Conservation management of Australian sandalwood (*Santalum spicatum*): using experts and a review of knowledge to develop future research priorities

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Abstract: Australian sandalwood (*Santalum spicatum*) is an ecologically important, economically valuable and culturally significant hemiparasitic plant, which is highly sought after for the aromatic oils contained within the heartwood. Naturally occurring populations occur across the rangelands and south-west agricultural region of Western Australia (WA) and the southern rangelands of South Australia. Due to historical over-harvesting, land-clearing, altered fire regimes, loss of seed-caching marsupials and overgrazing by introduced herbivores, sandalwood populations have declined across their range. As regeneration is now limited, some populations are threatened with extinction and active management is needed to secure their persistence. To inform future research and conservation management of Australian sandalwood in WA, we reviewed the literature to identify current knowledge gaps and then harnessed expert knowledge to: (1) define research topics based on these knowledge gaps; (2) define criteria for research prioritisation; and (3) score research topics. This process provided a consolidated and ranked account of key/critical research priorities, that highlights the need to dedicate more resources to improve Australian sandalwood management to stabilise and conserve populations. Recommended research directions include better understanding genetic structure and gene flow; further evaluating ecological functional roles; better understanding threats and the effectiveness of threat mitigation; further characterising population condition, distribution and trends; exploring methods to

enhance recruitment; identifying important habitat for targeted conservation; improving methods for population monitoring; and incorporating Traditional Owner knowledge into sandalwood research and future decision-making. Given the widespread and fragmented nature of Australian sandalwood, future efforts to conserve and protect this important species will require an integrated cross-tenure management approach.

Keywords: expert review, hemiparasitic plant, integrated management, population genetics, regeneration, research prioritisation, *S. spicatum*, threat mitigation

Introduction

Within Australia, where species endemism is remarkably high, biodiversity has rapidly declined since European colonisation (Dielenberg et al. 2023). To prevent further losses to biodiversity and conserve ecosystem processes, a coordinated cross-tenure management approach is being advocated to achieve conservation objectives for threatened species inhabiting multi-tenure landscapes (e.g. Australia's vast rangelands) (van Etten 2013; Foran et al. 2019; Kearney et al. 2022). Knowledge on biodiversity and threats, however, is often lacking (e.g. Carwardine et al. 2014), thus it is important to identify and address the critical knowledge gaps that will inform management strategies and deliver improved conservation outcomes. For species with commercial value, where knowledge needs extend across disciplines from biology, ecology, resource management, socioeconomics to compliance, effective management is complex (Huish et al. 2015; Bunney et al. 2022).

Australian sandalwood (*Santalum spicatum* [R.Br.] A.DC., Santalaceae; Sprague and Summerhayes, 1927) is a root-hemiparasitic woody shrub or small tree (typically 3–4 m high) with a preference for nitrogen-fixing species as hosts, particularly *Acacia* spp.

(Loneragan 1990; Barrett et al. 1996; Brand 2002b). Commercially sought after for the aromatic oils contained within the heartwood, Australian sandalwood is of international economic importance; sandalwood also has significant cultural, spiritual, medicinal and nutritional value to the Aboriginal peoples (DBCA 2023). One of five endemic *Santalum* species in Australia and four naturally occurring in Western Australia (WA) (George 1984), Australian sandalwood is slow-growing and may take over a century to reach current commercial harvest size (stem diameter ≥127 mm, 150 mm above ground), though maturation rates differ based on site and climatic conditions (Loneragan 1990). Germination is facilitated by seed dispersal and burial by seed-caching marsupials [notably the woylie (*Bettongia penicillata*), Murphy et al. 2005; and boodie (*Bettongia lesueur*), Chapman 2015] where these species are extant (i.e. western edge of the wheatbelt (woylies), fenced reserves and some islands); seeds are also dispersed by natural water flow across the landscape and emus (Murphy 2009; DBCA 2023). Successful regeneration is likely enhanced by seed burial close to a suitable host plant and reliant upon adequate winter rainfall over successive years and protection from grazing (Loneragan 1990; Kealley 1991; Sawyer 2013).

Populations of Australian sandalwood are distributed across the rangelands and south-west agricultural region (wheatbelt) of WA (Figure 1) and the southern rangelands of South Australia (SA) (McLellan et al. 2021). Isolated populations also occur on islands in the vicinity of Shark Bay in WA, including Dirk Hartog (DHI), Bernier and Dorre Islands (Ride et al. 1959; Burbidge and George 1978) (Figure 1). Note that this review excludes plantation sandalwood, which is cultivated as a commercial resource. Within WA, Australian sandalwood is distributed across 173 million hectares, with sandalwood records known from 15 of WA's 22 bioregions (DCCEEW 2023a; Interim Biogeographic Regionalisation for Australia (IBRA)) (Figure 1). Australian sandalwood populations in WA (excluding islands)

are genetically distinct from those in SA and have significantly higher genetic diversity (Crawford 2016).

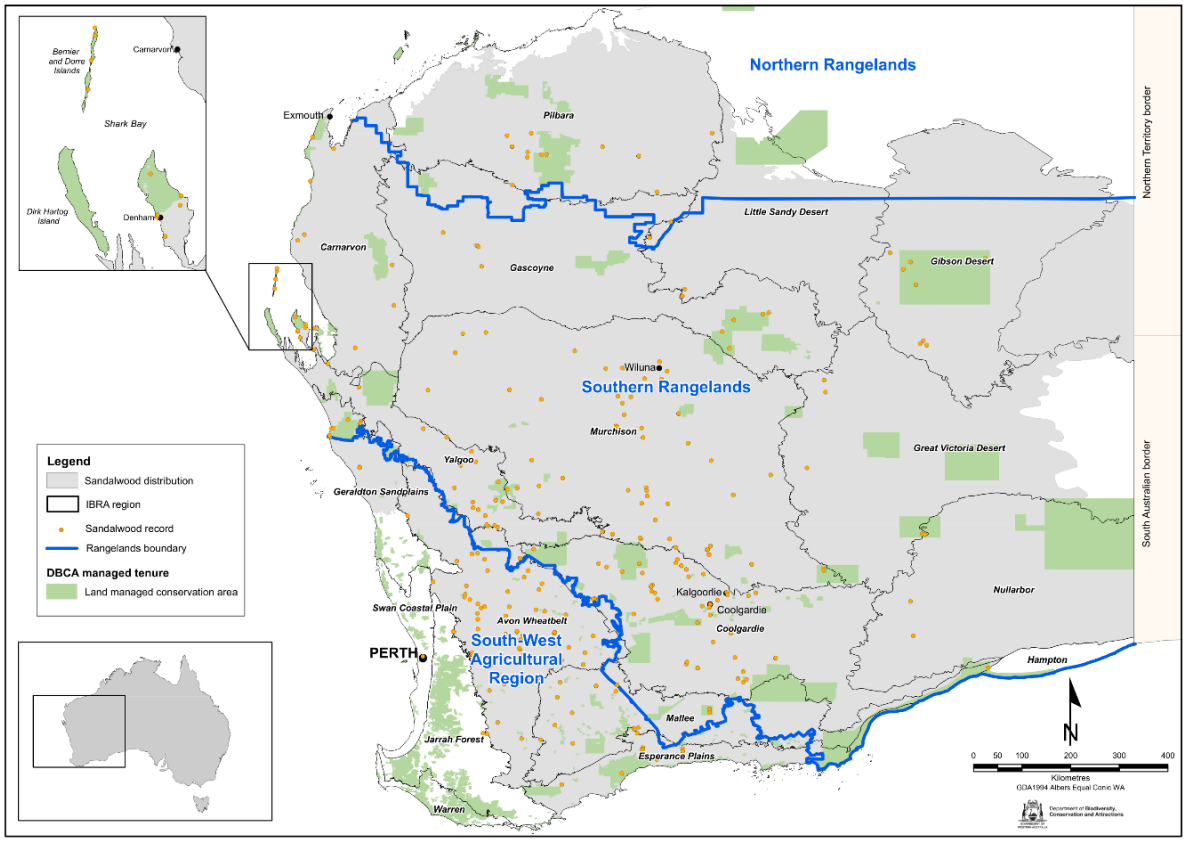

Figure 1. Map of Western Australia depicting Australian sandalwood (*Santalum spicatum*) occurrence records (specimens verified by the Western Australian Herbarium) from the Australasian Virtual Herbarium database (ALA, 2024).

Although Australian sandalwood is still broadly distributed across some bioregions (e.g. Coolgardie, Murchison, Gascoyne and Yalgoo), sandalwood occurrence in other areas (e.g. Avon Wheatbelt and Mallee) is severely fragmented (DBCA 2023). The largest and most contiguous extant populations are scattered throughout WA's arid and semi-arid rangelands where average annual rainfall is between 200–300 mm (Brand et al. 2014). The more mesic wheatbelt region (250–600 mm average annual rainfall) has been heavily cleared for

agriculture, with isolated and disjunct remnant populations now primarily confined to conservation reserves and private property (Anderson 2005; McLellan et al. 2021; DBCA 2023).

Like other *Santalum* spp. globally, Australian sandalwood is thought to be in decline (Gowland 2021; McLellan et al. 2021). Over the past 175 years, it is estimated that over six million mature live trees have been harvested from the wild (McLellan et al. 2021). In addition, low recruitment is recognised as a key contributing factor behind the species' ongoing decline (Kealley 1991; Brand et al. 2014; McLellan 2022). Most populations across Australia's rangelands are now dominated by mature trees (i.e. trees with an estimated stem diameter of > 100 mm), with few seedlings and saplings (< 20 mm stem diameter), and insufficient regeneration to stabilise the natural population (DPaW 2015; McLellan 2022; McLellan and Watson 2022). Lack of regeneration is not a recent phenomenon, with studies in the early 1980's reporting a skewed size-class distribution with a lack of small size stems, particularly on pastoral leases (Williamson 1982).

Failure to regenerate has been associated with a range of interacting threats including the loss of natural seed dispersers (particularly seed-caching marsupials), habitat loss, fragmentation and land degradation, grazing by domestic livestock and feral herbivores (particularly goats (*Capra hircus*) and rabbits (*Oryctolagus cuniculus*)), over-exploitation (both lawful and unlawful), altered fire regimes (specifically increased frequency, extent and intensity of fire), and climate change (reduced rainfall/drought) (Brand 2000; DBCA 2023). Artificial water points, which support elevated numbers of introduced and native herbivores (e.g. kangaroos), increase grazing pressure and may limit recruitment (DPaW 2015). Weeds, such as invasive grasses (e.g. buffel grass (*Cenchrus ciliaris*)), may also threaten populations indirectly via their influence on fire patterns (DBCA 2023). No diseases are currently known to have a significant effect on Australian sandalwood (DBCA 2023), although Cercosporoid

fungi, *Phoma* spp. (possibly *P. glomerata*) and an anthracnose (*Colletotrichum gloeosporioides*) have been isolated from trees in WA, with poor fruit development and defoliation associated with fungal infection (Fox and Reeve 1993).

Australian sandalwood is listed as 'Vulnerable' on the IUCN Red List of Threatened Species (Gowland 2021) and is currently being reviewed to determine its conservation status under the Commonwealth *Environment Protection and Biodiversity Conservation (EPBC) Act 1999* (DCCEEW 2023b). In the absence of management intervention to protect this important species, some populations (e.g. within the Murchison and Yalgoo regions) are considered at risk of local extinction within the next 50-60 years (Brand et al. 2014).

Although Australian sandalwood is a highly studied species, past research has been largely industry-focused (i.e. to improve management of Australian sandalwood cultivated on cleared land and used as a commercial crop in WA); see Loneragan (1990), McKinnell (1990), Havel Land Consultants (1993), Brand et al. (2001), Brand (2002a) and Clarke (2006) for an overview. While significant research by McLellan and colleagues has recently highlighted the ecological value of Australian sandalwood and quantified population structure in some stands, there remain critical knowledge gaps that constrain effective Australian sandalwood management (McLellan and Watson 2022; DBCA 2023).

To provide for the conservation, protection, and management of Australian sandalwood, the *Santalum spicatum* (Sandalwood) Biodiversity Management Programme (sandalwood BMP; DBCA 2023) was implemented in 2023 in accordance with the WA *Biodiversity Conservation Act 2016* (Government of Western Australia 2016). The sandalwood BMP contains objectives, strategies and actions that aim to stabilise Australian sandalwood populations. This review, which addresses Strategy 12 of the sandalwood BMP (DBCA 2023), seeks to (1) identify knowledge gaps in existing research relevant to sandalwood biodiversity conservation, and (2) provide recommendations for future research to inform the

conservation management of sandalwood in WA. The process for development of the research priorities for Australian sandalwood, and the priorities themselves, may also be useful elsewhere for the conservation management of commercially valuable trees in natural ecosystems.

Methods

We conducted a review of the published literature including peer-reviewed journals and books, and grey-literature (i.e. Government and industry documents/reports, theses, student reports, conference proceedings, websites and magazine articles). Literature was sourced from database searches and provided by the Department of Biodiversity, Conservation and Attractions (DBCA) staff, members of industry, university academics and environmental consultancies. Database searches involved searching for the terms 'sandalwood' and '*Santalum spicatum*' on Google Scholar and the DBCA library (DBCA 2025). Other relevant information was obtained from the Government of WA Environmental Protection Authority and Parliament of WA websites (DEC 2012; DPaW 2015). Knowledge gaps (presented below, in no particular order) were identified by the authors during the literature review considering two issues: (1) did the authors of the literature explicitly identify key areas of future work; and (2) is existing knowledge sufficient to inform on-ground Australian sandalwood conservation management.

In 2024, a series of online meetings were held with a group of experts selected based on their past/current involvement and/or research background with Australian sandalwood and relevant threatening processes. These DBCA and Forest Products Commission (FPC) staff included land and resource managers, policy officers, research scientists and ecologists (see '*Acknowledgements*'). At these workshops, experts refined the previously identified

knowledge gaps, developed research questions to address these knowledge gaps (Table 1), defined criteria for prioritisation and ranked the research questions according to these criteria (Figure 2).

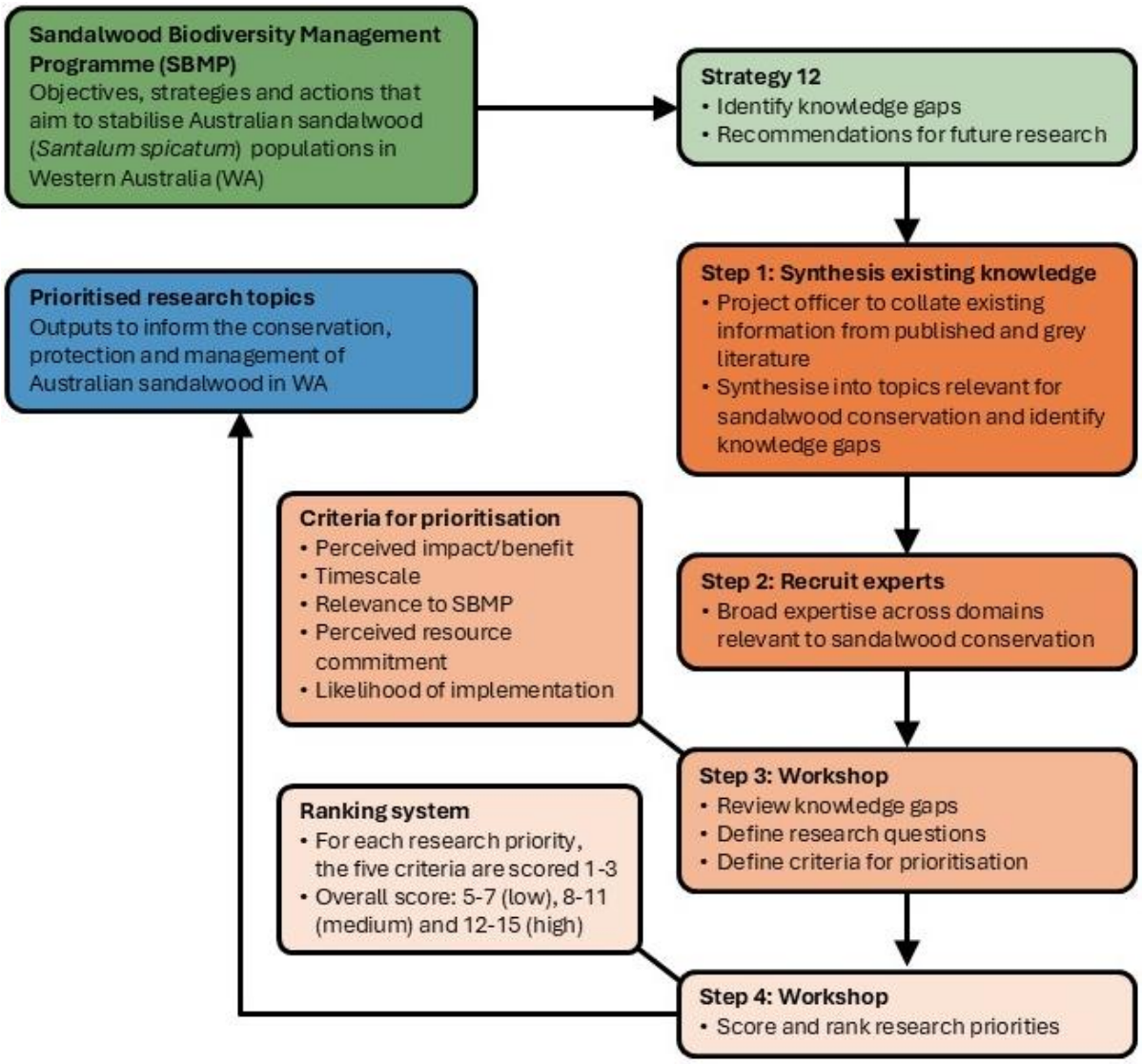

Figure 2. Protocol for development of prioritised future research directions for Australian sandalwood, outlining the policy framework for sandalwood management in Western Australia (green boxes), method steps for harnessing expert knowledge to prioritise research directions (orange boxes), and project outputs (blue). Further detail can be found in the Methods section and supplementary material (Table S1).

We used a systematic approach to prioritise research topics, including a grading system to rank priorities, with scores assigned verbally by attendees (see Figure 2; Table S1), with research questions ultimately categorised as high, medium, or low priority based on aggregated scores from five criteria (see '*Future research directions*'). A structured decision-making workshop (e.g. Hemming et al. 2018, 2022), in collaboration with other key stakeholders and Traditional Owners, is a future consideration to provide different perspectives, develop detailed collaborative research projects and help prioritise conservation actions.

Knowledge gaps

Better understanding population genetics and gene flow

An understanding of the patterns of distribution of genetic diversity and gene flow in species provides the basis for informing strategies for seed provenancing for restoration and responding to threats such as climate change. Studies on the genetic structure and genetic diversity of Australian sandalwood have been conducted using a variety of markers and across several scales. Across the entire range (excluding islands), populations in WA were found to be genetically distinct from populations in SA, and WA populations also demonstrated a higher degree of genetic structure and diversity (Crawford 2016), suggesting that WA populations may have high conservation value in terms of adaptive capacity and resilience to threats such as climate change and should therefore be a priority for conservation efforts. Within WA, two evolutionary significant management units or ecotypes have been identified, in northern and southern regions (Byrne et al. 2003a, 2003b; Crawford 2016), with suggestions of a third along the north-western coastline (from Shark Bay to

Exmouth) (Crawford 2016). These genetic clusters may partly align with observations of morphological variation between the northern and southern regions (Fox and Brand 1993), and distinctive functional and biochemical traits including the ability to coppice in the Shark Bay area (e.g. Doronila and Fox 1991; Brand and Ryan 2001), which is atypical at other sites (e.g. Loneragan 1990).

Australian sandalwood stands in the northern rangelands have higher levels of genetic diversity, a greater number of rare alleles and have achieved genetic drift-gene flow equilibrium, indicating that population structure has been stable in this region for an extended period (Byrne et al. 2003b). In the southern rangelands, greater genetic differentiation between populations was evident, though genetic diversity and the number of rare alleles was lower, suggesting that populations in the south had been more recently established (Byrne et al. 2003b). Within single populations in the northern and southern regions, genetic diversity was high in both populations but varied greatly between loci (Millar et al. 2012). Mating system studies using RFLP markers showed generally high levels of outcrossing and genetic diversity, while the ability of sandalwood to self-pollinate was also evident (Muir et al. 2007).

The implications of these genetic studies are that the distinct regional clusters – northern, southern and possibly north-western – could be considered different management units for conservation and restoration. Different seed provenancing strategies may be appropriate - climate change considerations aside. For northern populations, it is recommended that only locally sourced seed (i.e. within a 10 km radius of the place of planting; Byrne 2001) is used for regeneration programs to maintain the balance between drift and gene flow (Byrne et al. 2003b). In contrast, in southern populations, seed collection strategies should aim to collect samples across the range of populations to ensure adequate representation of genetic diversity (Byrne et al. 2003b).

To better understand the broader genetic structure of the WA sandalwood population and identify provenances with high conservation value, we recommend further genotyping to map the genetic structure of the WA population in more detail (Table 1). Confirming whether populations along the north-western coastline represent a separate ecotype should be a high priority (Table 1) so appropriate management can be implemented, as is including island populations, which have yet to be studied but potentially represent unique genetic lineages and mating systems (e.g. levels of inbreeding). In conjunction with other tools to support sustainable and legal forestry (e.g. isotopic provenancing), the creation of a larger DNA-marker set may also help to combat illegal harvesting through timber tracking (see Crawford 2016; Bunney et al. 2023).

New genotyping studies could be conducted in the context of morphological and functional trait variation across populations and to clarify propositions of clonality in some populations (e.g. Brunton et al. 2021). On DHI, for example, McLellan (2022) observed a '*densely clustered distribution pattern of smaller/younger plants under larger sandalwood plants*', which he proposed was indicative of growth from root suckers, rather than seed germination - a proposition which could be tested through genetic research. Root suckering of the *Santalum* genus is known to occur both naturally, and in response to harvesting and environmental stress, though this phenomenon is infrequently reported for *S. spicatum* compared to other *Santalum* species (e.g. *S. lanceolatum* and *S. album*) (McKinnell 1990; Fox 1997; CALM/AgWA 1998). Root coppicing of *S. spicatum* has been documented on Nanga Station, Shark Bay, following stump removal (Barrett 1989). Coppicing from root material has also been observed in the species' southern range, following tree removal in winter with immediate rain, though the ability to coppice varied between individuals (B. Sawyer personal observation).

Evaluating ecological functional roles

All species play functional roles in the ecosystems in which they occur. Some species, however, are thought to have disproportionally large effects relative to their abundance – these are referred to as keystone species (Power et al. 1996). Recent studies within the WA rangelands provide evidence that Australian sandalwood provides vital ecological functional roles including the provision of vegetation structure, microclimate refuge and elevated levels of nutrient-rich leaf litter (McLellan 2022). During warm weather conditions, fauna have been observed seeking microclimate refuge in sandalwood trees, and comparisons of localised canopy microclimatic conditions found that parasitic plants (sandalwood, quandong (*Santalum acuminatum*) and leafless ballart (*Exocarpos aphyllus*)) were significantly cooler than non-Santalaceae species, particularly during heatwave conditions (Gow 1997; McLellan 2022). The ability of sandalwood and other co-occurring Santalaceae species to provide microclimate refuge will become increasingly important in a changing climate, with the presence of short-term refuges vital for the persistence of fauna in the face of increasing temperatures and prolonged drought events.

The provision of litter fall, which drives nutrient dynamics, and enhances species diversity through nutrient enrichment and the creation of 'litter gardens' (Watson et al. 2022), also supports a diverse plant and faunal community directly under the canopy (McLellan 2022). Higher levels of nitrogen, potassium and phosphorus have been detected in the soil under sandalwood canopies (Hobbs and Atkins 1991). McLellan (2022) also highlighted the importance of Australian sandalwood as a food source (from fruit, foliage, flowers, nectar, stems, bark, seeds and litter) for ground dwelling marsupials and other fauna. Compared to other Santalaceae plants (quandong and leafless ballart) in the WA rangelands, sandalwood had the highest frequency of fauna visitation for foraging, particularly mammals (McLellan 2022).

While McLellan (2022) provides strong evidence that Australian sandalwood exhibits attributes of a keystone species, there have been no other studies evaluating the effect of sandalwood on ecological communities using controlled comparisons of species composition and diversity (e.g. Watson 2015). To conclude that Australian sandalwood is a keystone species, it must be empirically demonstrated that sandalwood has a disproportionally large effect relative to its abundance (Power et al. 1996), such that the removal of sandalwood will result in the loss of other dependant fauna (Mills et al. 1993). It is unknown whether any species depend solely on sandalwood for resources or if other co-occurring Santalaceae species, which provide similar ecological functions, fill such an ecological gap (McLellan 2022). We recommend further research to evaluate the ecological functional role of Australian sandalwood at other sites, including associations with other flora (i.e. key host species) and fauna (Table 1).

The role of dead Australian sandalwood (as opposed to dead wood from other trees) should also be evaluated, as dead sandalwood is included in the quota for commercial harvest, and there have been recommendations to commercially salvage sandalwood trees killed by bushfires (DPaW 2015). Dead trees and fallen logs provide habitat for other species (e.g. the southern pygmy spiny-tailed skink (*Egernia depressa*), which was exclusively recorded on Australian sandalwood during McLellan's studies) and are vital for healthy ecosystem functioning; their removal is considered a key threatening process in other Australian states (e.g. NSW; Department of Environment and Conservation New South Wales 2003). Studies to evaluate whether there are any direct or indirect benefits of dead sandalwood, to sandalwood seedlings (e.g. protection from the elements or enhanced soil quality) may also be warranted.

Lastly, as a species with documented knowledge dating back over a century, Australian sandalwood could potentially be used as an indicator species to monitor habitat quality or

wider rangeland vegetation health, particularly in response to climate change, but also other factors (e.g. salinity). As defined by Siddig et al. (2016), indicator species are living organisms whose status reflects the condition(s) of their environment. Sandalwood may be adept at reflecting overall ecosystem health due to its hemiparasitic relationship with other host plants, and strong interactions with other flora and fauna.

Altered fire regimes

Disturbance regimes play a key role in plant population dynamics. Across the range of Australian sandalwood, as is the case in many seasonally dry regions globally, fire is a dominant disturbance playing a role in driving plant mortality and recruitment. Understanding the effects of fire on Australian sandalwood is incomplete, with contradictory evidence of tolerance to fire, perhaps reflecting variation associated with fire characteristics such as severity and patchiness, and/or regional differences. Australian sandalwood has often been reported to be fire-killed because of observations of poor coppicing ability and survival after fire, and apparent susceptibility to fire effects (Loneragan 1990; Kealley 1991; DEC 2012), particularly when young (CALM/AgWA 1998). However, other sources suggest some tolerance to fire with variation in mortality rates with degree of canopy scorch and tree size (likely correlated with canopy scorch in surface fires) (Forests Department of Western Australia 1984; DEC 2012), suggesting sandalwood may be best viewed as a facultative resprouter (Prior and Bowman 2020). Moderate to high intensity fires and short fire return intervals often result in tree mortality (DBCA 2023) and large, intense wildfires may extirpate local populations (Pobke 2007).

A study that examined the effects of wildfire on Australian sandalwood regeneration in Salmon Gum (*Eucalyptus salmonophloia*) woodland, 10 km east of Kalgoorlie, revealed that

16% of sandalwood trees were immediately killed by fire (Loneragan 1990). While 64% of burnt trees initially survived, with some evidence of coppicing, long-term survival was low (20% after > 2 years). In late 2019, a sandalwood regeneration trial site located approximately 30 km south of Coolgardie was affected by a moderate intensity bushfire, with 10 to 12-year-old saplings burnt to cindered sticks (Figure 3A) (B. Sawyer personal observation). Following several late summer-autumn rain events, Australian sandalwood saplings at the site were observed in May 2020 to have new shoots mostly emerging at ground level (Figure 3B). Burnt mature Australian sandalwood was observed to have new epicormic shoots (Figure 3C). Follow-up monitoring is recommended to document the long-term survival of these individuals.

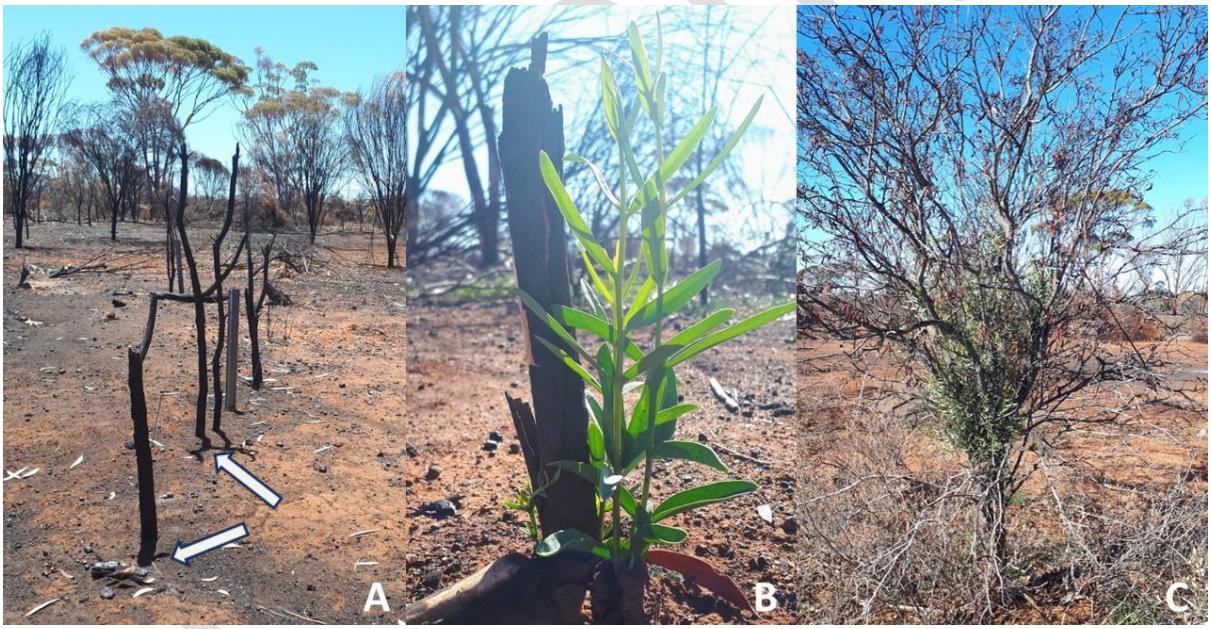

Figure 3. The response of Australian sandalwood (*Santalum spicatum*) to moderate intensity fire, including (A) 10 to 12-year-old saplings (location indicated by arrows) immediately post-fire, (B) new shoots emerging 18 months post-fire, and (C) new epicormic shoots on established sandalwood post-fire. Photographs © Ben Sawyer/DBCA.

Altered fire regimes (i.e. increased frequency, extent and intensity of fire) in the presence of a rapidly changing climate poses a serious threat to the regeneration and survival of Australian sandalwood (Gowland 2021). For example, the Great Western Woodlands, centred on the Coolgardie bioregion, which historically burned infrequently, has been subject to increasingly frequent and larger fires, with roughly 40% of extant woodland burned at least once over the past 50 years (Jucker et al. 2023). In the absence of seed-caching mammals, which bury and potentially protect seed from high temperatures produced by fire (e.g. Peterson and Parker 2016), surface seeds are likely to be highly vulnerable to fire (Pobke 2007); though the ability of soil-stored Australian sandalwood seed to persist through fire and germinate afterwards has not been investigated. Due to the hemiparasitic nature of sandalwood, consideration of the fire susceptibility of preferred host plants is also important. Within the species' southern distribution, for example, obligate-seeder *Acacia* spp. are the dominant hosts in many vegetation types, particularly eucalypt woodlands that are of low flammability, but subject to contemporary stand-replacing canopy fires (Burrows 2015; Gosper et al. 2018; DBCA 2023). Even if Australian sandalwood can successfully coppice, survival after fire when dominant host plants are temporarily absent while they regenerate from seed, is questionable.

Research to examine the fire response traits of a range of Australian sandalwood ecotypes/populations, in the context of individual plant-based fire intensity (defoliation), should be considered. Importantly, research to examine plant community composition and condition post-fire in less-studied vegetation types (e.g. WA mulga, rocky ranges and coastal limestone habitats) will help to determine the regenerative capacity of ecosystems with Australian sandalwood (i.e. recovery) and inform the type(s) and frequency of fire management needed. As the ability of soil-stored seed to survive fire and subsequently

germinate is also unknown, research that focuses on the regenerative strategies of Australian sandalwood post-fire should be a focus (Table 1).

Given the high susceptibility, typically poor regenerative capacity and low density of extant Australian sandalwood populations, appropriate fire management is crucial for sandalwood conservation. The distribution of Australian sandalwood across WA, however, encompasses a wide range of climates, landforms and vegetation types with differing flammability, plant fire response traits and contemporary fire regimes, along with varying land tenures and land uses (Burrows 2015; DBCA 2023). As Australian sandalwood is both fire sensitive (i.e. readily killed by fire) and fire independent (i.e. does not require fire as part of its life cycle), prioritising fire management to reduce the risk of wildfires burning vast areas of habitat should be a key priority to avoid further loss of populations, with a focus on the protection of core habitat and regeneration sites. Research is needed to determine the optimal temporal and spatial scale of fire mosaics and other fire mitigation and suppression approaches to achieve this outcome (Table 1). Consideration of the role of traditional burning practices would also be of value, as Indigenous peoples aimed to protect fire sensitive assets such as Australian sandalwood, by lightly burning around the base of trees or sweeping away leaf litter to reduce fuel loads, and fire was also deliberately constrained in some habitats with Australian sandalwood (e.g. mature *Eucalyptus* woodlands) (Prober et al. 2016).

Herbivore grazing

Herbivore grazing plays a key role in plant population dynamics. Of particular importance is where populations of herbivores are enhanced through artificial provision of resources, and where biological invasions and pastoralism expose plant populations to a functionally different suite of herbivores than with which they evolved. The provision of artificial water

points across arid and semi-arid Australia has increased total grazing pressure by supporting elevated numbers of introduced livestock (cattle (*Bos taurus*) and sheep (*Ovis aries*)), feral herbivores (goats, rabbits, camels (*Camelus dromedarius*), donkeys (*Equus asinus*) and horses (*Equus caballus*)) and native herbivores (e.g. kangaroos) (Fensham and Fairfax 2008). Introduced herbivores, particularly goats and rabbits, are widespread within the current Australian sandalwood distribution and heavily graze seedlings and trees. Goats are intermediate feeders and can browse sandalwood leaves and break branches up to 1.8 meters high (FPC 2016). Sheep have also had a significant long-term impact on Australian sandalwood establishment and recruitment in WA (DBCA 2023) and will also graze host plants, though sheep production in the southern rangelands has greatly declined since the 1990's, with a shift towards cattle grazing (Foran et al. 2019). At Paynes Find, in the mid-west of WA, only mature Australian sandalwood trees were detected on sheep grazing properties (with feral goats and rabbits) with access to permanent fresh water and bores, indicating lack of recruitment for at least 30 years (Brand 1999). Artificial water points also enable introduced predators (i.e. the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*)) to expand their range, which has played a key role in the decline and extirpation of important seed-caching marsupials and other native fauna (Woinarski et al. 2015). The control of dingoes (*Canis familiaris*) and other apex predators (e.g. the wedge-tailed eagle (*Aquila audax*)) by pastoralists has potentially limited top-down regulation of herbivores and introduced predators (Letnic et al. 2012; Glen et al. 2016), exacerbating their impact. Research is needed to evaluate the effects of artificial water point closure on feral herbivores, introduced predators and native fauna, including interactive effects on Australian sandalwood regeneration and weeds (Table 1).

While goats and rabbits have long been recognised as a significant threat to Australian sandalwood, camels are reported to be having an increasingly negative effect on Australian

sandalwood, particularly within the arid interior (Kealley and Chevis 2022; McLellan 2022; DBCA 2023). In the Mungilli Area, near Wiluna in the Gibson Desert, evidence of camel browsing was reported in all inventoried sites except protected gullies and rocky areas, with severe browsing leading to the death of mature and old sandalwood trees in open areas and sites with natural water sources (Kealley and Chevis 2022). Given there is potential for commercialisation of camels in WA (e.g. the Goldfields Esperance Region; Hanslow-Sells et al. 2019), studies are needed to quantify the effects of camels on Australian sandalwood. Similarly, with a shift from sheep to cattle grazing across the southern rangelands (Foran et al. 2019), the threat posed by cattle (and the management of pastoral land) may need to be evaluated (Table 1).

Understanding pastoralists' motivations or lack thereof to protect sandalwood is also worth exploring, as are incentives for actively managing herbivore grazing on private property (e.g. methods to reduce total grazing pressure on pastoral leases) to benefit Australian sandalwood conservation (Table 1). The Australian Carbon Credit Unit (ACCU) Scheme is a government incentive that encourages people and businesses to run projects that reduce emissions or store carbon (Clean Energy Regulator 2025). One such project on Gindalbie Station in the WA Goldfields, is acquiring carbon credits by reducing cattle numbers and actively managing pest animals, fire and weeds to promote regeneration (Salubris 2024). Projects such as this, which reduce total grazing pressure and concurrently manage other interacting threats, may indirectly benefit Australian sandalwood, but research to quantify outcomes on sandalwood survival and recruitment is needed.

Introduced and apex predators

Introduced predators (the red fox and feral cat) have played a key role in the decline and extinction of critical weight range terrestrial fauna, including important seed-caching marsupials (Woinarski et al. 2015). The absence of seed-caching marsupials across much of the Australian sandalwood distribution limits seed dispersal and burial away from parent trees, negatively affecting recruitment (Brand 2000; Murphy 2009). Seeds that are not dispersed fall directly under the canopy of parent trees, where survival is low (Brand 2000). Management actions to protect seed-caching marsupials where they still occur (e.g. baiting with 1080 or sodium fluoroacetate; *Probait®, Eradicat®*) or reintroduction projects to reestablish seed-caching marsupials in sandalwood habitat where they once locally occurred (e.g. managed reserves or on islands), may help to promote sandalwood recovery.

Research suggests that dingoes, as a long-naturalised apex predator, may regulate numbers of herbivores and introduced predators, which can have a positive effect on biological diversity by reducing total herbivory and suppressing mesopredator predation (Letnic et al. 2012; Nimmo et al. 2015; Campbell et al. 2022). Observations of dingo predation on feral goats and red kangaroos (*Osphranter rufus*) on the Wooleen Cattle Station, in the Murchison River district estimated a 90% reduction in kangaroos within 7 years of dingoes returning (Campbell et al. 2022); feral goats were eradicated within the same period and rapid native vegetation regeneration was subsequently observed. The use of dingoes as a management tool to reduce herbivore overabundance and thus total grazing pressure, may be a consideration to help Australian sandalwood to re-establish (e.g. on ex-pastoral estates). The mesopredator suppressive effects of dingoes (Ripple et al. 2014) may also be advantageous in areas where small native mammals persist and introduced predator control (e.g. 1080 baiting) is not used.

Eagles as apex predators may also help to reduce total grazing pressure, particularly from rabbits and kangaroos, which make up a significant portion of their diet (Olsen et al. 2014;

Glen et al. 2016); their impact on foxes may also be beneficial. In the Western Deserts of WA, some Traditional Owners have reported a decline in fox numbers following the return of apex predators (eagles and dingoes) across the landscape (K. Muir personal communication). The role of apex predators in Australian sandalwood habitat could be examined using occupancy studies and concurrent scat analyses (Table 1).

Climate change

Globally, climate change now poses an environmental, economic and social threat under all emissions scenarios. Australia is considered a notable hotspot with some changes now considered inevitable and irreversible (Government of Western Australia 2021). To make informed decisions about managing current and future climate risks, climate adaptation research is needed to enhance resilience to a changing climate. Projections of future climate change for Australia's rangelands and the south-west agricultural region include higher temperatures with hotter and more frequent hot days, reduced rainfall in winter (and spring in southern regions), increased intensity of heavy rainfall events, and more severe fire weather (Government of Western Australia 2021). The duration of drought events is also predicted to increase in the south (Government of Western Australia 2021). Climate change projections for Australian sandalwood in WA (estimated using MaxEnt models incorporating soil and climate variables) predict a southern shift in distribution (retreating into the Southwest Australian Floristic Region), with no suitable habitat projected to remain within the northern arid regions by 2090 (Crawford 2016).

Soil moisture levels are one of the main determinants of Australian sandalwood seed germination (DEC 2012). Predicted declines in winter rainfall (up to 45 percent by 2090 in the south) and increased evaporation rates, which will reduce soil moisture and runoff

(Government of Western Australia 2021), are expected to have a significant negative effect on sandalwood establishment and recruitment (DBCA 2023). Sawyer (2013) reported a statistically significant relationship between germination and rainfall, with a minimum threshold of ~264 mm rainfall per annum (including an autumn rainfall event of >12.5 mm) required for Australian sandalwood seed germination. Rainfall during autumn and early winter is crucial (Brand and Sawyer 2016; Brand 2017), though late-summer rainfall also plays a significant role in maintaining soil moisture during establishment (Sawyer 2013). For mature trees, reduced rainfall may also prevent or delay flowering and seed production and/or reduce overall seed yield (Barrett 1990). Bioclimatic modelling using MaxEnt also indicated the importance of precipitation in the coldest quarter (and slope) for the establishment of Australian sandalwood (Crawford 2016).

For hemiparasitic plants such as sandalwood, climate change may also impact nitrogen fixation and plant growth. Reduced soil moisture for instance, may reduce root nodule abundance and/or activity of the host (Norris 2005). A significant decrease in the nitrogen content of Australian sandalwood leaves has been associated with very low soil moisture levels (Struthers 1983). Competition for water between host plants and sandalwood during dry periods may be intense (Fox 1997). Given the critical reliance of sandalwood on host plants, testing the climate tolerance of sandalwood and common host species, particularly within more arid areas, should also be a consideration for future research (Table 1). Investigating the effects of extreme events (e.g. heat, drought) on adult, sapling and host survival is also important.

In accordance with Strategy 7 of the sandalwood BMP, '*Adapt sandalwood management to climate change*', research into innovative practices for reducing the reliance of sandalwood germination on the winter rainfall threshold (i.e. 100mm between April 1 and August 31 with a pre-June 15 'season-break' of >12.5mm) have been recommended (DBCA 2023). Other

strategies that may promote climate resilience by enhancing drought tolerance could also be evaluated (e.g. potassium supplementation; Xu et al. 2021).

One method to enhance resilience against the effects of a drying and warming climate is 'predictive or climate adjusted provenancing' (e.g. Sgrò et al. 2011; Prober et al. 2015), which for Australian sandalwood could involve the establishment of arid-provenance plants within more southern regions to effectively increase the proportion of pre-adapted genes that are suited to the predicted future climate of the site, enhancing genetic variability and adaptive capacity of the target population. Other methods to maximise adaptive potential include 'composite provenancing' and 'admixture provenancing' (see Breed et al. 2013), though these also involve transferring plant genotypes over large spatial scales (e.g. mixing of northern and southern ecotypes) to increase overall genetic diversity, which poses similar genetic risks (i.e. outbreeding depression and maladaptation; Aitken and Whitlock 2013). More recently, 'regional admixture provenancing' has been advocated as a compromise for ecological restoration (Bucharova et al. 2019) by mixing seeds from several local populations (i.e. those with similar environmental conditions), thereby maintaining regional adaptation and reducing the risk of unintended effects on dependent biota. Significant differences in the performance of Australian sandalwood from different provenances have been reported (Bamford 2001; Brand 2017), so the outcomes of provenance trials conducted to improve climate resilience should consider pre-existing differences in population performance.

Invasive weeds

Invasive weeds pose a significant threat to biodiversity via their impacts on plant community structure (e.g. inhibiting native plant establishment and growth) and ecosystem functioning

(e.g. altering fire regimes, hydrology and nutrient cycling) (Weidlich et al. 2020). Few studies have examined the effects of weeds on Australian sandalwood, though they are reported to smother seedlings, reducing survival and growth (Brand and Jones 1999). The presence of invasive buffel grass may indirectly threaten sandalwood by influencing fire patterns (i.e. reduced fire return intervals and increased intensity). While the current threat posed by buffel grass to Australian sandalwood is likely greatest at the periphery of sandalwood's distribution (Great Victoria Desert) and is typically concentrated in areas of disturbance, modelling studies predict that much of the range of Australian sandalwood will become increasingly climatically suitable for buffel grass with climate change (Martin et al. 2015). As sandalwood management activities such as harvesting and regeneration, and activities related to pastoralism and mining, have the potential to spread weeds such as buffel grass (DBCA 2023), strategies to manage and restrict the spread of invasive weeds (particularly flammable grasses) and reduce surface fuel loads to decrease the risk of large-scale intensive wildfires should be considered (Table 1).

Evaluating population condition and distribution

Effective implementation of species conservation strategies requires an understanding of current patterns of species distribution and population demographic structures. More consistent data across the broader distribution of Australian sandalwood will help to understand change in sandalwood populations over time and in varying environments, and the key reasons for these changes.

To provide a better understanding of Australian sandalwood population trends across WA, DBCA has recently undertaken monitoring to evaluate changes to populations over time (as per Strategy 2 of the sandalwood BMP; DBCA 2023). Focusing on plots established by

552 Australian sandalwood inventory programs over 20 years ago, this project remeasured ~ 300
553 plots to investigate population trends (e.g. rates of population increase or decline, the
554 occurrence and patterns of recruitment, and changes in spatial distribution within and across
555 the landscape) accounting for variables including exposure to threats and land tenure type
556 (B. Sawyer personal communication). While this was not a sandalwood inventory for the
557 purpose of calculating a total standing resource, better understanding the current population
558 size and distribution of Australian sandalwood will help to inform management and refine
559 recommendations for an 'acceptable yield' taking into account biodiversity, social and
560 economic considerations (DBCA 2023).

561 Ongoing monitoring of key populations and the establishment of new inventory sites is
562 encouraged to better understand population trends in response to threats and other
563 biotic/abiotic factors (Table 1). For example, establishing long-term monitoring sites with
564 the goal of concurrently evaluating potential drivers of population change over time.
565 However, as inventory studies inherently take decades or more to reveal demographic and
566 productivity trends, these could be combined with one-off sampling of a large range of plots
567 outside the network to increase the sample size to test models of demography (populations)
568 in relation to threats, harvesting history, land tenure etc. The incorporation of population
569 viability analyses may also help to evaluate which management scenarios may help to
570 stabilise populations.

571 The regulatory framework for the WA Australian sandalwood industry was reviewed by
572 Lingard and Perry (2018), who identified a potentially unsustainable commercial harvest
573 quota. Recent studies (McLellan et al. 2021) support this notion. Sandalwood is also
574 removed illegally, and unlawful harvesting has been recognised as a significant threat to the
575 species since the early 2000s (DBCA 2023). Prior to 2016, it was estimated that over 500
576 tonnes of living sandalwood was illegally harvested each year (FPC 2016); though the true

577 amount is unknown (Lingard and Perry 2018). Despite higher penalties for illegal
578 sandalwood activity (see Government of Western Australia 2016), prosecution is often
579 hindered by lack of tools to verify sandalwood origin (Bunney et al. 2022). Further genetic
580 provenancing to complement the existing genetic marker set developed by Crawford (2016),
581 for example, could enable higher resolution discrimination of geographic origin within WA
582 to help combat the illegal trade (Table 1). Developing genetic markers that can discriminate
583 between wild and plantation sandalwood would also be beneficial.

584

585 ***Enhance recruitment***

586 Observations of recruitment failure in sexually reproducing plants indicate a barrier at one or
587 more points along the pathway from flower production, pollination, seed maturation, seed
588 dispersal, germination and growth to reproductive maturity. Overcoming recruitment failure
589 requires an understanding of where this barrier occurs, and the cause. Low levels of
590 recruitment are recognised as a key contributing factor behind Australian sandalwood's
591 ongoing decline (Kealley 1991; Brand et al. 2014; McLellan 2022).

592 Bees, wasps, flies, butterflies, moths, ants and cockroaches have been observed on
593 sandalwood flowers in WA (Barrett 1987; Gow 1997). While pollination vectors are
594 unconfirmed, Australian sandalwood is presumed to be insect-pollinated (Byrne et al.
595 2003b). Research to identify and actively conserve key pollinators and determine if
596 pollination is a factor limiting sandalwood recruitment should be considered as this may aid
597 sandalwood regeneration (e.g. Taylor et al. 2018). Research to examine the breeding system
598 of sandalwood more holistically (i.e. patterns of pollen movement by primary vectors) will
599 help to address this knowledge gap and may be used to inform licensing guidelines relating

to the retention of an optimal number of mature reproductive trees and adequate spacing to enable cross-pollination (Table 1).

The low density and fragmented nature of extant populations may reduce genetic variability and gene flow (i.e. dispersal of pollen or seeds between populations), which can decrease population resilience to climate change, pests and disease and elevate extinction risk (Pobke 2007; Frankham et al. 2017). Chevis and Kealley (2024) provide evidence that seed germination and recruitment can occur where seed is physically buried by natural water flow or under mulch near mature trees, and threatening processes (particularly browsing and fire) are controlled. Trials to reintroduce seed-caching marsupials into mature sandalwood stands where they have become locally extinct (e.g. managed reserves) should be considered to aid seed dispersal, burial and establishment away from parent trees (e.g. Chapman 2015; Murphy et al. 2015) (Table 1). Reintroduction projects for the purpose of restoring ecosystem processes are becoming increasingly common (IUCN/SSC 2013) and can be achieved if appropriate landscape-scale control of threatening processes is implemented (e.g. Lohr et al. 2021). Genetic techniques could be used to examine gene flow across landscapes of different connectivity.

Emus are capable of dispersing sandalwood seed over large distances (Davies 1978; Loneragan 1990), which could have important consequences for gene flow and genetic structure within and between populations (Calviño-Cancela et al. 2006) as emus remain widespread across the rangelands. However, the reported ability of sandalwood seeds to successfully germinate following excretion by emus, is mixed (Murphy et al. 2005). McLellan (2022) found that most sandalwood seeds in emu scats had been wholly or partially destroyed during passage, and for those that did pass intact, there was no evidence of successful germination at any site due to desiccation (i.e. scats deposited on the soil surface were exposed to the sun). In contrast, there are reports that sandalwood seedlings

have successfully germinated across the Charles Darwin Reserve in the northern edge of the wheatbelt in response to introduced herbivore control and seed dispersal by emus (Allen 2018). In a landscape largely devoid of seed-caching marsupials, the role of emus in sandalwood regeneration, particularly long-distance seed dispersal, may be an area for further investigation (Table 1). For example, experimental trials of gut passage effects by emus could be conducted controlling for fruit maturity/age and the effects of habitat and microsite on recruitment from emu scats. As emus also disperse the seed of host (*Acacia* spp.) plants and other nitrogen-fixing host genera (e.g. *Daviesia* spp.) (Calviño-Cancela et al. 2008), their continued presence within remaining stands of Australian sandalwood may be important.

With the aim of improving Australian sandalwood regeneration in harvested areas, a research program known as 'Operation Woylie' was implemented by the FPC in 2007 (SCEPA 2014). The FPC now employs mechanical seeding, which was designed to mimic the role of the woylie (see below) in seed burial, as the primary method to regenerate Australian sandalwood post-harvesting; noting that this occurs on pastoral land with no sheep/goats and unallocated Crown land where feral ungulates/rabbits are regulated by dingoes/wild dogs (DBCA 2023). Over the 2022-2023 season, 20.4 tonnes (~6.5 million seeds) were sown across the WA rangelands (FPC 2023). In response to low winter rainfall, however, germination rates and the number of seedlings established per annum has been lower than anticipated in some years (e.g. target 50,000 with a cumulative average of 39,000 seedlings over the first 10 years of the program; FPC 2021). In response to good rainfall over the 2022 winter, however, the FPC reported strong sandalwood establishment, with approximately 150,000 new seedlings established from the 2022 seeding program (FPC 2023).

As there are no published reports detailing long-term survival of germinants (i.e. beyond the seedling stage to become saplings/reproductively mature trees), follow-up studies are recommended to determine the level of successful recruitment occurring at regeneration sites (Table 1). Observations from plots established between 1925 and 1930 at Karamindie State Forest (22 km ESE of Coolgardie) suggest that successful recruitment may be low, with less than 5% of planted seed reaching maturity, and less than 3% of plants surviving to 98 years of age at this site (B. Sawyer unpublished data). The FPC is currently revisiting some of the first mechanically seeded sites to evaluate long-term survival, which will help to address this knowledge gap. Revisiting other historic plots or establishing new monitoring plots across the sandalwood distribution may help to provide important data regarding long-term survival to better inform management (e.g. key attributes of sites with higher success rates).

At present, 'Operation Woylie' remains the most cost-efficient and practical method to re-establish Australian sandalwood on a large scale. This process involves machine ripping a 250 mm deep rip line into which fresh seed is sown (FPC 2016). Impacts of machinery movements across the landscape can be mitigated by operator judgement to avoid unnecessary vegetation damage and effects on the host trees. Monitoring of the program by the FPC over the past 12 years indicates no obvious ongoing environmental concerns. On some land systems, especially the sandy-surfaced soil types, it is often difficult to see the rip-lines after only 2-3 years (J. Brand personal observation). As there are no studies that quantify the short- and long-term impacts of machinery, including mechanical harvesting, on the flora and fauna within sandalwood communities, research that examines species composition and diversity pre- and post-harvest and in response to mechanical seeding is recommended (Table 1).

Further research into seed priming techniques that promote germination and growth may also be a consideration. Hormonal seed priming using gibberellic acid (GA_3) significantly

enhanced sandalwood germination in some studies (Brand and Sawyer 2016) but not others (Brand 2017). Osmopriming, where seeds are soaked in aerated, low-water-potential chemical solutions, has been shown to enhance *ex-situ* germination and seedling growth of *Santalum album* (Debta et al. 2023) and could be investigated for *S. spicatum*. Likewise, other techniques with demonstrated benefits in *S. album*, for example nutripriming (Jijeesh et al. 2022), or inoculation with mycorrhizal fungi (Binu et al. 2015), may be worth investigating to help maximise Australian sandalwood recruitment success (Table 1).

Improved methods for population monitoring and identifying important habitat

Developing effective methodological approaches for population monitoring and identifying important and potential habitat are key components of programs to assess changes in species abundance, distribution, demographic structures and conservation status. Australian sandalwood occurs on a broad range of substrates, particularly loam, or sandy loam soils, in the presence of nitrogen-fixing host plants (Loneragan 1990; DEC 2012). In the northern arid regions of WA, sandalwood mainly occurs on alluvial plains and drainage lines associated with *Acacia* shrublands (Anderson 2005; DBCA 2023). In the southern semi-arid regions, sandalwood is associated with a more diverse range of vegetation types, typically *Acacia* dominant understories that occur in *Eucalyptus* woodlands (Loneragan 1990; Brand 2000); though naturally occurring populations are also known from granite outcrops, ridgetops, lateritic breakaways and creek lines (Fox 1997; McLellan 2022). Slope is important in determining sandalwood presence, likely due to naturally formed drains enabling seed dispersal/burial and/or providing sites with higher soil moisture (Brand and Jones 2002; Crawford 2016).

There can be a high variability in population demography between sites, over time and even within discrete populations. Over-bark stem diameter is currently used as a proxy to estimate Australian sandalwood age/size-class and is an accepted means of understanding population demography (e.g. Brand et al. 2014), however stem diameter growth rates can vary between sites (e.g. 0.5 mm per annum in the western rangelands (Brand et al. 2014) and 4 mm per annum at Dryandra in the more mesic wheatbelt (Loneragan 1990)). McLellan (2022) observed putatively very old trees with relatively small stem diameters, and stark variation in stem diameter and tree height between sandalwood populations on the mainland versus DHI. Follow up monitoring of two plots established at Karamindie State Forest also revealed that growth rates may change over time (e.g. average of 1.43-2.16 mm stem diameter growth per year during the first 44-49 years (from 1930 and 1925, respectively, to 1974), compared to ~ 0.5 mm growth per year from 50 years of age (from 1974 to 2023); B. Sawyer unpublished data). While measuring stem diameter may be useful for monitoring growth over time, it is less accurate for inferring tree age across the sandalwood distribution and can be extremely labour intensive. Even within discrete populations, sandalwood growing in a creek system, for example, may grow faster than sandalwood positioned 200 m away on top of a rocky breakaway (B. Sawyer personal observation). To better understand population structures and condition, analysing over-bark stem diameter in conjunction with additional environmental predictors should be considered, and research to identify more accurate methods to measure tree age may be warranted (e.g. analysing non-invasive timber core samples by radiocarbon dating or utilising dendrochronological techniques) (Table 1). Research to examine life history traits including maturation rates and peak fecundity of different sandalwood populations across the landscape is recommended to help determine the ideal size-class distribution and better inform commercial harvesting guidelines.

As sandalwood population size and health varies considerably across WA (DBCA 2023), identifying key habitat attributes of more robust populations may lead to better management. Better understanding the distribution of sandalwood and how it relates to physical habitat characteristics (e.g. topography, soil properties, vegetation types) and other variables (e.g. presence of threats, climate change) may also help to identify important and potential habitat for targeted conservation. Understanding the extent and condition of potential and existing host species throughout the rangelands is particularly important. Bioclimatic modelling, similar to Crawford (2016), could also be expanded upon to incorporate additional variables (as above) and include representative samples across the full WA distribution, as a high number of presence points within the species' northern distribution were omitted from the Crawford (2016) model.

To build knowledge of the sandalwood distribution and conduct population condition monitoring across the vast and remote WA landscape, aerial survey techniques have been explored. While these approaches, using RGB + near-infrared and hyperspectral aerial imagery, had some success in distinguishing Australian sandalwood from other vegetation, the degree of incorrect attribution was too high for widespread application (van Dongen et al. 2020; Barnes et al. 2023; FPC 2023). As such, the ability of these techniques to be applied to the broader rangelands with differing vegetation communities, soil types and landscape characteristics remains questionable. However, as remote sensing tools have the potential to map the occurrence of sandalwood over large areas more efficiently and cost-effectively than ground-based approaches and may be used to characterise important landform and vegetation associations (i.e. the identification of host species and potential sandalwood habitat), further research in this field should be considered as remote sensing surveillance and plant recognition technology continue to evolve (Table 1).

Australian sandalwood knowledge acquisition and dissemination

This review identified that significant information/data (e.g. Brand 2017) is not publicly available. As such, we recommend capturing, consolidating and analysing existing information/data and finalising work for publication in relevant peer reviewed journals where appropriate. Greater availability of contemporary consolidated information will enable informed decision making and aid Australian sandalwood conservation.

Exploring opportunities to gather and respectfully incorporate Traditional Owner knowledge into Australian sandalwood research and future decision making is also recommended (e.g. Goolmeer et al. 2024) (Table 1). Lingard and Perry (2018) identified the need for ongoing funding for regeneration initiatives, which could provide an opportunity to incorporate Traditional Owner knowledge and provide economic and cultural benefits from their involvement in sandalwood management programs such as the Sandalwood Dreaming project (FPC 2024; Government of Western Australia 2024).

Future research directions

Based on our review of existing knowledge and the input of experts into developing and ranking research questions, we propose a set of research priorities to address current knowledge gaps and guide conservation management of Australian sandalwood (Table 1). Research directions are prioritised as high, medium or low based on scoring by experts on five criteria, namely (1) the perceived likelihood of providing the greatest positive effect on sandalwood biodiversity conservation; (2) timescale (i.e. estimated length of time required to complete a research project); (3) relevance to meeting the management actions identified in the sandalwood BMP (DBCA 2023); (4) the perceived resource commitment required to complete a research project; and (5) the likelihood of research outputs being

implemented/used to inform future management actions (see Supplementary Table S1 for further detail regarding the prioritisation process).

Concluding remarks

Australian sandalwood is an ecologically important, economically valuable and culturally significant hemiparasitic plant. Due to a range of threats, sandalwood populations have declined across their range. On-ground recovery action is needed to conserve sandalwood populations, however as this review demonstrates, there are still large knowledge gaps regarding Australian sandalwood and its management. Critical to the ongoing persistence of sandalwood is better understanding population genetics and gene flow across the species' distribution, further evaluating the ecological functional role of sandalwood *in situ* and investigating ecological patterns and processes, particularly pollination, seed dispersal and recruitment. Research to inform best practice management of introduced herbivores and fire to benefit sandalwood communities is also important, as is better understanding population trends in response to other threats and biotic/abiotic factors. A coordinated cross-tenure management approach, incorporating Traditional Owner knowledge into future decision making, is likely to provide the greatest positive effect on sandalwood conservation across the vast WA landscape.

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Table 1: Suggested research priorities for Australian sandalwood (*Santalum spicatum*) in Western Australia (WA), ranked as high, medium or low (see Table S1 for more detail on rankings) based on (1) perceived impact/benefit (likelihood of providing the greatest positive impact on sandalwood biodiversity conservation); (2) timescale (estimated length of time required to complete a research project); (3) relevance to SBMP (research topic supports management action(s) identified in the sandalwood BMP; (4) perceived resource commitment (estimated resources/funding required to complete a research project); and (5) likelihood of implementation (probability of research outputs being implemented/used to inform future management actions).

Priority	Research topic	Objective	Expected outcome
High	Population genetics – mapping the genetic structure of the Australian sandalwood population, including on islands	Build a reference database of DNA samples to better understand the broader genetic structure of the Australian sandalwood population in WA. Determine whether populations along the north-western coastline represent a separate ecotype.	Higher resolution genetic discrimination within WA to inform management of regionally distinct genetic provenances and to build resilience against climate change. May also be used to trace the geographic origin of timber products to help combat illegal harvesting.
High	Enhance recruitment –dispersal ecology and pollination	Investigate the dispersal ecology (including the role of biotic and abiotic vectors) and pollination ecology (patterns of pollen movement by primary vectors) of Australian sandalwood. Determine if pollination is a factor limiting sandalwood recruitment.	Help to inform management strategies that promote natural pollination, seed dispersal and enhance recruitment within remaining stands of Australian sandalwood. Contribute to guidelines relating to the retention of an optimal number of mature seed-bearing trees and optimal spacing within populations.
High	Population dynamics – better understand population trends/life-history traits in response to threats and other biotic/abiotic factors	Continue to monitor existing sites and establish additional long-term monitoring sites, and resurvey at regular intervals (i.e. every 10 years), to better understand population trends over time. Concurrent monitoring of threats, and habitat condition, will enable the identification of potential factors influencing population dynamics.	Improved understanding of long-term population trends including changes in population status (e.g. in response to threats), the success of regeneration programs, and the effectiveness of threat mitigation programs. Provide information to inform Australian sandalwood management and refine recommendations for harvesting.

Priority	Research topic	Objective	Expected outcome
		Explore more accurate methods to monitor population age (e.g. radiocarbon dating or dendrochronological techniques) and examine life-history traits (maturation rates and peak fecundity) to determine the ideal size-class distribution of Australian sandalwood across the landscape.	
High	Threat mitigation – impacts of machinery on Australian sandalwood habitat	Examine species composition and diversity (and other habitat attributes) pre- and post-harvest, and following mechanical seeding, to determine the short- and long-term impacts on sandalwood communities.	Provide information to inform future sandalwood harvesting (e.g. frequency of harvesting intervals) and management strategies that promote habitat rehabilitation and sandalwood recovery (e.g. optimal spacing of mature trees).
High	Threat mitigation – influence of climate change	Better understand how climate change is likely to impact Australian sandalwood and key host spp. across the WA distribution. Investigate adaptation strategies that may promote climate resilience.	Provide improved understanding of the impact of climate change to inform adaptation strategies (e.g. provenance seed sourcing strategies and establishment with reduced winter rainfall).
High	Survey and monitoring – further evaluate the use of remote sensing techniques to better understand the distribution of Australian sandalwood and key host spp.	As technology evolves, further investigate remote sensing as a tool for the broad-scale detection of Australian sandalwood and potential sandalwood habitat across WA. Sampling to determine age and/or genetic structure of select populations (e.g. north-western coastline) could also be conducted during ground truthing.	Provide a more accurate estimate of total population size, demography and distribution to help inform an acceptable level of Australian sandalwood harvesting in different IBRA bioregions. Identify sandalwood populations and potential sandalwood habitat (i.e. native vegetation associations where Australian sandalwood is likely to occur) in need of targeted conservation management.
High	Threat mitigation – total grazing pressure	Conduct occupancy modelling to determine the level of threat posed by introduced and native herbivores, particularly camels (*Camelus dromedarius*). Compare occupancy before and after management intervention (e.g. closure of artificial water points, culling, exclusion fencing or land management that is sympathetic to the occurrence of dingoes) and robustly quantify impacts on Australian	Provide information to develop effective threat mitigation strategies to reduce total grazing pressure in sandalwood habitat and enable regeneration, including private property and Crown land leased for pastoralism. Consider innovative approaches for herbivore control in key areas.

Priority	Research topic	Objective	Expected outcome
		sandalwood regeneration, key host spp. and cohabiting fauna. Consider incentives for pastoralists and other stakeholders to protect Australian sandalwood.	Better understanding of the interactive effects of management intervention on cohabiting fauna (e.g. non-herbivores), key host spp., weeds and fire.
High	Ecological functional roles – evaluating the ecological functional role of Australian sandalwood *in situ*	Conduct controlled comparisons of species composition and diversity across the sandalwood distribution to evaluate the ecological functional role of Australian sandalwood *in situ*, with a focus on the importance of sandalwood as a food source, the role of dead wood and the potential of sandalwood as an indicator species of wider ecosystem health.	Provide evidence to support the keystone/indicator species hypothesis and identification of habitat (including key host spp.) important for targeted conservation management.
Medium	Enhance recruitment –informing seeding regimes and optimising survival	Conduct long-term monitoring at sandalwood regeneration sites to determine germination rates, seedling survival and successful recruitment. Consider innovative approaches to enhance seedling germination and establishment (e.g. seed priming techniques). Determine optimal seeding regimes across the various land systems and Beard vegetation associations.	Provide information to develop successful regeneration strategies to help stabilise sandalwood populations, including innovative approaches to enhance recruitment. Contribute to seeding guidelines and identification of areas where recruitment is likely to succeed.
Medium	Traditional Owner knowledge acquisition – using Traditional Owner knowledge to inform Australian sandalwood biodiversity conservation	Research to investigate and adopt Traditional Owner knowledge to help conserve and manage Australian sandalwood.	Respectful incorporation of Traditional Owner knowledge into future decision making and sandalwood management in WA.
Medium	Threat mitigation – the role of apex predators	Determine the occupancy of apex predators (dingoes, wild dogs and their hybrids, and eagles) within known sandalwood stands. Conduct concurrent predator scat analyses to determine prey components. Robustly quantify impacts on sandalwood regeneration, key host spp. and cohabiting fauna.	Provide a better understanding of predator-prey dynamics (i.e. the impact of apex predators on feral herbivores/predators) to inform threat management and promote Australian sandalwood regeneration. Provide evidence to support the retention of apex predators in the landscape to reduce total herbivory.

Priority	Research topic	Objective	Expected outcome
Medium	Threat mitigation – fire ecology of Australian sandalwood and key host spp. and landscape fire management	Investigate post-fire recovery within sandalwood habitat, including the ability of Australian sandalwood and key host spp. to regenerate. Identify appropriate landscape fire management approaches to protect sandalwood habitat i.e. the optimal temporal and spatial scale of fire mosaics to reduce surface fuel loads and fire mitigation and suppression responses to decrease the risk of large-scale intensive wildfires.	Provide improved understanding of the ability of Australian sandalwood to regenerate (e.g. via coppicing) in some habitats. Provide information to develop fire management strategies that protect important sandalwood habitat and regeneration sites.
Low	Threat mitigation – invasive weeds	Better understand the direct impacts of weeds on Australian sandalwood and explore methods to control invasive weeds within sandalwood habitat (e.g. selective weed control of flammable grasses such as buffel grass (*Cenchrus ciliaris*)).	Help to inform strategies for targeted management of invasive weeds to restore habitat, reduce direct competition with sandalwood, and decrease the risk of large-scale intensive wildfires.

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