araucaria bidwillii*) genetic diversity at pre-colonial versus colonial sites. Diversity was calculated from 5 individuals across 5894 SNPs per site. ar=allelic richness per locus, Ho=observed heterozygosity per locus, uHe=unweighted expected heterozygosity per locus, fis=inbreeding coefficient, pA=private alleles.

	ar*p	ar*c	Ho*p	Ho*c	uHe*p	uHe*c	fis*p	fis*c	pa*p	pa*c	%p*p	%p*c
Mean	1.32	1.36	0.09	0.11	0.20	0.21	0.43	0.35	50.14	42.00	25.86	27.67
Variance	0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.01	525.14	237.50	10.53	7.33
Observations	7.00	9.00	7.00	9.00	7.00	9.00	7.00	9.00	7.00	9.00	7.00	9.00
Hypothesized Mean												
Difference	0.00		0.00		0.00		0.00		0.00		0.00	
df	12.00		13.00		12.00		14.00		10.00		12.00	
t Stat	-1.01		-2.09		-1.31		1.98		0.81		-1.19	
P(T<=t) two-tail	0.33		0.06		0.21		0.07		0.44		0.26	
t Critical two-tail	2.18		2.16		2.18		2.14		2.23		2.18	



Supplementary Figure 3. Linearised pairwise F_{st} distances plotted against $\log_{10}$ geographic distance between samples in Bunya Pine (*Araucaria bidwillii*) datasets (a) all SEQ sites with 5-6 samples and (b) SEQ pre-colonial sites with 5-6 samples.

Supplementary Table 4. Tests of range expansion and founder effects in Bunya Pine (*Araucaria bidwillii*). q is the strength of the founder effect, which positively increases with distance from the origin of range expansion and approaches zero with time since expansion and/or migration between demes; $r1/r10/r100$ is the decrease in diversity over 1/10/100 km; d is the effective founder distance in km (the deme size for which N_e is reduced by 1% during a founder event) and a low value indicates a strong founder effect; $Rsqr/pval$ are the correlation coefficient and p-value for the most likely origin ($P < 0.001$).

dataset	q	$r1$	$r10$	$r100$	d	$Rsqr$	P-value
SEQ	0.000528	0.998945	0.989548	0.904467	9.563228	0.049268	54.08206
SEQ pre-colonial	0.00011	0.999781	0.997809	0.978517	46.00945	-0.00525	4006.831

Supplementary Table 5. Contemporary N_e estimated for populations of Bunya Pine (*Araucaria bidwillii*) using N_e estimator v2. n =sample size, $n(hm)$ =harmonic mean sample size. SEQ= Southeast Queensland. Mt Lewis and Cannabullen representative of Australian Wet Tropics.

	Singletons in included				Singletons removed	
	n	SNPs	$n(hm)$	N_e	$n(hm)$	N_e
Mt Lewis	22	8038	15.6	11.4	15.6	7.2
Cannabullen	10	11737	4.9	inf	5.0	27.0
SEQ	23	6257	79.1	371.3	79.1	378.3
SEQ colonial	23	11844	34.5	311.5	34.5	218.4
SEQ pre-colonial	28	4421	28.5	140.0	28.4	118.9

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Chapter 5. Indigenous Peoples in eastern Australia facilitated dispersal and range expansion of the culturally significant Black Bean tree (*Castanospermum australe*; Fabaceae)

Abstract

Retracing the dispersal of culturally important plants by precolonial Indigenous Peoples can illuminate biocultural knowledges and the long-term genetic consequences of translocations, and hence guide contemporary restoration. *Castanospermum australe* (A. Cunn. & C. Fraser ex Hook.) or Black Bean is a culturally significant riparian tree with edible nuts that traditionally formed the staple diet of many Indigenous groups in northeast and central eastern Australia. Based on the large size of its seed and riparian dispersal syndrome, the species is assumed to have a limited potential for non-human dispersal between catchments. Yet findings from earlier studies raised the hypothesis that Black Bean underwent a recent and/or rapid spatial expansion in its southern range in part facilitated by Indigenous people in the region. This study built on previous work to investigate chloroplast and nuclear DNA evidence of dispersal within and between the range extremes of Black Bean, including between catchments, to evaluate the influence that pre-colonial Indigenous people had on the species' current distribution. Strong chloroplast divergence was detected within the northern range, suggesting that upslope seed dispersal has been limited in the absence of human influence. In the southern range, I found evidence of between catchment and upslope dispersal in both genomic datasets, supporting a scenario of recent anthropogenic-mediated range expansion. However, there were no consistent signals of founder effects or elevated outbreeding at upland sites of putative anthropogenic origin. Additional sequencing and coalescent models are likely to reveal the continent-wide dispersal history of Black Bean, including anthropogenic dispersal pathways.

Introduction

Castanospermum australe (A. Cunn. & C. Fraser ex Hook.), commonly known as Black Bean or Moreton Bay Chestnut, is a long-lived riparian tree with a disjunct distribution along the east coast of Australia. The tree carries strong cultural significance for many Indigenous groups across parts of its range (1). At the time of European colonisation in 1788, the large nutritious though toxic seeds of Black Bean provided a seasonal staple food for Indigenous Peoples of the Australian Wet Tropics (AWT), southeast Queensland (SEQ) and northern New South Wales (NNSW; Figure 1; sources listed in (2)). While Black Bean seed pods can float and naturally disperse downstream along riparian corridors, the tree is known to inhabit isolated upland patches, sometimes away from watercourses, leading to speculation that some

of these populations were established by pre-colonial Indigenous Peoples (1). This theory is consistent with the Bundjalung story that told of ancestors that dropped Black Bean seeds along the Nguthunguli songline between coastal NNSW and upland to the western Border Ranges in SEQ (1).

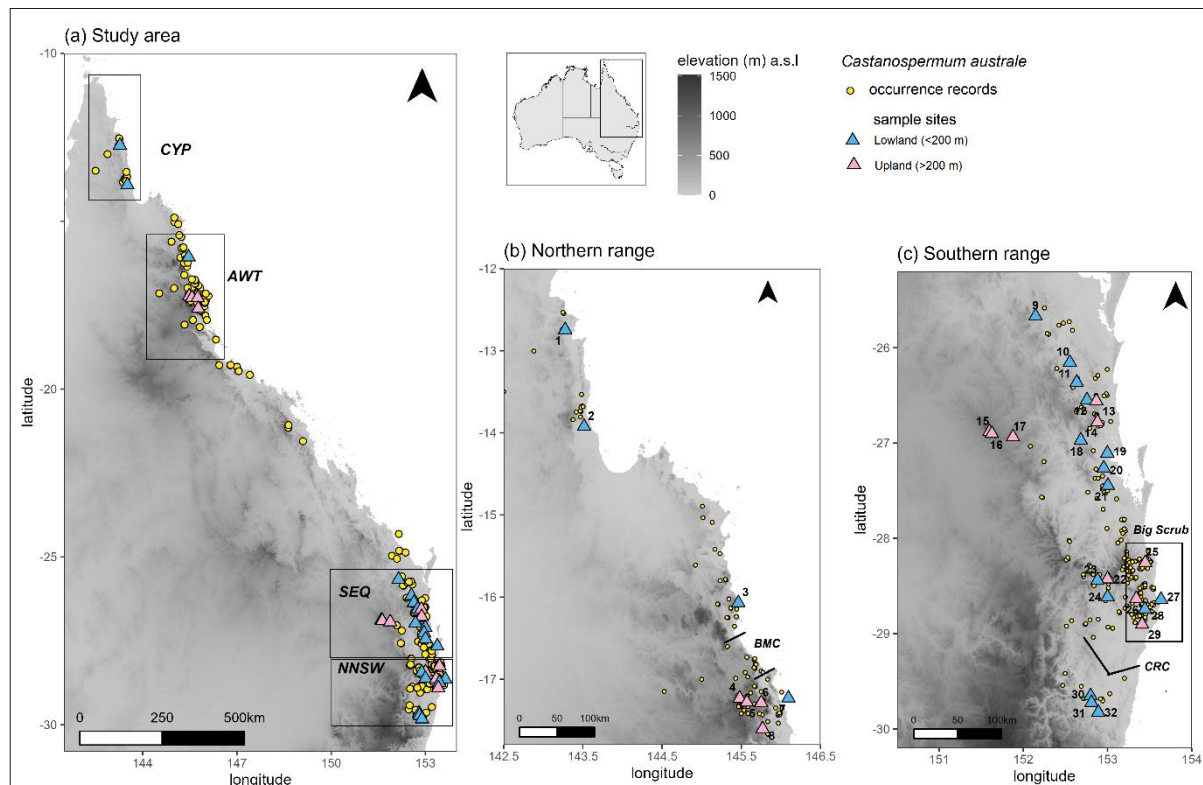


Figure 1 Distribution and sample sites of *Castanospermum australe* in eastern Australia. (a) The study area includes CYP= Cape York Peninsula, AWT= Australian Wet Tropics, SEQ= Southeast Queensland, NNSW= Northern New South Wales. (b) The northern range contains the biogeographic barrier BMC= Black Mountain Corridor, the extent of which is indicated by two black lines. (c) The southern range contains the biogeographic barrier CRC= Clarence River Corridor, marked with a black line.

In addition to the Indigenous biocultural evidence of past dispersal, recent genomic studies have revealed contrasting patterns between the northern and southern range of Black Bean (1, 2) that may reflect different anthropogenic interactions across the two regions. Pooled-sample chloroplast (cpDNA) genotyping revealed widespread haplotype-sharing in NNSW that suggests recent and/or rapid range expansion in the southern part of the species' distribution (1). Additionally, low nuclear DNA (nDNA) differentiation and putative admixture was found in populations from NNSW, albeit with some structure between upland and lowland sites (2). These findings have led to the hypothesis that Indigenous Peoples either directly introduced Black Bean to its southernmost range or facilitated a range expansion in NNSW from an earlier natural founder event, particularly to upland sites. Long-distance dispersal of Black Bean

may have occurred as a consequence of trade and/or ancient migrations. For instance, Dreaming stories (orally transferred creation stories) told by Quandamooka people in coastal SEQ describe the Black Bean pod as a watercraft that carried ancestral beings from the mainland to a cluster of islands in Moreton Bay (3). This potentially alludes to the original migration of the Quandamooka ancestors to the islands, bringing Black Bean with them. Alternatively, these stories may refer to the natural dispersal of Black Bean via oceanic currents, as the seed pods resemble miniature canoes.

By contrast, strong haplotype structure was previously detected between three sites in AWT, suggesting limited anthropogenic or natural dispersal in the northern range of Black Bean (1). However, ethnohistorical and archaeological records indicate that Black Bean seed was a seasonal staple, and the tree carries ancient cultural significance for various Indigenous groups in the region (see Materials & Methods). At the time of European colonisation (post-1788), annual inter-group ceremonial gatherings took place in cleared pockets within the dense rainforest of the AWT tablelands during the Summer and at lowland coastal sites in the Winter (4, 5). At these ceremonial grounds, often known as bora grounds, women stored and processed large volumes of edible nuts to feed the gathering attendees (6). Present-day stands of Black Bean can be observed adjacent to some of these upland bora grounds (M. Fahey, pers. obs), such as near Site 8 in this study (see Figure 2) or at Lake Barrine on the Atherton Tableland and ‘Gourka Gourka’ on the western slope of upper Bellenden Ker (7). This raises the possibility that the trees were intentionally or incidentally translocated in connection to the hosting or migration to the ceremonial gatherings. This hypothesis is supported by the putative signal of nDNA admixture observed at an upland site in the Atherton Tableland (2), potentially the outcome of anthropogenic dispersal from multiple sources.

As a step toward uncovering the influence of east Australian Indigenous Peoples on the distribution and genetic diversity of Black Bean, this chapter investigates genetic signatures of recent dispersal within and between the northern and southern ranges of the species, that cannot be attributed to riparian or faunal vectors. I use the terms ‘ancient’ and ‘recent’ in reference to an evolutionary timescale, with ‘ancient’ indicating hundreds of thousands to millions of years in the past (i.e., prior to the arrival of humans on Sahul) and ‘recent’ indicating after the arrival of humans to Sahul, from ~65 kya onwards (8). Although it is not possible to determine the timing of events in this chapter, I assume that detectable signatures of human influence are most likely to have occurred during the Holocene, as people responded to the environmental and botanical shifts associated with Holocene warming.



Figure 2. Mamu Traditional Owners and project collaborator Gerry Turpin collecting Black Bean (*Castanospermum australe*) leaf samples at bora grounds near Gooligan's Ck (Site 8), Wooroonooran National Park, Queensland, Australia.

First, I sought to determine whether a new, expanded and combined cpDNA and nDNA dataset supported the question raised by Rossetto et al. (2017): (1) Was the southern range recently colonised via long-distance dispersal from northern populations? In addition, I built on Rossetto et al. (2017) with individual-based data that can be used to quantify variation within populations. Specifically, I explored the following three hypotheses of anthropogenic dispersal within the northern and southern ranges; (2) Does gene flow primarily occur within catchments (riparian dispersal) or is there evidence of gene flow between catchments (anthropogenic dispersal)?; (3) Do upland sites show signs of founder effects (single dispersal event) or elevated outbreeding (multiple dispersal events/sources)?; (4) Do analyses of co-ancestry and admixture between sites support introgression between geographically distant populations?

Materials and Methods

Study species

Black Bean is the only member of the genus *Castanospermum*, with its closest relatives in the tropical South American genus *Alexa* (9). It grows to 35 m tall in pluvial forests, mostly on riverbanks in lowland and mountainous regions, from the Cape York Peninsula (CYP; 12°42'S) to the mid north coast of NSW (30°22'S; Figure 1), as well as Papua New Guinea and Norfolk Island (Australian territory), Vanuatu, and New Caledonia in the Pacific. Black Bean thrives on well-drained, fertile, moist alluvial soils and deep loams on basalt in sunny positions, though will tolerate partial shade. The species occurs in a wide range of subtropical to tropical climes, and will tolerate light frost, though prefers climates with a mean annual temperature of 28°C and mean annual rainfall of 1,000–3,800 mm (10).

The fruits develop between March and May (Autumn) and are 10-25 x 4-6 cm woody cylindrical pods that contain 3-5 round seeds similar in appearance to chestnuts (11). The seeds are 3-5 cm in diameter and contain castanospermine, an indolizidine alkaloid that inhibits alpha- and beta-glucosidase activity and causes severe gastrointestinal upset in some mammals (12).

Known animal dispersers of Black Bean

The common bush rat (*Rattus fuscipes*) has been identified as a major predator of Black Bean seeds (10, 13), and can promote seed germination rates in some rainforest species (14). However, bush rat movements are restricted to the densely forested slopes and gullies surrounding creeks and rarely disperse seed beyond a range of 200-400 m (15, 16). Therefore, native rats are not likely to move Black Bean seed over ridgelines or between catchments.

I could not find reports on the impacts of castanospermine on birds. Cockatoo species (*Cacatua spp.*) are reported to occasionally feed on Black Bean seeds in some locations (17), though it is not their typical food source and so dispersal by Cockatoos would be sporadic. Furthermore, the Southern Cassowary (*Casuarius casuarius johnsonii*) can ingest seeds up to 6 cm whole (18) and might be able to consume Black Bean seed without processing them and therefore without ingesting castanospermine. Therefore, in continuous rainforest, cassowaries can potentially disperse Black Bean up to 2 km per day (19, 20). Regardless, across most of the Black Bean distribution (south from AWT), there are no birds with a sufficiently large gape to swallow the seed whole (see (2, 21). Finally, the buoyant seed pods are reportedly able to travel long distances via oceanic currents and may account for the species' presence in the Pacific, though I could not find a source for this claim.

Black Bean pollen grain morphology appears to be adapted for bird pollination (22). The large showy racemes of yellow-orange flowers emerge between September and November (Spring) and contain abundant nectar that attracts butterflies, flying foxes (*Pteropus* sp.) and parrots such as lorikeets (*Trichoglossus* sp.). Lorikeets are widespread in eastern Australia and their foraging behaviour is likely to facilitate long-distance pollen dispersal (23). Therefore, I anticipated greater potential for nDNA connectivity between catchments and across habitat barriers across the study area, while cpDNA dispersal was anticipated to be primarily constrained within catchments in the absence of human intervention.

Known Indigenous uses of Black Bean

Indigenous Peoples in eastern Australia are known to have historically consumed Black Bean seeds in multiple locations across the species' range. Although archaeobotanical studies are sparse in the southern range of Black Bean, ethnographic sources and contemporary knowledge point to Black Bean exploitation and cultural significance to the Kabi Kabi, Jagera, Yugambeh and Bundjalung people (3, 24, 25). Amongst these groups, it is women's 'business' (role) to learn how to remove the toxins from Black Bean seed and prepare them into flour for consumption (Bundock, 1978; Madonna Thompson (Jagera) pers. comm. 2022). Meanwhile Black Bean features in Bundjalung (NNSW) and Quandamooka (SEQ) Dreaming stories that imply a link between human migrations and Black Bean dispersal (1, 3). I could not find ethnographic or other sources that indicate Indigenous groups in the CYP or central QLD exploited Black Bean, although the now extinct Warungu language (central QLD) had a name for Black Bean, indicating some form of cultural importance (26).

In the AWT, ethnographic reports describe Black Bean seed detoxification and consumption by several groups during the early colonial period (27–30). This included lowland coastal groups, such as the southern clans of the Girramay, Warrgamay (31, 32), and Jirrbal (33) and the northern coastal Kuku-Yalanji (34–36). The upland Jirrbal people on the western side of the Atherton Tablelands also exploited Black Bean (5) and archaeobotanical research has dated Black Bean seed processing on the tablelands to at least 2.5 kya (37). It has been noted that detoxification techniques vary considerably between locales (38) and linguistic analyses have revealed little homology between names for Black Bean seed amongst the various dialects of the region (1). All of this suggests that Indigenous AWT peoples have an ancient relationship with Black Bean that has diversified amongst clans and language groups.

Sample scheme

The sampling scheme was intended to capture the full breadth of diversity across the east Australian distribution of Black Bean, and to target multiple lowland and upland sites within each catchment to gauge whether gene flow primarily moves downstream (riparian dispersal) or upstream within and between catchments (anthropogenic dispersal). However, travel restrictions imposed by the Covid-19 pandemic prevented the ability to sample the central QLD region or multiple sites per catchment in the northern range. Nevertheless, I obtained Black Bean leaf tissue samples from 9 sites (6 catchments) in the northern range and 23 sites (10 catchments) in the southern range. Sample sizes varied between 1-13 samples per site (average = 7), depending on the number of trees and their accessibility (Table 1).

Generation of genomic data

cpDNA

Chloroplast DNA was obtained for 3 samples from each of 16 sites across the study area (Supplementary Table 1). Whole-genome skim sequencing was undertaken at Deakin Genomics Research and Discovery Facility (Geelong, Australia) and I extracted chloroplast reads by mapping against a library of chloroplast genomes with GetOrganelle (39), using *Angylocalyx braunii* (Papilionoideae) chloroplast plastid as a seed (Accession: MN709877). I used CLC Genomics Workbench 20.0 (QIAGEN, Denmark) to assemble the chloroplast genomes de novo by taking an initial mapping against the *A. braunii* reference. CLC was also used to inspect read quality and depth, identify inverted repeat regions and map reads against annotated Papilionoideae sequences obtained from GeSeq (40), using default settings. For read conflicts, I used the quality score and vote options to determine the consensus sequence and variants with a coverage <20 or read consensus <60% were marked as 'N' for ambiguous.

The sequences were aligned with the MUSCLE alignment function in Geneious Prime 2022.2 (Biomatters, New Zealand) to identify variant sites. As the alignment function can't handle repeat regions, the inverted repeats were removed from the sequences prior to alignment. To eliminate potential sequencing errors, non-synonymous variants in coding regions were marked ambiguous as were variants within 5 base pairs from repeat regions > 5 base pairs long. After removing the inverted repeats and areas of low coverage, the cpDNA sequences ranged between 99,148 and 102,044 base pairs (Table S1).

Table 1. Sample sites and genetic diversity estimates for Black Bean (*Castanospermum australe*). Sites with less than 5 samples were excluded from diversity analysis. Orara and OraraN were merged for diversity calculations. ar=allelic richness, Ho=observed heterozygosity, He=expected heterozygosity, Fis=inbreeding coefficient, pa=private alleles, %p=proportion of polymorphic loci. CYP= Cape York Peninsula, AWT = Australian Wet Tropics, SEQ= Southeast Queensland, NNSW= Northern New South Wales.

Region	Sub-region	Site	Locality	Lat	Long	Elevation (m)	Catchment	Riparian	n	ar	Ho	He	Fis	pa	%p
CYP	NBMC	1	Iron Range NP	-12.75	143.28	34	Lockhart	Y	6	1.19	0.08	0.08	-0.07	11	19
		2	Kulla	-13.92	143.52	34	Stewart	Y	5	1.24	0.10	0.09	-0.11	4	24
AWT		3	Cape Tribulation	-16.07	145.46	33	Daintree	Y	8	1.21	0.09	0.08	-0.06	54	21
AWT	SBMC	4	Tolga	-17.23	145.48	772	Barron	N	10	1.27	0.11	0.11	0.02	24	28
		5	Curtain Fig	-17.28	145.57	755	Barron	N	7	1.28	0.11	0.11	0.03	11	28
		6	South Curtain Fig	-17.29	145.75	615	Mulgrave-Russell	N	10	1.25	0.09	0.11	0.15	2	27
		7	Russell Island	-17.23	146.09	41	Mulgrave-Russell	Y	4	NA	NA	NA	NA	NA	NA
		8	Gooligan's Ck	-17.60	145.77	385	Johnston	Y	10	1.3	0.12	0.12	-0.03	77	32
SEQ	MV	9	Eel Ck	-25.67	152.14	130	Mary	Y	6	1.19	0.09	0.08	-0.12	11	18
		10	Glastonbury Ck	-26.15	152.55	63	Mary	Y	6	1.24	0.10	0.01	-0.05	1	23
		11	Amamoor	-26.36	152.64	113	Mary	Y	5	1.23	0.09	0.09	0.02	2	21
		12	Moy Pocket	-26.55	152.76	87	Mary	Y	10	1.24	0.10	0.09	-0.07	1	22
		13	Mapleton	-26.56	152.87	288	Mary	N	1	NA	NA	NA	NA	NA	NA
		14	Mary Cairncross	-26.78	152.88	440	Mary	Y	10	1.25	0.10	0.10	-0.03	6	24
	DD	15	Bunya Mtns D	-26.88	151.59	980	Burnett	Y	8	1.17	0.06	0.07	0.10	0	15
		16	Bunya Mtns MC	-26.90	151.63	970	Burnett	N	8	1.18	0.07	0.07	0.01	3	16
		17	The Palms NP	-26.94	151.88	508	Brisbane	Y	7	1.20	0.09	0.08	-0.07	0	19
	MOR	18	Neurum	-26.97	152.68	130	Stanley	Y	8	1.24	0.10	0.10	-0.06	1	23
		19	Morayfields	-27.11	152.99	3	Caboolture	Y	2	NA	NA	NA	NA	NA	NA
		20	Rollo Petrie	-27.26	152.96	20	Pine	Y	6	1.24	0.02	0.10	0.13	0	22
		21	Bancroft Park	-27.45	153.00	7	Enoggera	Y	6	1.23	0.07	0.09	0.21	3	22
NNSW	NR	22	Razorback	-28.427	153.00	313	Richmond	N	2	1.25	0.11	0.10	-0.10	4	22
		23	Moore Park	-28.44	152.88	116	Richmond	Y	5	NA	NA	NA	NA	NA	NA
		24	Fawcetts Ck	-28.61	153.00	58	Richmond	Y	10	1.23	0.10	0.09	-0.10	1	21
	BS	25	Hogan's Scrub	-28.25	153.45	209	Tweed	N	5	1.28	0.11	0.11	-0.03	24	27
		26	Big Scrub	-28.63	153.34	213	Richmond	Y	8	1.26	0.11	0.10	-0.10	28	25
		27	Byron Bay	-28.64	153.64	26	Richmond	N	10	1.21	0.07	0.09	0.23	0	22
		28	Booyong	-28.74	153.44	29	Richmond	Y	13	1.26	0.10	0.10	0.02	21	24
		29	Victoria Park	-28.90	153.41	171	Richmond	N	10	1.25	0.11	0.10	-0.10	3	53
	NR	30	Ramornie	-29.65	152.80	23	Clarence	Y	2	NA	NA	NA	NA	NA	NA
		31	Orara N	-29.72	152.81	25	Clarence	Y	4	1.24	0.10	0.09	-0.04	7	21
		32	Orara	-29.83	152.89	33	Clarence	Y	4	1.24	0.10	0.09	-0.04	7	21

nDNA

For all samples, nDNA extraction from leaf samples and SNP genotyping using DArTseq technology (41) was undertaken at Diversity Arrays Technology Pty Ltd (Canberra, Australia). Markers were filtered according to reproducibility average (proportion of technical replicates for which the marker score is consistent) and call rate (proportion of individuals with non-missing scores). I retained markers with a

minimum reproducibility average of 0.96 and a call rate greater than 0.9, and randomly selected one SNP per CloneID to minimise the influence of linkage disequilibrium in the dataset. After quality filtering, this yielded 24,121 SNPs from 216 samples across the full study (2.63% total missing data). To explore regional hypotheses of dispersal, I subset the data for separate analyses of the full study area, North, and South (Figure 1).

Haplotype inference (cpDNA)

To visualise cpDNA variation amongst samples, I employed POPART 1.7 (42) to construct a median-joining haplotype network with epsilon=0. This method shortens the overall length of the network, by iteratively adding inferred nodes with 'median' sequence variation to the observed haplotype nodes (43). Sites where one or more samples were ambiguous were excluded from the haplotype calculation. Although pollen dispersal via birds and bats may facilitate widespread nDNA connectivity, seed (cpDNA) dispersal is expected to follow riparian corridors in the absence of human assistance. I anticipated widespread haplotype sharing amongst catchments in the southern range as an indication of recent and/or rapid range expansion potentially facilitated by anthropogenic dispersal. By contrast, the northern range was anticipated to display greater haplotype structure as a more ancient lineage.

Population structure (nDNA)

I employed the sNMF genotype assignment algorithm implemented in R package LEA 3.6.0 (44) to identify population structure across the Black Bean distribution, with a particular focus to identify "admixed" individuals and sites, as an indication of co-ancestry (incomplete lineage sorting) or introgression. I ran models that assumed K=2-6 ancestral genotypes, with 10 replicates per model. To verify population groupings based on allelic covariances, I used the discriminant analysis of principal components (DAPC) method implemented in R package adegenet 2.1.7 (45, 46). I also performed a principal components analysis (PCA) on the allelic variance amongst samples and visualised this using a three-dimensional ordination of the first three principal components. Under a scenario of recent range expansion in the southern range, I anticipated that nDNA population structure would correspond with the cpDNA groupings and reveal gene flow between catchment areas. Meanwhile, different gene flow rates associated with pollen versus seed dispersal was anticipated to have produced some nDNA vs cpDNA genomic differences in the northern range, as a putatively more ancient lineage.

Genetic diversity (nDNA)

To eliminate the effects of sampling bias on the calculation of diversity statistics, I filtered the dataset such that there were 6 samples per site. Those with less than 6 samples per site were excluded from analysis. To quantify genetic distance between sample sites, I calculated pairwise F_{ST} values in R package BEDASSLE 1.6 (47). I used the R package *diveRsity* 1.9.9 (48) to estimate the observed heterozygosity, expected heterozygosity, proportion of polymorphic loci, allelic richness (confidence interval = 0.05, 999 bootstraps), and inbreeding coefficient for each site. The number of alleles unique to each site (private alleles) was calculated in *poppr* 2.9.3 (49, 50). I anticipated that anthropogenic translocation of Black Bean to upland sites would have produced either elevated outbreeding or founder effects, depending on the dispersal scenario. For instance, reinforcement translocations (multiple dispersal events or seed sourced from multiple locations) were anticipated to result in a negative inbreeding coefficient along with elevated heterozygosity and allelic richness compared with the species' average, particularly if dispersal was recent. On the other hand, if Indigenous people introduced Black Bean to upland sites with a small number of propagules and no additional dispersal (introduction or assisted migration), these sites were anticipated to display high inbreeding coefficients and lower diversity estimates than the species' average. To account for geographic influences on diversity, I performed a Pearson's correlation (two-tailed t-test of significance, $P=0.05$) between diversity estimates and latitude, longitude, elevation.

Migration

I applied TreeMix (version 1.13, Pickrell and Pritchard 2012) to test for and visualise co-ancestry and admixture between sites. TreeMix uses allele frequency data and a Gaussian approximation for genetic drift among populations to estimate a maximum likelihood tree (Pickrell and Pritchard 2012). Admixture between branches of the tree is determined in a stepwise likelihood procedure, where the tree is searched for the optimal placement of each migration event (Pickrell and Pritchard 2012). The proportion and directionality of gene flow events are estimated from the asymmetries in the relationships inferred by the tree (Martin et al. 2015). It should be noted that Treemix assumes a strict tree-like divergence between sites and that post-divergence gene flow events are discrete and instantaneous. Therefore, populations with ancestry from multiple sources or continuous gene flow with other sites will make tree topology estimation unstable. The model also underestimates branch lengths as it does not consider drift between the parental populations (only the observed derived populations). The fit of the phylogeny inferred by Treemix is evaluated, with pairwise residuals above zero indicating populations are more closely related than represented in the best-fit tree and residuals below zero indicate populations are less related. I estimated a separate maximum likelihood tree for the northern and southern range, with 34 samples from the other range as the outgroup and assuming zero up to 24 discrete migration events. The aim was

to investigate whether the northern and southern ranges conform to tree-like divergence assumed by Treemix and evaluate support for co-ancestry versus introgression (or a combination) in admixed sites identified by sNMF. I anticipated that the southern range would display shallow divergences and high residuals as a consequence of either extensive gene flow or multiple source populations. By contrast, the greater antiquity of the northern range led to the expectation of tree-like divergence between sites, and that anthropogenic dispersal would facilitate introgression between diverged populations.

Results

Full Study

nDNA population structure

Overall, the nDNA population structure was consistent across each of the clustering analyses and indicated four population groups: Big Scrub (northeast NNSW), SEQ and W Northern Rivers (west NNSW), SBMC (south of BMC in AWT), and NBMC (north of BMC and CYP). However, some substructure varied between analyses and the number of clusters assumed in each analysis, suggesting incomplete lineage sorting. The PCA revealed strong population structure between the northern and southern range of Black Bean (Figure 3), suggesting vicariance between regions. Differentiation between NBMC and the southern range accounted for 62% (PC1) of the total variation within the study area, with SBMC sites as a cluster. This pattern was supported by the DAPC ordination, including the best-fit model that assumes four clusters (Figure 4) and the sNMF genotype assignments (Figure 5).

There was some putative evidence of long-distance dispersal against the background of strong population structure. The Russell Island (Site 7) samples clustered most closely with NBMC sites in each of the analyses, despite the closer geographic proximity to SBMC, potentially a result of dispersal from further north. In addition, one Victoria Park (Site 29) sample from the southern range clustered with northern samples in the PCA (Figure 3) and had an intermediate probability of clustering with Big Scrub versus SBMC in each DAPC analysis (Figure 4). It also had a distinct genotype in the sNMF models and didn't clearly cluster with any group (Figure 5).

The between-site pairwise F_{st} values were low to moderate within the northern and southern ranges (0.01-0.35), and very high (>0.75) between them (Figure 6). The greatest genetic differentiation in the northern range was across BMC, while sites north of the barrier showed relatively low F_{st} values considering the large geographic distances between them. There was very low genetic differentiation amongst sites south of BMC, commensurate with the short geographic distances between them. In the

southern range, Eel Creek (Site 9) and Darling Downs (sites 15-17) showed the greatest pairwise differences with other sites, while sites 10-14 within Mary Valley showed low genetic differences.

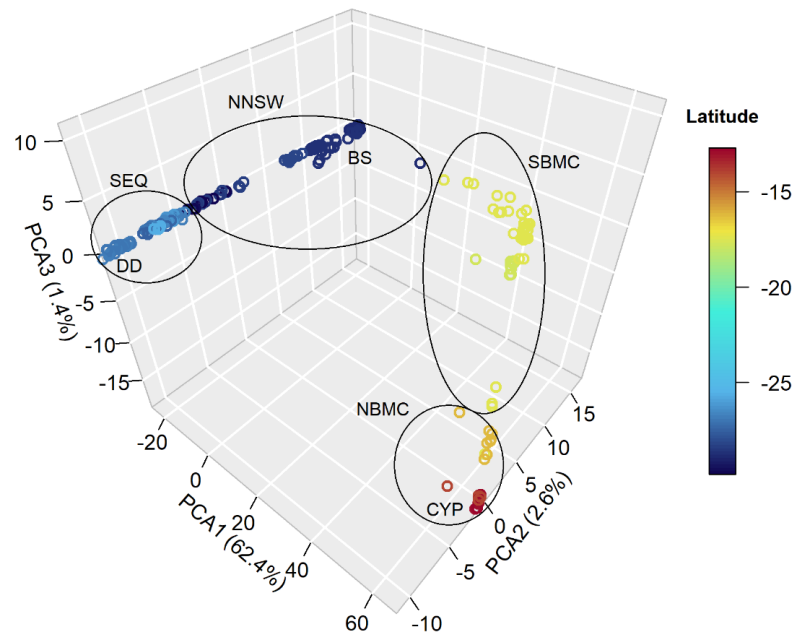


Figure 3. Principal components analysis of *Castanospermum australe* nDNA genomic variation across the full study area, ordinated by first three primary axes of variation. Samples are coloured according to latitude. SEQ=south east QLD, DD=Darling Downs, NNSW=northern NSW, NR=Northern Rivers, BS=Big Scrub, SBMC=south of Black Mountain Corridor, NBMC=north of Black Mountain Corridor, CYP=Cape York Peninsula (see Table 1 for sites within each regional cluster).

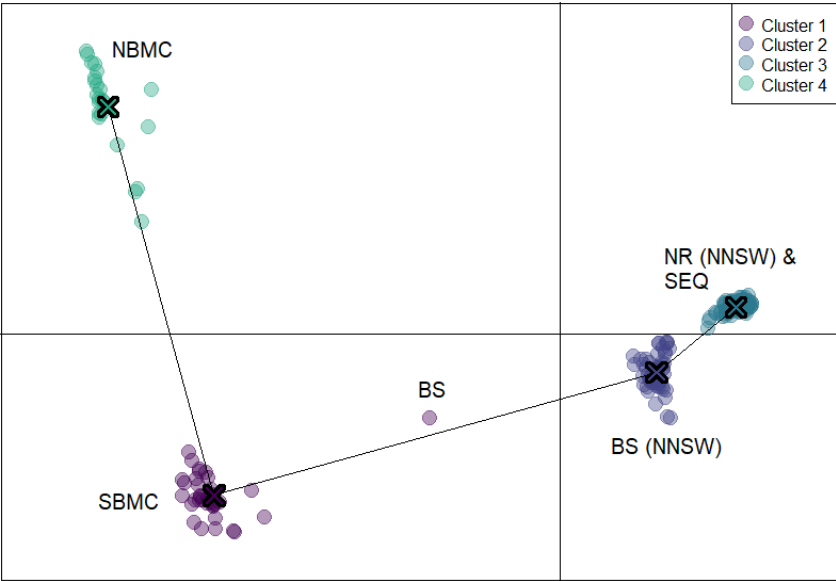


Figure 4. DAPC clustering of *Castanospermum australe* samples across the full study area, assuming 4 clusters. NR=Northern Rivers, SEQ=south east QLD, BS=Big Scrub, SBMC=south of Black Mountain Corridor, NBMC=north of Black Mountain Corridor (see Table 1 for sites within each regional cluster).

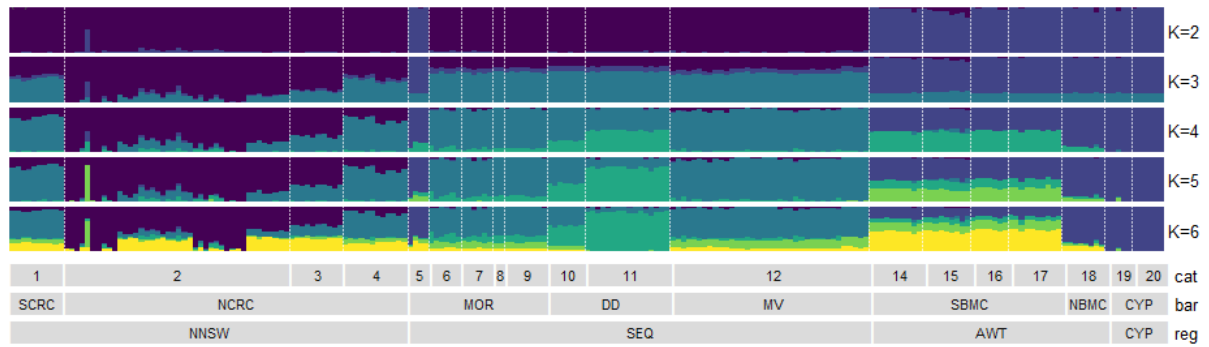


Figure 5. Genotype assignment of *Castanospermum australe* samples across the study area. Genotype algorithm implemented in sNMF and averaged across 10 replicate runs, assuming 2-6 clusters. The algorithm fails to find additional genotype clusters greater than K=4. cat=catchment, bar=barrier or range disjunction, reg=region.

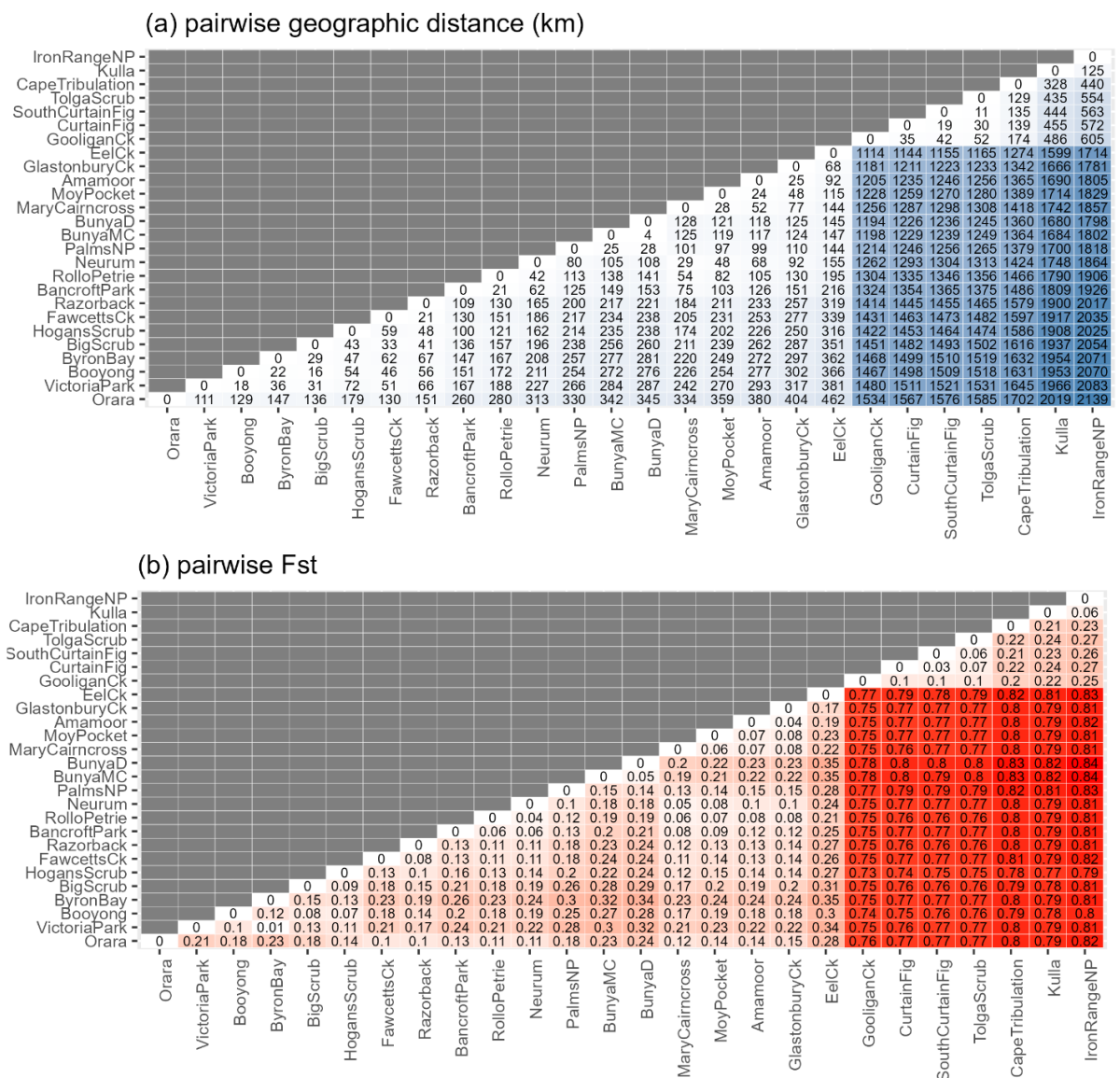


Figure 6. Heatmap of pairwise distance estimates between *Castanospermum australe* sample sites. Sites were subsampled to include 6 samples, and sites with less than 6 samples were excluded from analysis. (a) Pairwise geographic distances (km), with darker blue indicating greater distances and pale blue indicating shorter distances. (b) Pairwise Fst values, with dark red indicating high genetic distance and pale red indicating small genetic distances.

Overall, cpDNA variation was consistent with long-term isolation between the northern and southern ranges of Black Bean, although a number of individuals were identified as likely candidates of recent dispersal between the regions (Figure 7). The haplotype network suggests recent long-distance dispersal from AWT to the southern range, whereby Hogan's Scrub (Site 25, NNSW) and Bunya Mountains (sites 15-16, SEQ) displayed haplotypes closely related to Gooligan's Creek (Site 8, AWT).

Southern range

NNSW

- VictoriaPark
- Hogan'sScrub
- OraraN
- Ramornie
- Razorback

SEQ

- RolloPetrie
- Neurum
- ThePalmsNP
- BunyaD
- BunyaMC
- MaryCairncross
- MoyPocket
- EelCk

Northern range (AWT)

SBMC

- Gooligan'sCk
- Russell
- Tolga

NBMC

- CapeTribulation
- IronRange

Phylogenetic tree showing relationships between populations. Bootstrap values are indicated at the nodes. The tree is rooted on the left with a pie chart node representing the Southern range. The tree branches out to show relationships between various populations, with bootstrap values indicated at the nodes. A legend identifies the populations by color and shape.

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Within-region population structure

Northern range

The northern range displayed weaker nDNA population structure compared with the cpDNA dataset, supporting the hypothesis of different rates of seed versus pollen gene flow in the region. In addition, the high elevation sites in SBMC clustered together in all analyses as evidence of extensive between-catchment gene flow. The primary structure was across BMC, which accounted for 12.6% of total variance amongst samples in the PCA ordination (Figure 8). Secondary structure was evident between Cape Tribulation (Site 3) and CYP (PC2=5.2%) and between Gooligan's Creek (Site 8) and sites further upland in SBMC (PC3=4.4%). The best fit DAPC assumed K=2 and corresponded to division across BMC. The sNMF genotype assignments supported division across BMC and a distinct Gooligan's Creek genotype assuming $K \geq 3$ (Figure 9). Russell Island (Site 7) showed an admixed genotype between SBMC, Cape Tribulation and CYP assuming K=2-4.

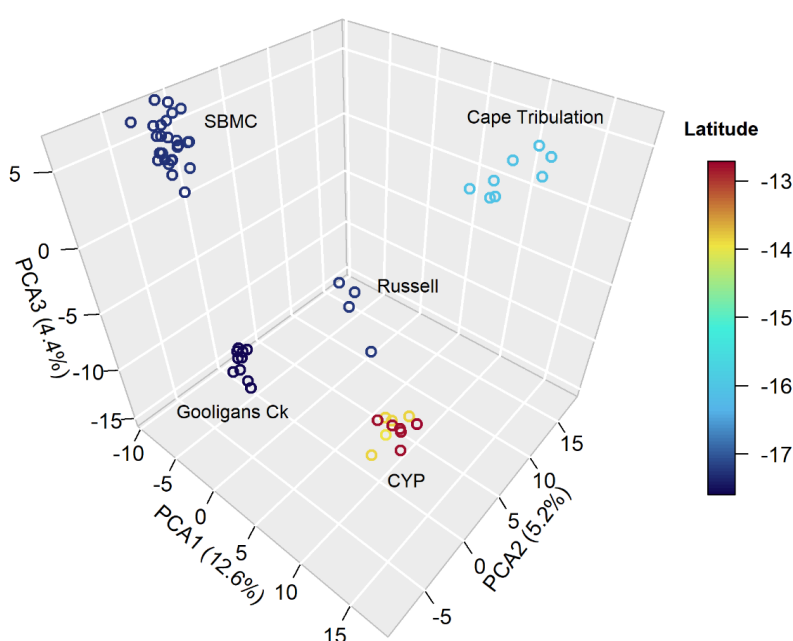


Figure 8. Principal components analysis of Black Bean (*Castanospermum australe*) nDNA genomic variation in the northern range, ordinated by first three primary axes of variation. Samples are coloured according to latitude. SBMC=South of Black Mountain Corridor, CYP=Cape York Peninsula (see Table 1 for sites within each regional cluster).

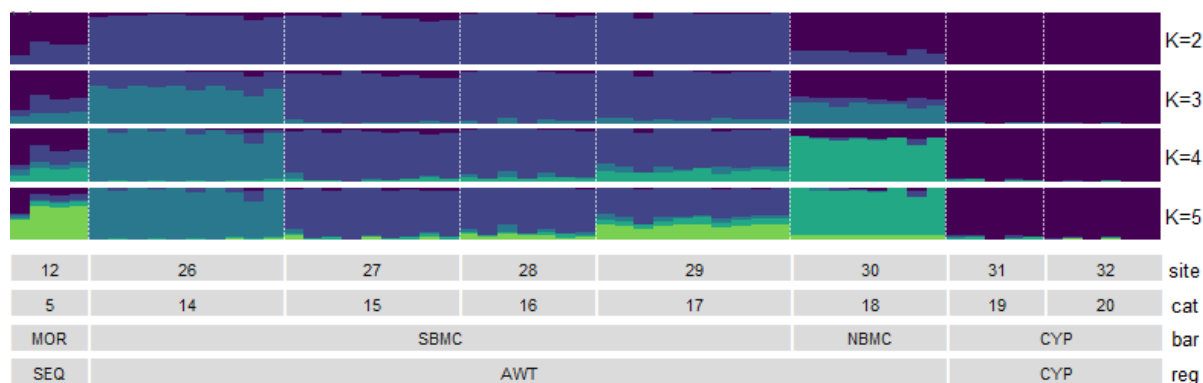


Figure 9. Genotype assignment of Black Bean (*Castanospermum australe*) samples from the northern range. Genotype algorithm implemented in sNMF and averaged across 10 replicate runs, assuming 2-5 clusters. Site numbers are stated in Table 2. cat =catchment, bar=sub-region demarcated by habitat barrier or range disjunction, reg=region.

Southern range

The southern range displayed continuous latitudinal and longitudinal nDNA variation in each of the analyses, with greater sub-structure than evident in the cpDNA data. The PCA ordination showed tight clustering of the WNR sites, with intermediate variation between Big Scrub and SEQ (PC1=10.2%, Figure 10). The Palms NP (Site 17) showed intermediate variance with other Darling Downs sites and the SEQ cluster (PC2=4.8%), while SEQ showed continuous latitudinal variation along PC3 (3.2%). The best supported DAPC analysis (and the most consistent with the PCA) identified 3 clusters, with WNR and SEQ grouped together as intermediate to Big Scrub and Darling Downs (Figure 11). The sNMF was consistent with the first two analyses and showed WNR as “admixed” between Big Scrub and SEQ genotypes (Figure 12). The Palms NP also showed putative admixture between the Darling Downs and SEQ sites assuming $K > 3$, while Victoria Park (Site 29) and Byron Bay (Site 27) in NNSW had a distinct genotype assuming $K \geq 4$. The algorithm failed to identify additional genotypes beyond $K = 4$.

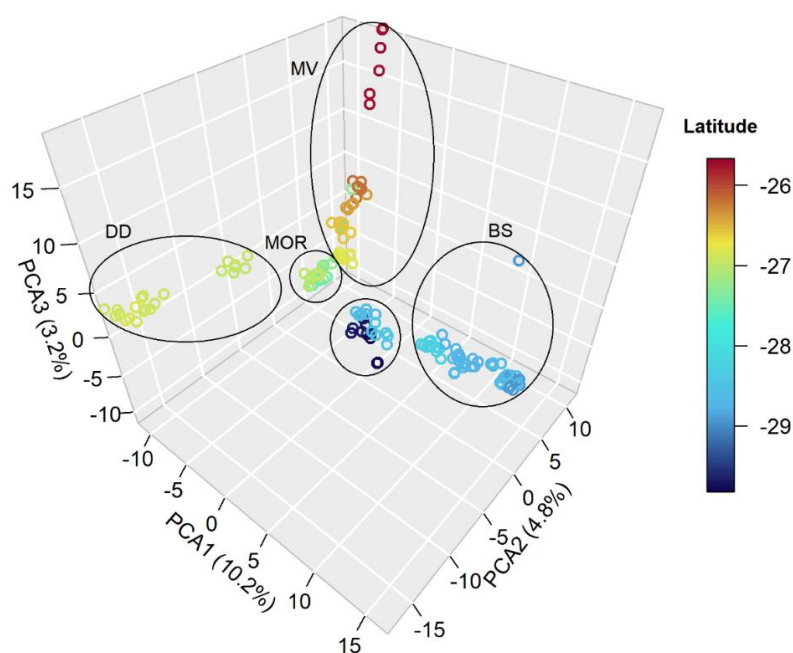


Figure 10. Principal components analysis of Black Bean (*Castanospermum australe*) nDNA genomic variation across the southern range, ordinated by first three primary axes of variation. Samples are coloured according to latitude. BS=Big Scrub, WNR=Western Northern Rivers, MV=Mary Valley, MOR=Moreton Bay, DD=Darling Downs (see Table 1 for sites within each regional cluster).

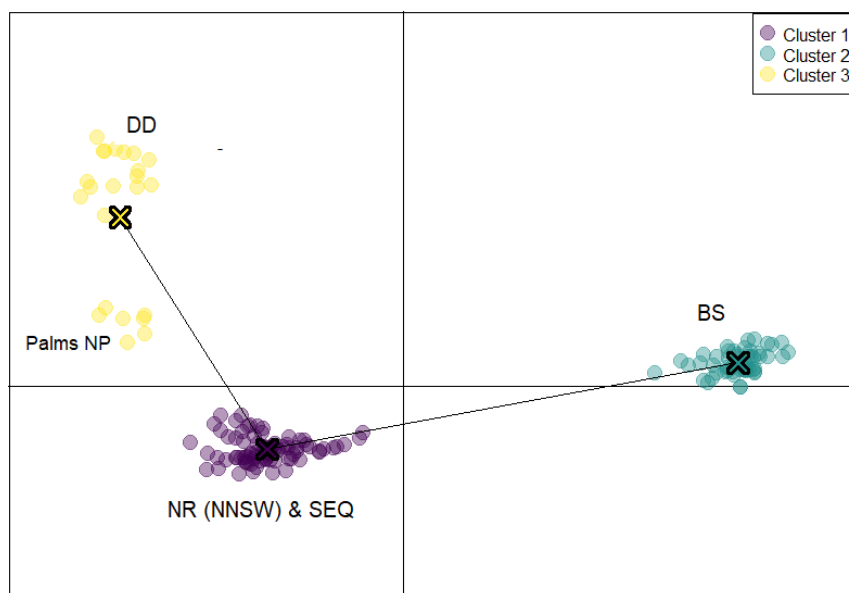


Figure 11. DAPC cluster analysis of Black Bean (*Castanospermum australe*) samples in the southern range, assuming 3 clusters. DD=Darling Downs, NR=Northern Rivers, SEQ= south east QLD, BS=Big Scrub (see Table 1 for sites within each regional cluster).

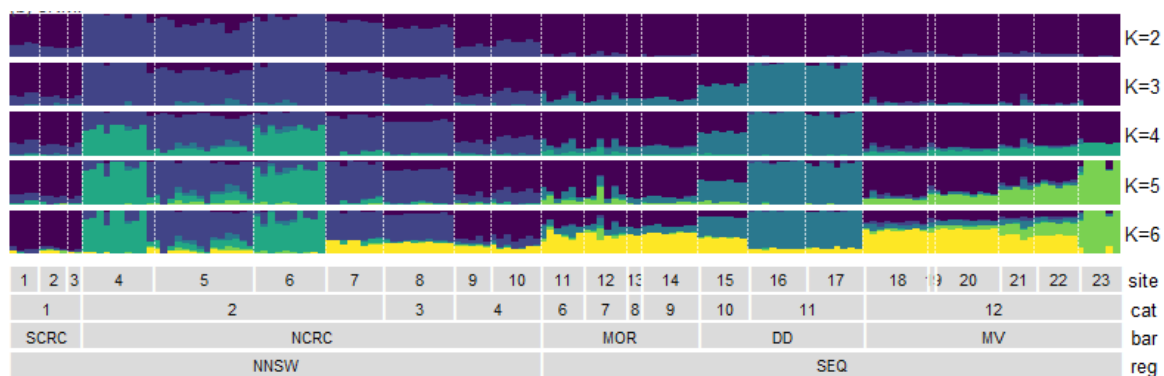


Figure 12. Genotype assignment of Black Bean (*Castanospermum australe*) samples from the southern range. Genotype algorithm implemented in sNMF and averaged across 10 replicate runs, assuming 2-5 clusters. Site numbers are stated in Table 1. cat =catchment, bar=sub-region demarcated by habitat barrier or range disjunction, reg=region.

Genetic diversity

I calculated diversity estimates for each site (Table 1) and averaged them across the northern and southern regions, as well as sub-regions identified in the previous analyses (Table 2). On average, Black Bean showed greater genetic diversity within the northern range compared to the south, consistent with expectations for a more ancient lineage (Table 2). However, there was considerable variation between sites within each region and sub-region, with a high standard deviation of the estimated private alleles and F_{is} .

Table 2. Black Bean (*Castanospermum australe*) genetic diversity estimates averaged by region. Standard deviation in brackets. ar=allelic richness, H_o =observed heterozygosity, H_e =expected heterozygosity, F_{is} =inbreeding coefficient, pa=private alleles, %p=proportion of polymorphic loci.

	ar	H_o	H_e	F_{is}	pa	%p
Big Scrub	1.252 (0.022)	0.100 (0.017)	0.112 (0.007)	0.006 (0.121)	15 (11)	30 (12)
SEQ	1.223 (0.026)	0.090 (0.014)	0.099 (0.011)	-0.014 (0.093)	3 (3)	21 (8)
South	1.232 (0.027)	0.093 (0.015)	0.102 (0.011)	-0.009 (0.100)	6 (8)	23 (7)
SBMC	1.274 (0.018)	0.106 (0.013)	0.124 (0.004)	0.041 (0.068)	28 (29)	29 (2)
NBMC	1.211 (0.022)	0.09 (0.008)	0.092 (0.008)	-0.078 (0.019)	23 (22)	21 (2)
North	1.247 (0.037)	0.099 (0.014)	0.110 (0.017)	-0.01 (0.08)	26 (26)	25 (4)
Full study	1.236 (0.032)	0.094 (0.015)	0.104 (0.014)	-0.009 (0.095)	11 (18)	23 (7)

The significant Pearson's correlations revealed some geographic structure in the distribution of genetic diversity (Table 3). However, I did not find consistent evidence of founder effects or excessing outbreeding at upland sites that could be putatively attributed to recent anthropogenic translocations.

Within the northern range, elevation positively correlated with *He* and *Fis* and the upland SBMC sites had high diversity estimates although with a heterozygote deficit ($Ho < He$). NBMC sites (all low elevation) also had many private alleles and negative *Fis* values, suggesting that outbreeding has generated unique heterozygotes in those sites. The greater diversity in SBMC drove a negative correlation between latitude and allelic richness, *He* and % polymorphic loci. This was primarily attributed to Gooligan's Creek (Site 8), which had the greatest allelic richness and private alleles across the whole study, and a slight heterozygote excess ($Ho > He$). The high number of novel heterozygous alleles are potentially the outcome of admixture with other sites.

Table 3. Pearson's correlation of genetic diversity estimates with geographic variables in the northern and southern ranges of Black Bean (*Castanospermum australe*). Statistical significance determined at $p < 0.05$ and p-values in brackets. ar=allelic richness, Ho=observed heterozygosity, He=expected heterozygosity, Fis=inbreeding coefficient, pa=private alleles, %p=proportion of polymorphic loci.

	ar	Ho	He	fis	p alleles	%p
North						
longitude	0.65 (0.116)	0.45 (0.314)	0.75 (0.051)	0.64 (0.121)	0.44 (0.316)	0.68 (0.091)
latitude	-0.79 (0.033)*	-0.58 (0.171)	-0.87 (0.01)*	-0.65 (0.118)	-0.38 (0.399)	-0.81 (0.026)*
elevation	0.71 (0.07)	0.41 (0.364)	0.80 (0.03)*	0.75 (0.049)*	-0.15 (0.75)	0.69 (0.09)
South						
longitude	0.80 (>0.001)*	0.50 (0.01)*	0.89 (>0.001)*	0.1 (0.619)	0.42 (0.038)*	0.54 (0.005)*
latitude	-0.38 (0.058)	-0.32 (0.123)	-0.45 (0.024)*	0.01 (0.949)	-0.32 (0.11)	-0.34 (0.097)
elevation	-0.62 (>0.001)*	-0.40 (0.045)*	-0.67 (>0.001)*	-0.004 (0.983)	-0.14 (0.506)	-0.26 (0.201)

Although allelic richness, *Ho* and *He* were negatively correlated with elevation in the southern range (Table 3), there was no consistent pattern of elevated outcrossing or founder effects at upland sites. All diversity estimates excluding *Fis* were strongly correlated with longitude (Table 2), which can be attributed to the elevated number of private alleles and negative *Fis* at the coastal upland Big Scrub sites (Table 1). The relatively high inbreeding and low diversity observed in Byron Bay (Site 27) was an exception. Victoria Park (Site 29) stood out with a high % polymorphic locus, few private alleles and negative *Fis* consistent with extensive outbreeding. By contrast, the upland Bunya Mountains sites (15-16) to the west showed low overall diversity and moderate *Fis*, suggesting founder effects or a slight bottleneck. All SEQ sites had few private alleles and *Fis* values that suggested outbreeding in Mary Valley and inbreeding in Moreton Bay.

Migration models

To investigate whether the low genetic structure identified in the prior analyses can be attributed to introgression between diverged populations, I used TreeMix to construct a maximum likelihood tree featuring varying numbers of migration or admixture events. Overall, the northern range showed model stability that supports a history of population divergence with introgression (Figure 13). By contrast, the southern Treemix models indicated shallow branching and incomplete lineage sorting that supports the hypothesis of co-ancestry under rapid expansion (Figure 14).

For the northern range, adding 1-5 migration events improved the log-likelihood of the phylogenies inferred by Treemix (data not shown). Although the log-likelihood only marginally increased beyond 5 migration events, phylogenies with $m \geq 14$ had residuals close to zero, indicating that models with many discrete migration events fit the data well. The phylogeny with $m=14$ was consistent with the population structure identified in previous analyses – Russell Island (Site 7) and NBMC formed a clade distinct from SBMC; and Gooligan’s Creek (Site 8) showed some drift from the remaining SBMC sites at the base of the northern clade (Figure 13a). Treemix inferred multiple weak introgression events between SBMC and NBMC, and from the southern outgroup to both northern clades. Strong introgression was inferred from Iron Range (Site 1, CYP) to Russell Island and from NBMC to Gooligan’s Creek. The residual values were close to zero, indicating the phylogeny is a good representation of the data (Figure 13b). A comparison of phylogenies showed that tree topology was not affected by the number of migration events (data not shown). While migration increased the drift parameter, the relative branch lengths were unaffected. The stability between models suggests that the tree-like divergence and discrete migration assumed by Treemix accurately represents the co-variance amongst sites.

The log-likelihood of the southern Treemix phylogenies greatly increased by adding between 1-10 migration events, while additional migration brought marginal improvements (data not shown). In contrast to the northern range, the topology and branch lengths varied depending on the number of migration events and all models showed strong residuals (Figure S4), indicating that the southern populations violate tree-like divergence and/or discrete migration. All phylogenies including $m=10$ (Figure 14a) placed Big Scrub sites as the basal clade and Mary Valley and Darling Downs as the most derived clades. Branching was shallow in most phylogenies, and Mary Valley showed minor drift along a single branch, consistent with rapid population expansion. The phylogenies suggested that the admixed profile of the Richmond and Clarence catchment sites of NNSW can be attributed to both co-ancestry and gene flow with Big Scrub. The admixed profile of The Palms NP (Site 17) appears to be due to co-ancestry

with other SEQ sites rather than introgression. The residual values ranged between ± 3.2 , indicating that tree-like divergence does not perfectly represent the data (Figure 14b).

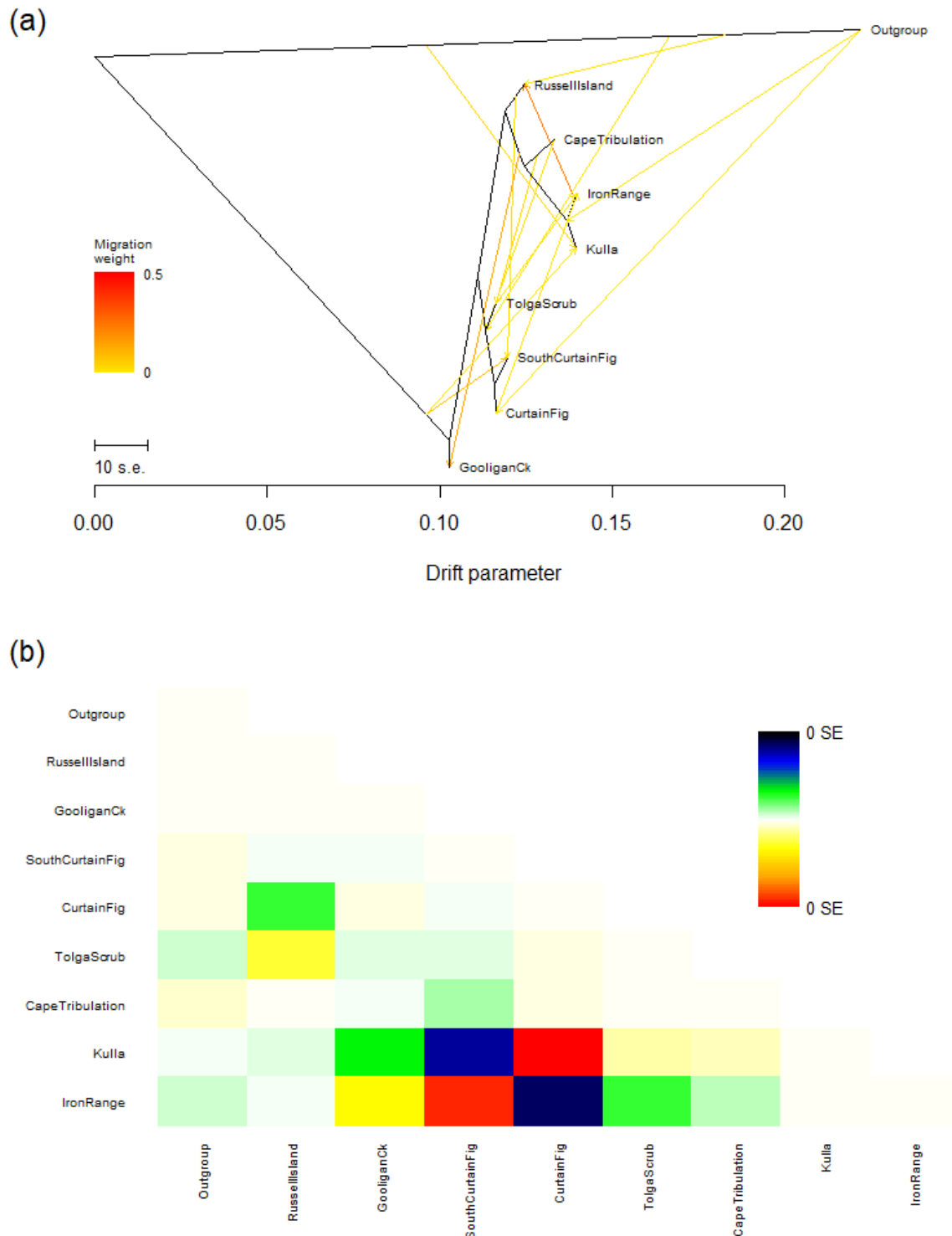


Figure 13. TreeMix analysis of the northern range of Black Bean (*Castanospermum australe*) based on 24,999 SNPs, with 34 southern samples as an outgroup and assuming 14 migration events. (a) The inferred maximum likelihood phylogeny tree. Directionality of gene flow is indicated by arrows and coloured according to their weight. (b) The residual fit plotted from the maximum likelihood tree. The colour bar to the right of the matrix indicates the degree of relatedness between populations, with residuals above zero indicating populations are more closely related than represented in the best-fit tree (i.e. bluer shades indicate population pairs that are candidates for admixture events), while residuals below zero indicate populations are less related than represented in the best-fit tree.

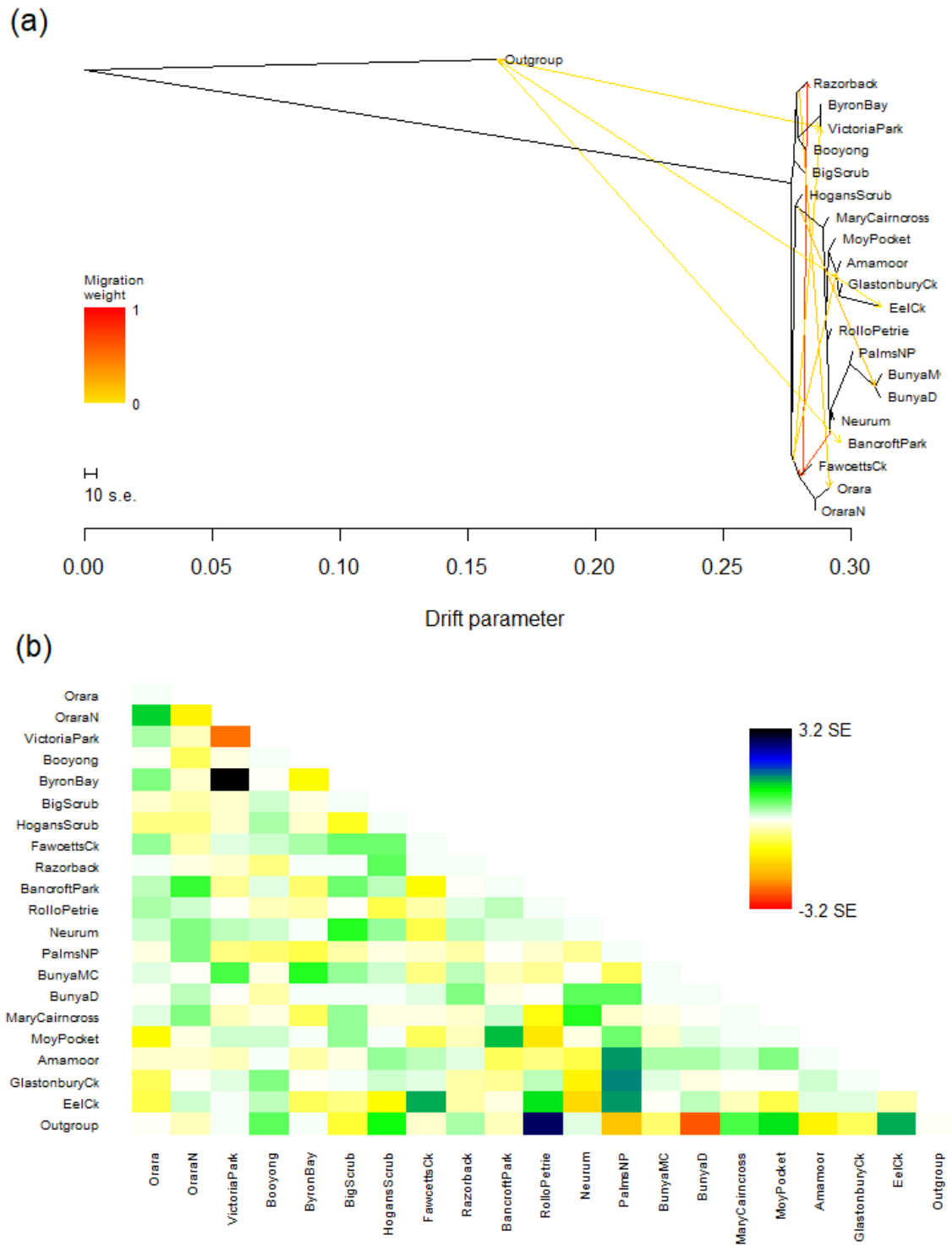


Figure 14. TreeMix analysis of the southern range of Black Bean (*Castanospermum australe*) based on 25,773 SNPs, with 34 northern samples as an outgroup and assuming 10 migration events. (a) The inferred maximum likelihood phylogeny tree. Directionality of gene flow is indicated by arrows and coloured according to their weight. (b) The residual fit plotted from the maximum likelihood tree. The colour bar to the right of the matrix indicates the degree of relatedness between populations, with residuals above zero indicating populations are more closely related than represented in the best-fit tree (i.e. bluer shades indicate population pairs that are candidates for admixture events), while residuals below zero indicate populations are less related than represented in the best-fit tree.

Discussion

I evaluated nDNA and cpDNA variation within and between the northern and southern ranges of Black Bean to gain insight to the dispersal history of the species. I found evidence of long-distance dispersal from the north to south, against a background of long-term vicariance between regions. The strong cpDNA differentiation between sites in AWT indicated that uphill and between-catchment seed dispersal was very limited in Black Bean, and that Cassowaries and other animals played a limited role in moving seed over long distances. Consequently, signals of seed-mediated long-distance dispersal can be plausibly attributed to translocation by people. Meanwhile the nDNA patterns suggest Black Bean had potential for pollen-mediated admixture over greater distances than naturally facilitated by seed movement. Various hypothetical dispersal scenarios are discussed below.

Long-term vicariance rather than recent southward expansion

Consistent with the findings of (1), I found strong nDNA and cpDNA differentiation between the northern and southern ranges of Black Bean, suggesting long-term vicariance rather than recent colonisation of the south directly from the north. However, with the current dataset, it is not possible to rule out recent colonisation of the southern range from central eastern QLD, which could be plausibly attributed to anthropogenic dispersal. Given that shallow divergence between NNSW and SEQ was observed in both the chloroplast and nuclear genomes, it is most plausible that the southern range was initially colonised by a single maternal lineage. Alternatively, NNSW and SEQ could have been colonised in two distinct events, either by dispersal from two closely related though distinct source populations, or in two distinct phases of dispersal from the same source population.

Instances of long-distance dispersal from AWT to two upland sites in the southern range were also inferred from the cpDNA data. Given the elevation and distance of these sites from the coast, oceanic dispersal is not considered a likely vector. The migrant samples do not show evidence of their northern origins in the nDNA dataset, suggesting that multiple generations have passed to enable homogenisation with their respective populations. Therefore, these samples are identified as candidates of precolonial anthropogenic dispersal. In addition, one Victoria Park (Site 29) sample showed a genotype most similar to the northern range, although I did not have haplotype data for this sample to determine if this is reflected in the cpDNA. It should be noted that Victoria Park was restored from a very small remnant population, and it is possible that the individual originated from a nursery with stock obtained somewhere in QLD.

Northern range

In the AWT, Black Bean was found at upland sites adjacent to bora grounds and away from watercourses (*pers. obs.*). Therefore, it is conceivable that precolonial Indigenous people intentionally or incidentally introduced Black Bean to some of these upland sites to prepare food for large gatherings. However, the deep haplotype divergence observed between Gooligan's Creek (Site 8) and Tolga (Site 4) on the Atherton Tableland was much greater than expected for the 52 km that separated them, suggesting an ancient presence of Black Bean on the range. It is worth noting that Black Bean may have been planted at Tolga as part of a restoration project c. 2005 (Andrew Ford, *pers. comm.*, 2022) which may contribute to the strong differentiation observed. However, significant chloroplast variation was also observed between Gooligan's Creek and Curtain Fig (Site 5), another upland site on the Atherton Range sampled by Rossetto *et al.* (2017).

Unless Black Bean was introduced to Atherton Tableland from an unsampled location south of the AWT study sites, the current data would suggest that either Indigenous people moved Black Bean to the upland bora grounds from neighbouring creeks or that Cassowary and/or other megafauna facilitated a gradual and ancient upland expansion of Black Bean. Additional sampling in the upland and lowland areas of SBMC could elucidate a signal of recent upslope haplotype dispersal that could verify the anthropogenic origin of Black Bean on the Atherton Tableland, since the cpDNA data already indicated that non-anthropogenic upslope dispersion was very slow. It would be interesting to determine whether there is extensive haplotype sharing between Tolga Scrub and other upland sites on the Atherton Tableland, as an indicator of recent seed dispersal, or, if the upland sites were highly differentiated, indicating ancient refugia. The nDNA patterns indicated co-ancestry amongst these upland sites, however this may have been the outcome of extensive pollen-mediated gene flow over time.

Black Bean could have arrived on the elevated part of Russell Island (Site 7), 40 m above sea level, via oceanic dispersal in extremely large waves. More likely, the rainforest population was remnant from prior to the Holocene sea-level rise c. 7-12 kya, when the eastern coastline of northern Australia was up to 250 km wider than today (Ulm, 2011). The low chloroplast variation between Russell Island and Gooligan's Creek suggested recent seed dispersal between the lower southern slopes of Atherton Range and the adjacent coastal plains, which would have once connected to Russell Island. While present-day catchment connectivity is limited by the proximity of the high elevation ranges to the coastline, the expanded coastal plains likely enabled more widespread riparian dispersal of Black Bean prior to the Holocene. However, it is curious that the population at Russell Island displayed strong haplotype divergence though nDNA similarity with the Cape Tribulation (Site 3) and CYP populations, which

would also have been connected to the low-lying coastline during the Late Pleistocene. Additional sampling on the coastal lowlands immediately south of BMC could reveal nDNA and cpDNA co-ancestry with Russell Island, intermediate between the NBMC and upland SBMC genotypes. Meanwhile pollen dispersal could potentially account for the gene flow with Cape Tribulation.

In contrast to the low rate of seed dispersal inferred across the AWT, Black Bean displayed unusually high nDNA similarity between the two low-lying sites in CYP, located over 125 km apart. The annual monsoonal flooding of the coastal swales is likely to facilitate cross-catchment dispersal of Black Bean seed in the region, although the considerable distributional gap and intervening raised elevation suggested that flash flooding was not likely the source of connectivity between the two sample sites. Recent oceanic seed dispersal is an alternative explanation for the genetic similarity between sites, though requires verification by cpDNA similarity. Based on the ethnographic literature, anthropogenic dispersal appears to be unlikely. The CYP sample sites are located within the historical range of multiple closely linked Indigenous groups that collectively identify themselves as *pama malnkana* or “beach people” (51). Reportedly Black Bean was not consumed by the people Indigenous to the Lockhart region of CYP where Iron Range (Site 1) is located (34), and the species does not appear to have featured in the domiculture practiced in the northern part of the peninsula (51).

The low haplotype variation between Cape Tribulation and Iron Range in CYP suggested recent long-distance dispersal or a rapid stepwise diffusion of Black Bean between the regions, although currently it is not possible to determine the direction of expansion. The Treemix phylogenies suggested a scenario in which Russell Island underwent drift from Gooligan’s Creek, and diverged to form the northern clade, suggesting a northwards range expansion. This was consistent with the much higher present-day abundance of Black Bean in AWT compared to CYP. Whole-genome sequence data and coalescent models can be used to verify a northward expansion and to date the timing of dispersal. Based on the chloroplast divergence across BMC, I anticipate these models would reveal an ancient divergence between Russell Island and Cape Tribulation, followed by a rapid Holocene expansion into CYP, potentially facilitated by Indigenous people or sea level rise.

Southern range

I found stronger evidence for anthropogenic dispersal of Black Bean in the southern range compared to the north, and the genetic patterns are consistent with the hypothesis that the region underwent a recent and rapid range expansion. The greater haplotype diversity in NNSW may indicate Black Bean had a longer presence in the region than SEQ, and that the initial colonisation of the southern range occurred

somewhere in NNSW. Haplotype diversity was not geographically structured across NNSW, which suggested seed dispersal was rapid and widespread in the region. This interpretation is consistent with the Treemix models for the southern range, which revealed shallow divergence in NNSW as the ancestral clade, and SEQ as the derived clade. Prior to logging in the 19th Century, the Clarence and Richmond catchments were abundant with Black Bean (52), and so, a rapid diffusion across the valley could explain the haplotype sharing observed between the Big Scrub and NR sites.

One potential explanation is that following an ancient founder event in the Big Scrub area, the southern Black Bean population remained small and isolated by the highly dissected McPherson and Nightcap Ranges and the periodically dry Clarence River Corridor, until Indigenous groups facilitated dispersal as they moved across the landscape. This scenario is compatible with the story of the Three Brothers, which describes the arrival of Bundjalung people to coastal NNSW and how they populated the region with three major language groups: Bundjalung in the Tweed and south to the Clarence River, the Githabul to the north-west, and Yugambeh to the north-east in SEQ (53). All three languages share the name *bugam* for Black Bean seed, suggesting a rapid transfer or shared ancestral connection to the species (1).

Although I found low haplotype variation that suggested the southern range of Black Bean was colonised by a single maternal lineage, the slight structure observed between the NNSW and SEQ haplotypes indicated that some temporal isolation allowed for mutational differences to accumulate between the two regions. Temporal isolation could have accrued across the McPherson Range, identified as a biogeographic barrier for other taxa (54). The presence of NNSW haplotypes in two SEQ sites may either correspond with the initial range expansion from NNSW into SEQ or more recent seed dispersal (possibly including restoration activities) after the two regions became isolated and differentiated.

The low cpDNA diversity in SEQ suggested this region underwent a rapid range expansion. This was reflected in the nDNA data for Mary Valley sites, which suggested outbreeding and continuous variation along a latitudinal gradient (with the exception of Eel Creek/Site 9). This included two upland sites Mapleton (Site 13) and Mary Cairncross (Site 14) which displayed connectivity in both nDNA and cpDNA genomes. Black Bean carries cultural significance to Kabi Kabi people in this region, who may have facilitated the upland dispersal of Black Bean to multiple sites across the Blackall Range. Gene flow would also be maintained by the extensive riparian connectivity along the low-lying Mary River, and ongoing pollen dispersal facilitated by birds and bats. Meanwhile, the somewhat geographically isolated populations in Darling Downs displayed some nDNA differentiation from the other SEQ sites, suggesting that pollen flow was limited between Mary Valley and Darling Downs.

Following the hypothesis that Indigenous people introduced Black Bean upland during the Holocene, I sought to investigate whether upland sites in the southern range displayed evidence of either founder effects (introductions) or outcrossing and/or admixture (reinforcement). Founder effects were anticipated in instances where Black Bean was introduced to an upland site in a single founder event, since gene flow to downstream sites would be possible via riparian dispersal, though upland gene flow was expected to be limited. This pattern was found in the high elevation Bunya Mountains sites of SEQ, which displayed higher inbreeding and lower diversity values than the species' average. By contrast, the upland Big Scrub sites located adjacent to the Nguthungulli songline and in the downstream catchments, displayed high outbreeding and elevated diversity and private alleles compared to most other sites. Furthermore, the Treemix phylogenies suggested shallow divergence and continuous gene flow rather than discrete dispersal events. This pattern of greater admixture in Big Scrub could be attributed to genetic reinforcement following multiple translocation events associated with the Nguthungulli songline. Alternatively, more contemporary restoration activities in the highly cleared Big Scrub rainforest may also have contributed to the elevated outbreeding amongst these sites.

Conclusions

I investigated the nDNA and cpDNA evidence of dispersal within and between the range extremes of Black Bean to evaluate the influence that pre-colonial Indigenous people had on the species' current distribution. The extreme north-south divergence and extensive gene flow within the southern range is consistent with three putative scenarios: (1) The southern range was colonised via ancient long-distance dispersal from AWT and the founder population remained small and geographically restricted until Indigenous people (and/or Holocene warming) facilitated assisted migration; (2) The southern range was colonised via recent or ancient dispersal from central QLD and underwent a recent range expansion; or (3) Black Bean had an ancient presence across the eastern coastline, until Pleistocene glacial cycles drove population contraction and vicariance, followed by a recent southern expansion. The combined cultural and genomic data presented here suggested that Indigenous people played an important role in this recent southern expansion, although with variable impacts on the genetic diversity of anthropogenic sites. I could neither negate nor verify the hypothesis that Indigenous people introduced Black Bean to the Atherton Tableland or other upland sites in the AWT with the current dataset. However, the strong cpDNA differentiation across the region suggested that non-anthropogenic uphill seed dispersal has been limited. Further studies will focus on additional chloroplast sequencing or long-read sequencing to determine the continent-wide demographic history of Black Bean, and to test the likelihood of the proposed dispersal scenarios.

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Supplementary Materials

Supplementary Table 1. Black Bean (*Castanospermum australe*) samples sequenced for chloroplast DNA.

Voucher	Site	locality	latitude	longitude
NSW1036043	2	OraraN	-29.724	152.810
NSW1036044	3	Ramornie	-29.652	152.800
NSW1036045	3	Ramornie	-29.652	152.800
NSW1036135	4	VictoriaPark	-28.902	153.410
NSW1036138	4	VictoriaPark	-28.902	153.410
NSW1036139	4	VictoriaPark	-28.902	153.410
NSW1036165	8	HogansScrub	-28.255	153.448
NSW1036166	8	HogansScrub	-28.255	153.448
NSW1036167	8	HogansScrub	-28.255	153.448
NSW1036033	11	Razorback	-28.427	153.000
NSW1036034	11	Razorback	-28.427	153.000
NSW1036040	11	Razorback	-28.427	153.000
NSW1036093	12	Russell	-27.654	153.376
NSW1036096	12	Russell	-27.654	153.376
NSW1036097	12	Russell	-27.654	153.376
NSW1076767	14	RolloPetrie	-27.262	152.956
NSW1076772	14	RolloPetrie	-27.262	152.956
NSW1076807	14	RolloPetrie	-27.262	152.956
NSW1071359	16	Neurum	-26.970	152.683
NSW1071362	16	Neurum	-26.970	152.683
NSW1071363	16	Neurum	-26.970	152.683
NSW1071327	17	ThePalmsNP	-26.936	151.878
NSW1071336	17	ThePalmsNP	-26.936	151.878
NSW1071337	17	ThePalmsNP	-26.936	151.878
NSW1071302	18	BunyaMC	-26.901	151.628
NSW1071303	18	BunyaMC	-26.901	151.628
NSW1071347	18	BunyaMC	-26.901	151.628
NSW1071317	19	BunyaMtnsD	-26.881	151.597
NSW1071338	19	BunyaMtnsD	-26.881	151.597
NSW1036055	20	MaryCairncross	-26.778	152.881
NSW1036060	20	MaryCairncross	-26.778	152.881
NSW1036059	20	MaryCairncross	-26.778	152.881
NSW1071370	22	MoyPocket	-26.547	152.756
NSW1071374	22	MoyPocket	-26.547	152.756
NSW1071380	22	MoyPocket	-26.547	152.756
NSW1070246	25	EelCreek	-25.667	152.145
NSW1070247	25	EelCreek	-25.667	152.145
NSW1070266	25	EelCreek	-25.667	152.145
NSW1036176	26	GooliganCreek	-17.603	145.769
NSW1036177	26	GooliganCreek	-17.603	145.769
NSW1036111	29	SouthTolga	-17.231	145.480
NSW1036112	29	SouthTolga	-17.231	145.480
NSW1036113	29	SouthTolga	-17.231	145.480
NSW1036157	30	CapeTribulation	-16.069	145.462

NSW1036158	30	CapeTribulation	-16.069	145.462
NSW1036159	30	CapeTribulation	-16.069	145.462
NSW1036087	32	IronRangeNP	-12.746	143.277
NSW1036090	32	IronRangeNP	-12.746	143.277
NSW1036092	32	IronRangeNP	-12.746	143.277

Chapter 6. General discussion and conclusions

Thesis summary

Indigenous Biocultural Knowledge (IBK), archeological and ethnohistoric records from around the world indicate that a suite of culturally significant and/or useful plant species were targeted by human niche construction efforts throughout the Holocene, though appear 'wild' in terms of an absence of obvious genetic and/or morphological modifications (1–6). However, there is a paucity of information on precolonial plant translocations by Indigenous Peoples in Australia and the genomic legacies of these processes remain poorly understood. As retracing Indigenous plant translocations is a culturally sensitive and novel area of research, Objective 1 of this thesis was to develop ethical protocols for collaborating with Indigenous Peoples on genomics-based projects and Objective 2 was to outline a genomic screening approach that can be used to identify plant species that warrant investigation. These objectives were met in Chapters 2 and 3 respectively and provide a valuable framework for Australian-based genomics research, for which such guidelines are otherwise lacking. As part of Objective 3, the work presented in this thesis was the first to combine genomic techniques with IBK data to investigate how Indigenous Peoples influenced the distribution of east Australian rainforest trees through seed dispersal. Chapter 4 was also the first Australian phylogeographic study to demonstrate that Indigenous Peoples modified translocation practices in response to colonial displacement.

The genomic case studies presented in Chapters 3–5 broaden our understanding of how pre-industrial societies shaped Holocene vegetation shifts by adding information from the Australian continent. The dispersal patterns I inferred for Bunya Pine (*Araucaria bidwillii*) and Black Bean (*Castanospermum australe*) in Chapters 4 and 5 support the position that prior to colonial displacement, Indigenous Peoples and pre-industrial human populations played important functional roles in the landscapes they inhabited. I observed geographically and temporally varied signatures of plant translocation patterns, depending on the species targeted for dispersal or the Indigenous groups involved. These findings indicate that subsistence modes were not uniform amongst rainforest-dwelling peoples in east Australia and raise interesting cultural and ecological questions about why past Indigenous groups adopted translocation practices in some cases, and not in others. In the section below, I adopt a human niche construction framework to postulate some of the factors that may have contributed to this apparent variation in Indigenous translocation practices and link with parallel examples from North and South America. I suggest that cultural factors were equally as important as ecological constraints in determining past human-plant interactions. Finally, I describe how the work presented in this thesis establishes pathways for developing cross-cultural restoration workflows and propose future research avenues.

Indigenous plant translocation practices vary between species and Country

The genomic analyses in Chapters 3, 4 and 5 revealed both a spatial and temporal variation in plant translocation practices by Indigenous Peoples in eastern Australia. Black Bean and Bunya Pine dispersal signals varied between geographically disparate groups of Indigenous Peoples, with stronger evidence of anthropogenic influence in the southern part of the study area (Southeast Queensland (SEQ) and Northern New South Wales (NNSW)) compared with the Australian Wet Tropics (AWT) in the north. Additionally, the translocation practices of Indigenous groups within the southern region appear to be dynamic – dispersal distances varied depending on the plant species in question and were adapted through time (prior to or during European colonisation). This is in line with the perspective put forth in human niche construction theory (or landscape domestication (7)), that the sociocultural preferences of past and present Indigenous populations are an important driver of ecological transformation and landscape variation (8–10).

The anthropogenic dispersal patterns detected in Bunya Pine and Black Bean corroborate conclusions drawn from the literature on Indigenous foodways to suggest that customs related to the consumption and sharing of food guide Indigenous plant management practices (11). Different dietary preferences between Indigenous groups in the study area is one plausible explanation for the limited evidence of anthropogenic Black Bean dispersal in the AWT compared to the south. For instance, on the Bloomfield River just north of the Cape Tribulation sample site, one colonial source described Black Bean seeds as, ‘...nearly always obtainable, but... not relished. It is one of the worst foods to prepare, a long time being required to wash away the disagreeable flavour’ (12). According to contemporary Kuku-Yalanji, who inhabit this northern end of AWT, *Beilschmiedia bancroftii* followed by *Aleurites moluccana* and *Elaeocarpus bancroftii* were traditionally favoured over Black Bean as a carbohydrate source during the wet season, and were actively protected through fire management on the rainforest margins (13). Interestingly, I identified *B. bancroftii* and *E. bancroftii* as candidates of past Indigenous dispersals in the genomic screening study (Chapter 3). Additional chloroplast sequencing and interviews with contemporary biocultural knowledge holders can be used to investigate whether these two species were translocated by the Kuku-Yalanji or other Indigenous Peoples of the northern AWT, or alternatively, if translocation was not a significant practice in the region.

Different dietary preferences have also been observed between groups within the northern part of the study area, which is reportedly related to the presence of Melesian tuberous plants and fruits in CYP and their absence in AWT (13). It has been previously hypothesised that the dietary incorporation of carbohydrate-rich tree seeds was an adaptation by Indigenous clans in the AWT (14). Different resource

availabilities also appear to have influenced dietary preferences within the southern part of the study region. For instance, there is a distinction between neighbouring groups, in which the more southern Bundjalung and Kabi Kabi utilise Black Bean while the Batchalla utilised cycad (*Cycas media*) as the primary carbohydrate source. These plants are not just considered carbohydrate sources, they also form part of the identity of the groups, and learning to process the toxins from their seeds is an important part of women's initiation ((15); Madonna Thompson pers. comm. to M. Fahey, 2022). Based on this, I speculate that the Batchalla and groups in central Queensland did not utilise or disperse Black Bean seed, as they would have had access to abundant cycad seed. If this hypothesis is accurate, we would expect evidence of limited Black Bean dispersal in central QLD compared with the populations further south, which can be tested by genotyping Black Bean populations in the region.

In contrast to other explanatory models that emphasise ecological (16), population density and technical constraints (17), the historical translocation patterns inferred in this thesis support the notion that during the Holocene, east Australian Indigenous societies organised their plant exploitation protocols to meet social needs in addition to subsistence (18, 19). Chapter 4 demonstrated that Bunya Pine translocation practices were adapted by Indigenous groups in southern Queensland to maintain cultural integrity following European settler-colonialism. Although located in a very different ecological context, the Bunya Pine case study is consistent with the Hynes and Chase concept of "domiculture" (20) to describe how north Australian Indigenous societies utilise resources as localised social groups according to hearth-based areas of exploitation (domuses). Here domiculture refers to the localised interaction between people and resources, governed by location- and time-specific restrictions on exploitation (for instance according to spiritual prohibitions) and technologies purpose fit to each domus. Under this arrangement, as appears to be the case with Bunya Pine, the maintenance of kinship relations is valued over the exploitation of plants as a resource (21).

Species-specific cultural restrictions linked to social structure govern the plant management protocols of various Indigenous groups across Australia (for example (21–24)), and may explain the different precolonial translocation practices that I inferred for Black Bean and Bunya Pine. Prior to European colonization, there may have been little motivation to translocate Bunya Pine trees when the aim of the Bunya Gatherings was to connect geographically distant kin. As discussed in Chapter 4, some sources suggest that the allocation of Bunya Pine nut was strictly controlled and its dispersal without permission may have caused a rift in kinship relations (25, 26). Cultural restrictions on the procurement and use of wild harvested species have also been observed amongst Indigenous groups in CYP (20) and other parts of Australia (22, 23, 27, 28); as well as amongst Indigenous Peoples in North America (29, 30). By contrast,

Black Bean displayed genomic signals of a southern range expansion that might have been linked to the seasonal or territorial migration of ancestral Indigenous groups. The Three Brothers story mentioned in Chapter 5 and a prior linguistic analysis of language groups in the region suggest Bundjalung people migrated northward from NSW to SEQ (31), roughly coincident with the dispersal patterns inferred for Black Bean.

However social relationships in Indigenous Australian societies are embedded within a spiritual understanding of the environment. Therefore, I hypothesise that precolonial plant translocation protocols were guided by an effort to emulate and cultivate natural processes. From an Indigenous perspective, the natural environment (including flora and fauna) is the legacy of the creative acts of ancestral beings or Dreaming Heroes, who are understood to have become part of the landscape (32). Replicating patterns observed in the environment is therefore a spiritual practice that perpetuates or restores the Dreaming (33). Many Indigenous groups practice “increase rituals” in varying forms, which aim to re-energise the spiritual forces that ensure continuity in the production of important resource species, as well as maintain the relationship between people and the ancestral beings responsible for the resource species (34, 35). However, as posited by Elkin (36), these rituals are “not an attempt to bring about the irregular and extraordinary, but to maintain the regular.” In this regard, locally restricted Bunya Pine translocation may have reflected the observation that the species lacks a natural mechanism for long-distance dispersal. By the same token, wider Black Bean translocation may have been permitted because the species readily germinates in a range of conditions and can disperse along waterways. This is reflected in the Dreaming stories that describes the Black Bean seed pod as a watercraft on both Bundjalung (37) and Kabi Kabi Country (38).

Although I have emphasised social dimensions of plant selection, the seed longevity of different species may be an alternative factor that influenced the translocation activities of precolonial Indigenous Peoples in the study area. It has been speculated that the poor storability of *Asimina triloba* (pawpaw) provided incentive for Indigenous Peoples in North America to plant its seeds along well-travelled routes and settlements (39). Conversely, in the current study, the poor seed storability of many Australian rainforest species would have limited the likelihood of *incidental* long-distance tree dispersals as a consequence of human migrations. Germination trials have demonstrated that fleshy fruited Laurel tree species (such as those genotyped in Chapter 3) are more likely to have desiccation sensitive seeds with reduced viability after dry storage (40); and thus may be poor candidates for anthropogenic long-distance dispersal. On the other hand, Bunya Pine kernels are known to store well if kept dry. I could not find information on Black

Bean seed longevity; however, the species has non-fleshy fruit and low seed moisture content that supports the prediction that its seed have some desiccation tolerance and a capacity for storage.

Implications for restoration

The findings in this thesis and from other studies discussed above indicate that anthropogenic translocations likely served to expand or maintain the distribution, abundance, and genetic diversity of various dispersal-limited plants since the late Pleistocene (49, 50). This underscores the important custodial role that past and contemporary Indigenous Peoples have played in forest assembly processes (10, 51, 52), particularly in landscapes where megafauna dispersers have largely gone extinct (43, 53). Evidence from North America indicates that species translocated by precolonial Indigenous Peoples have persisted in “unsuitable” habitat for centuries, suggesting that some species may be more dependent on dispersal vectors or absence of competitors than specific habitat requirements (54). This is corroborated by ecological niche models that found Indigenous-consumed though dispersal-limited plants occupy greater geographic ranges and rainfall gradients compared with their non-utilised congeners (49, 50).

However, until recently, the prevailing models of biodiversity conservation have failed to consider the influence that ancestral human populations have had on the landscape (8, 55). Unfortunately, many of the biodiversity losses that have accrued since the 17th century can be attributed to the cessation of long-term Indigenous vegetation management practices in Australia (56–60) and elsewhere (53, 61–63). To redress these cultural and ecological losses, numerous authors have advocated for the uptake of pragmatic and historically informed approaches to manage emerging and novel ecosystems (64–66), particularly as species’ distributions will continue to shift under projected climate change (67).

Future directions

Numerous dispersal-limited plant species already inhabit their upper thermal limits (67, 68), and will require assisted migration to reach suitable habitat (69) or adapt *in situ* (70). By reconstructing the demographic impacts of past natural and anthropogenic dispersals, molecular techniques can be utilised to design historically and bioculturally informed translocation strategies. Collaborations between Indigenous Peoples and molecular ecologists can jointly rediscover past translocations to develop restoration goals, strategies, and monitoring techniques. Positive examples are emerging out of a project in New Zealand that utilises Māori IBK of historical translocations to guide selection of source populations for the assisted migration of a number of freshwater crayfish species (71–73).

Currently, there are no such projects for vulnerable or threatened plant species in Australia. However, the preceding chapters illustrated the customary nature of Indigenous plant translocation practices in eastern Australia and offer a foundation from which to develop restoration strategies that incorporate biocultural values of the relevant Indigenous groups. As an example, Kabi Kabi Traditional Owners may wish to bolster the Blackall Range population of Bunya Pine that was almost entirely decimated by logging in the 19th Century. Consultation with Kabi Kabi and other local Indigenous groups can be used to determine whether seed stock should be locally obtained to maintain the slightly distinct Blackall Range genotype in respect of the pre-colonial dispersal pathways. This would not have detrimental impacts on genetic diversity, as heterozygosity and allelic richness was equivalent between Bunya stands across SEQ. Alternatively, as Bunya is valued for its power to connect people, emphasis may be placed on the continued translocation of Bunya through kinship networks outside of its natural range.

Concluding statement

Overall, the work presented in this thesis has provided a foundation and template for the genomic reconstruction of cryptic tree dispersal histories by precolonial Indigenous Peoples. Furthermore, it has established pathways for cross-cultural restoration projects that can be used to develop biocultural-informed plant restoration strategies.

This work has provided novel insights to the influence of Indigenous Peoples on the distribution of east Australian rainforest trees and was the first genomics-based study to demonstrate that Indigenous translocation practices in Australia were modified in response to European colonisation. The Bunya Pine and Black Bean case studies add an important contribution to the human niche construction literature by highlighting the role that kinship, cultural identity and spiritual worldviews can play in niche construction activities. It is worth investigating whether social signatures are evident in the translocation practices of other Indigenous groups in Australia, and to identify whether there were broadscale trends of anthropogenic dispersals throughout the continent, as has been uncovered in precolonial South American societies.

Finally, the geographic variation in dispersal patterns demonstrates the dynamic nature of Indigenous interactions with plants. Given that Indigenous Peoples have been present on the Australian continent for over 60 Ky, it is likely that translocation practices were adapted over much deeper timescales. Black Bean shows promise as a study species, and an expansion on the current dataset is likely reveal anthropogenic dispersal pathways throughout the Holocene.

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