Title:

Ecology and conservation of a living fossil: Australia's Wollemi Pine (*Wollemia nobilis*)

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Abstract

The iconic Wollemi Pine (*Wollemia nobilis*) is a critically endangered Australian conifer and one of the world's rarest trees with only 46 mature individuals remaining in the wild. The species is regarded as a 'living fossil' and was discovered on the brink of extinction following a natural historical decline. While its discovery has enabled crucial intervention for its long-term conservation, it has also created novel threats. *Wollemia nobilis* is facing extinction in the wild due to its highly restricted distribution, extremely small population size, and ongoing impacts from exotic pathogens, inappropriate fire regimes, unauthorised site visitation, and anthropogenic climate change. A highly successful, collaborative program combining *in situ* management, ecological research and monitoring with public education and *ex situ* conservation strategies, such as translocation and commercial cultivation, is enhancing the species' long-term survival. The extended longevity and slow growth and maturation of wild Wollemi Pine present unique challenges to effective *in situ* conservation, including the multidecadal timescales required to deliver certain conservation objectives. The continued success of the conservation program depends on strong forward planning, intergenerational commitment and collaboration, and ongoing public support.

Keywords

adaptive management, Araucariaceae, clonality, commercial cultivation, conifer, conservation genomics, critically endangered, dendrochronology, *ex situ* conservation, fire frequency, fire severity, pathogens, recruitment failure, recovery plan, resprouter, translocation

List of relevant web pages

https://www.rbgsyd.nsw.gov.au — Royal Botanic Gardens and Domain Trust (RBGDT) — Wollemi Pine Conservation Program

https://www.threatenedconifers.rbge.org.uk — Threatened Conifers of the World

https://www.iucnredlist.org — IUCN Red List of Threatened Species — *Wollemia nobilis*

https://www.bgci.org — Botanic Gardens Conservation International (BGCI)

1. Introduction

1.1. *Discovery of the Wollemi Pine*

In 1994, the discovery of a small grove of unusual conifers in a remote canyon, deep inside the Wollemi wilderness of south-eastern Australia, made international headlines. The trees were discovered during an exploratory canyoning expedition by an off-duty National Parks and Wildlife Service officer named David Noble. The significance of the find was soon recognized and led to the description of an entirely new genus and species within the ancient conifer family, Araucariaceae. The new taxon was named *Wollemia nobilis* W.G.Jones, K.D.Hill & J.M.Allen (Jones *et al.*, 1995) and ascribed the common name 'Wollemi Pine' (although it is not a true pine). The generic epithet is a reference to the Wollemi National Park where the trees occur, and the specific epithet honors David Noble (Jones *et al.*, 1995). The Wollemi Pine's closest living relatives are *Agathis* spp., followed by *Araucaria* spp. (Escapa and Catalano, 2013), including many well-known members such as the Monkey Puzzle Tree (*Araucaria araucana*) in Chile, Kauri (*Agathis australis*) in New Zealand, and Bunya Pine (*Araucaria bidwilli*) and Norfolk Island Pine (*Araucaria heterophylla*) in Australia.

1.2. *Fossil record*

The Araucarian fossil record dates back over 200 million years to the late Triassic period and the discovery of *W. nobilis* has enabled the re-evaluation of a number of important fossil specimens. Early palaeobotanical studies reported a striking resemblance between the pollen of *W. nobilis* and that of *Dilwynites*, a fossil pollen taxon that first appeared in the fossil record during the late Cretaceous c. 91 Mya and peaked in abundance in the early Paleocene to late Eocene c. 65–34 Mya, with the last known records from the late Tertiary c. 2 Mya (McLoughlin and Vajda, 2005). *Dilwynites* has been identified in sediments from Australia, New Zealand, Antarctica, and Patagonia, and was thought to have gone extinct; that is, until the discovery of *W. nobilis*. This sparked a worldwide media frenzy with *W. nobilis* dubbed the 'Dinosaur Pine' in the popular press and variously declared 'the botanical find of the century', 'a living fossil from the age of the dinosaurs' and 'the equivalent of finding a small dinosaur still alive on earth' (Woodford, 2005). Although no macrofossils have been definitively assigned to *Wollemia*, the stratigraphic distribution of *Dilwynites* has been used to construct a fossil record for the genus (Macphail and Carpenter, 2014). However, at least some records of *Dilwynites* are attributable to *Agathis*, the sister group to *Wollemia* (Macphail and Carpenter, 2014). While it seems apparent that the genus *Wollemia* has an extensive fossil record and was once much more widely distributed in the Southern Hemisphere, there is no evidence to indicate when the extant species *W. nobilis* evolved. Nevertheless, *W. nobilis* is a highly significant species of outstanding biodiversity value. It is one of several palaeoendemic conifers recognized as 'living fossils' — sole survivors of ancient lineages thought long extinct — with another well-known example in the remarkable Dawn Redwood (*Metasequoia glyptostroboides*) from China.

2. Conservation status

2.1. *National and international assessments*

Wollemia nobilis is listed as critically endangered in Australia under the New South Wales (NSW) *Biodiversity Conservation Act 2016* (BC Act) and the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act). It is also listed internationally as a critically endangered species on the IUCN Red List of Threatened Species (Mackenzie and Auld, in press). The species is highly susceptible to anthropogenic disturbance and stochastic events due to its extremely small population size, highly restricted geographic distribution, limited dispersal capacity and low recruitment of new genetic individuals. Impacts from introduced pathogens, inappropriate fire regimes, unauthorised site visitation, and anthropogenic climate change are further increasing the risk of extinction (NSW Threatened Species Scientific Committee, 2015; Figure 1).

Wollemia nobilis was discovered on the brink of extinction following a natural historical decline (Section 2.4). While its discovery has enabled crucial intervention for its long-term conservation, it has, ironically, also created novel threats associated with publicity and unauthorised site visitation (Benson, 1996).

2.2. *Population structure and geographic distribution*

The Wollemi Pine is one of the world's rarest trees. At the time of writing, a total of 89 individuals of *W. nobilis* are known to exist in the wild, only 46 of which are mature (Table 1). The population has been reduced to four closely occurring stands within an isolated catchment, equating to a single location *sensu* (IUCN Standards and Petitions Committee, 2019). Extensive ground and helicopter searches of the Wollemi Pine catchment and neighbouring areas have failed to locate any additional populations. The species has a very highly restricted geographic distribution (the extent of occurrence and area of occupancy *sensu* IUCN Standards and Petitions Committee (2019) are less than 4 km^2 each).

A comprehensive demographic inventory was undertaken between 2020–2021, involving a combination of ground, rope access, RPA (remotely piloted aircraft), and helicopter surveys. The inventory included updated assessments of the boundaries between putative individuals in addition to their reproductive status (adult, juvenile or functionally juvenile; Section 4.1). A number of previously undetected individuals growing on high cliffs adjacent to two of the known stands were also identified. The size distribution of the population (not shown) is distinctly bimodal with an apparent bottleneck at c. 10m in height where it seems that few large juveniles successfully transition into adult trees (Mackenzie, Clarke and Auld, unpubl.). Impacts from recent wildfires (Section 4.4) and ongoing recruitment failure suggest a gradual and continuing population decline (Mackenzie and Auld, in press).

2.3. *Biotic threats*

Two aggressive, exotic, soil-borne pathogens, *Phytophthora cinnamomi* and *P. multivora*, were detected in the largest subpopulation in 2005 and 2009, respectively, and are thought to have been introduced by unauthorized visitors via contaminated footwear, clothing, and/or equipment. These *Phytophthora* species infect and colonize the root system of *W. nobilis*, disrupting the uptake of water and nutrients. This has led to extensive stem and canopy wilt and dieback in a number of mature individuals, although none are known to have died as a result (NSW Threatened Species Scientific Committee, 2015). The incidence of mortality in seedlings (including germinated but pre-emergent individuals) and smaller juveniles is unknown; however, these life history stages are thought to be more susceptible as the pathogens are attracted (via zoospores) to plant exudates leaked into the soil environment, most readily via actively growing roots.

Two species of *Botryosphaeria*, a native, stem-infecting fungal pathogen, have also been detected in the largest subpopulation (Slippers *et al.*, 2005). *Botryosphaeria* is an opportunistic endophyte that primarily affects stressed or wounded plants, and is known to be pathogenic to *W. nobilis* (Bullock *et al.*, 2000). During a 2012 translocation of *W. nobilis* (Section 5.4), 74 % of the mortality observed during the first two years of establishment was attributed to impacts from *Botryosphaeria* (Zimmer *et al.*, 2016). *Botryosphaeria* is seldom considered a problem to healthy undisturbed plants in the wild; however, it can be a significant threat to plants under other biotic or abiotic stress factors.

Interactions with co-occurring threats in the landscape such as drought and fire may exacerbate the effects of *Phytophthora* and *Botryosphaeria* on *W. nobilis*. The species is further imperiled by unauthorized site visitation which carries the risk of spreading existing pathogens into uninfected areas; introduction of novel pathogens and invasive weeds; trampling of exposed roots, seedlings, and small juveniles, which are difficult to detect in the understory; compaction and erosion of fragile soils; and theft of plant material due to its horticultural value (NSW Threatened Species Scientific Committee, 2015).

2.4. *Abiotic threats*

Wollemia nobilis is thought to be a paleoendemic species that has declined over an extensive period due to major climatic changes (McLoughlin and Vajda, 2005), the evolution and rise in dominance of the angiosperms (Kershaw and Wagstaff, 2001), and increasing fire activity in the landscape (Kershaw *et al.*, 2002), consistent with other Araucariaceae. Inappropriate fire regimes — in particular, high fire frequency and high fire severity — continue to threaten the remaining stands. Climatic warming (Lewis *et al.*, 2015) and extreme weather events such as heatwaves (Offord, 2011) and drought (Zimmer *et al.*, 2015), pose additional threats to the species that, in conjunction with wildfires, are predicted to increase in frequency and severity in the region due to anthropogenic climate change.

3. *In situ* conservation and management

3.1. *Species recovery team*

The Wollemi Pine Recovery Team was formed shortly after the species' discovery and comprises a collaborative expert panel of scientists and conservation managers from the NSW Department of Planning Industry and Environment (DPIE), the NSW National Parks and Wildlife Service (NPWS), the NSW Royal Botanic Gardens and Domain Trust (RBGDT), and a range of expert scientists from various universities. The team are responsible for ensuring the species' long-term persistence in the wild and their collective expertise includes plant ecology; extinction risk; experimental design and analysis; environmental survey; plant pathology; population genomics; horticulture; *ex situ* conservation and seed banking; reserve management (including fire, pest and weed management); specialist helicopter and rope-access operations; expedition planning; and minimal-impact ('leave no trace') wilderness skills.

3.2. *Species recovery plan*

A detailed species recovery plan was developed for *W. nobilis* in 1998. It synthesized existing knowledge regarding the species' life history and ecology and clearly documented the recovery actions and research required to effectively manage key threats and reduce extinction risk. The NSW recovery plan was revised in 2006 (NSW Department of Environment and Conservation, 2006) with a new updated version due for release in early 2022. It remains an indispensable tool in the conservation program for the species.

3.3. *Restricted site access*

In response to the immense public interest in the species, the fragility of its habitat, and the risk of inadvertent or deliberate damage, the extant population of *W. nobilis* and a buffer of surrounding habitat within the catchment have been protected through their declaration as Critical Habitat (now incorporated as an 'Area of Outstanding Biodiversity Value' under the

BC Act). This prohibits unauthorized entry into the area and severe penalties apply for non-compliance, including fines of up to $330,000 and two years' imprisonment for harming the species or its habitat. Additional protective measures include ongoing site surveillance and compliance enforcement, and restricted site access for minimum essential personnel undertaking the minimum essential management, research, and monitoring activities.

3.4. *Site hygiene*

Strict phytosanitary protocols are observed by all approved personnel visiting the sites to prevent the introduction and/or spread of pathogens and exotic species. These protocols include thoroughly cleaning and disinfecting footwear, clothing, and equipment prior to every site visit using a mixture of ethanol or denatured alcohol diluted to 70% with water. Guidelines apply regarding the maximum level of antecedent rainfall for planned visits to proceed in order to minimize physical impacts on the sites and spread of soil-borne pathogens. Designated routes of within-site movement involving multiple decontamination points, and use of separate sets of equipment for each site, and for certain parts of sites, further restricts soil movement and the transfer of pathogens (NSW Department of Environment and Conservation, 2006).

3.5. *Fire management*

The NSW National Parks and Wildlife Service conducts regular prescribed burning for bushfire hazard reduction within Wollemi National Park. This applies to the sclerophyll vegetation surrounding the Wollemi Pine catchment but not the rainforest community the species occupies. Rainforest communities are occasionally impacted by wildfire; however, this occurs at a significantly lower frequency than the highly fire-prone, eucalypt-dominated sclerophyll forests on the ridgetops above. Periodic reduction of surface fuels is an effective strategy for reducing the risk and spread of unplanned fires under milder conditions; however, it becomes ineffective during severe to catastrophic fire danger conditions.

During south-eastern Australia's catastrophic 2019–2020 'Black Summer' bushfire season, the wild population of *W. nobilis* came under threat from what would eventually become Australia's largest ever recorded forest fire. The wild sites were the focus of an intensive, multi-agency fire suppression effort which included installation of irrigation systems in the main grove to increase the moisture content of surface fuels and reduce fire severity; use of large air tankers to lay fire retardant around the catchment; strategic water bombing with helicopters and fixed-wing aircraft as the fire fronts approached; and winching specialist remote-area firefighters into the sites to extinguish active fires immediately after the main fire-fronts had passed. The groves were still impacted by understory fires to varying degrees (Section 4.4); however, the intervention likely reduced the severity of impacts.

This extraordinary effort to protect an important biodiversity asset during a national emergency was critically lauded and set an important precedent for planning and protection of other biodiversity values during future major fire events. An independent inquiry into the causes of, and responses to, the 2019–2020 bushfires noted that the success of the Wollemi Pine protection operation was aided by the existence of a detailed species recovery plan and fire protection strategies (de Bie *et al.*, 2021). Other key factors in the success included the species' iconic profile and associated public awareness and interest; strong advocacy from recovery team members who raised awareness of the impending threat and negotiated support and resources ahead of time; access to additional funding; and ecological knowledge and data from species experts (de Bie *et al.*, 2021).

The risk of unplanned fire to the wild population has been substantially reduced by the 2019–2020 bushfires and will remain low for approximately five years until surface fuels reaccumulate. Beyond this time, long-term fire exclusion (in the order of 50-100 years or more; Mackenzie, Clarke and Auld, unpubl.) remains a key objective to facilitate population recovery. Strategies to achieve this include rapid detection and suppression of ignitions within the national park and surrounds; an ongoing program of implemented fires for bushfire hazard reduction purposes; and strategic, manual removal of surface fuels from within the *W. nobilis* sites. In case of an imminent threat to the groves, wrapping the bases of *Wollemia* trunks in fire retardant material, as was done to protect Giant Sequoias (*Sequoiadendron giganteum*) during the 2021 wildfires in California, may be effective at minimizing the risk of serious basal charring and/or trunk collapse.

3.6. *Management of pests and weeds*

The NSW National Parks and Wildlife Service undertakes annual monitoring and treatment of invasive weeds in Wollemi National Park, with special attention to incursions of perennial weeds that have the potential to adversely affect the Wollemi Pine population and habitat. Vertebrate pest control programs targeting pigs and deer are undertaken to minimize direct and indirect impacts of these species, including site disturbance, pathogen and weed introductions, and physical damage to seedlings and juveniles.

3.7. *Additional legislative protection*

Between 58–65% of the world's threatened and near-threatened conifers are at risk from direct exploitation, agriculture and forestry (Royal Botanic Garden Edinburgh, 2021). *Wollemia nobilis*, via its fortuitous location within Wollemi National Park, is afforded protection from such threats under the NSW *National Parks and Wildlife Act 1974* (NPW

Act). The national park is situated inside the Greater Blue Mountains World Heritage Area and Gondwanan relicts such as the Wollemi Pine and another primitive and critically endangered gymnosperm, the Dwarf Mountain Pine (*Pherosphaera fitzgeraldii*, Podocarpaceae), are among the outstanding floristic diversity for which the region is internationally recognised.

In January 2021, *W. nobilis* became the first species to be declared an 'Asset of Intergenerational Significance' in NSW under the NPW Act. This is a statutory mechanism to reinforce existing protection measures to conserve the species for future generations, including a detailed, species-specific fire management strategy for both prescribed and unplanned fires.

4. Ecology

4.1. *Life history*

Wollemia nobilis is an emergent rainforest tree that can reach up to 40 m in height (Jones *et al.*, 1995) and has distinctive, deep-red, bubbly bark (Figures 2a,f). Growth is rhythmic, and the pattern of architecture and reiteration in *W. nobilis* is unlike any other extant Araucariaceae, and is possibly unique among plants (Hill, 1997). Two main types of foliage are evident: juvenile-phase foliage, which is arranged in two rows on opposite sides of the branch, and adult-phase foliage, which is arranged in four rows with branches exhibiting a unique diamond-shaped pattern that reiterates along their length due to the production of markedly shorter leaves at the beginning and end of each growing season.

The Wollemi Pine is monoecious with male pollen and female seed cones ('strobili') borne on the ends of upper branches (Jones *et al.*, 1995; Figures 2b,c). Female cone production signals maturity and only commences once juvenile trees reach the rainforest canopy and gain access to the sunlight above. In cultivation, males cones may develop from five years of age and females cones from eight years of age (NSW Department of Environment and Conservation, 2006); however, juvenile-to-adult transitions appear to occur infrequently in the wild (none have been recorded since monitoring began in 1994) and, thus, the primary juvenile period of wild individuals remains unknown.

Seeds disperse in late summer with most seedlings (Figure 2d) emerging within 30 m of adult trees (NSW Department of Environment and Conservation, 2006). Germination is epigeal and bimodal with a pulse of emergence in autumn and in spring (Offord *et al.*, 1999). Seeds are short-lived (< 1 year) and there is no persistent seed bank; however, the species maintains a bank of shade-tolerant, slow-growing juveniles that sit largely dormant in the understory awaiting the formation of canopy gaps (Zimmer *et al.*, 2014). This strategy of intermittent recruitment in response to occasional disturbance, coupled with extended adult longevity (see below), is consistent with many other Southern Hemisphere conifers, including Araucariaceae (Kershaw and Wagstaff, 2001).

A key life history trait of *W. nobilis* is its prolific copping habit, both in the absence of, and in response to, disturbance (Jones *et al.*, 1995; Burrows *et al.*, 2003; Figures 2e,g). As a consequence, most individuals are multi-stemmed (Jones *et al.*, 1995), with some individuals comprising over 40 trunks $\geq$ 2 m tall, in addition to numerous smaller coppice stems (Mackenzie, Clarke and Auld, unpubl.). This makes it difficult to delineate genetic individuals in the field (Mackenzie and Auld, in press).

The ability to resprout is likely to have been pivotal to the long-term persistence of *W. nobilis* by providing a buffer against disturbance and decreasing population turnover and reliance on seedling recruitment (Bond and Midgley, 2001). Vegetative regeneration is rare in conifers; however, other notable exceptions include various species of *Araucaria* and *Agathis* that are able to coppice, sucker and form epicormic shoots — but usually only in response to severe trauma (Burrows *et al.*, 2003). Very few trees have the ability of *W. nobilis* to produce secondary trunks in the absence of disturbance (Burrows *et al.*, 2003). Individual trunks of *W. nobilis* can live in excess of 400–450 years (Banks, 2002) and may be replaced by other trunks when they fall. Hence, the rootstock of individual trees could be much older than their standing trunks, with some of the larger trees potentially many hundreds — if not thousands — of years old.

Adult trees that suffer complete loss of their mature trunks (e.g., due to fire, windthrow or impacts from falling rocks) may enter a secondary juvenile phase while replacement stems resprout and mature (Mackenzie, Clarke and Auld, unpubl.). Given the benefits of well-developed adult root systems, these functionally juvenile individuals are expected to have higher survival and faster growth and maturation than true juveniles.

4.2. *Genetic variation*

An early genetic study prior to the widespread use of genomic sequencing detected no variation in *W. nobilis* despite exploration of hundreds of loci and concluded that the species has exceptionally low genetic variation. One of four hypotheses proposed to explain this was that the entire extant population comprised only one to a few clones (Peakall *et al.*, 2003). However, following sequencing of the chloroplast genome (Yap *et al.*, 2015), exceptionally low — yet detectable — genetic diversity was found in a whole-chloroplast analysis

(Greenfield *et al.*, 2016). More refined population genetic studies based on reduced representation genome sequencing approaches are ongoing but preliminary investigations have identified low-level variation within and between subpopulations (Bragg *et al.*, unpubl.). This information is being used to guide the composition of *ex situ* collections and translocated populations to maximize their genetic diversity.

4.3. *Habitat*

Wollemia nobilis is restricted to narrow, steep-sided sandstone canyons and gorges dominated by warm temperate rainforest (Benson and Allen, 2007). Soils are shallow, acidic and relatively infertile (NSW Department of Environment and Conservation, 2006). Most individuals occur within the rainforest or at its margins, perched on steep slopes and benches up to 30 m above the canyon floor. Very few individuals persist on the lower rainforest slopes and flats. The remainder grow on higher benches or cling precariously to exposed ledges and cliff faces within the periphery of eucalypt-dominated sclerophyll vegetation which is drier and more fire-prone. Warm temperate rainforest is common throughout the gullies and gorges of the Blue Mountains; however, the elevated terraces and benches presently favored by the Wollemi Pine are quite rare within this community (Clarke and Mackenzie pers. obs.) and are likely to play a key role in the species' persistence in these sites.

The moist and stable conditions within these relatively sheltered habitats (especially within the rainforest) have enabled *W. nobilis* to survive past climatic changes as the landscape dried and became increasingly more fire-prone, particularly during the Pleistocene (McLoughlin and Vajda, 2005). Today, the canyons continue to provide important refugia from the drought, temperature extremes, and frequent fires that affect the surrounding eucalypt forests and woodlands.

The fact that such a distinctive and conspicuous tree species as the Wollemi Pine eluded discovery on the edge of Australia's largest city throughout two centuries of botanical exploration is a testament to the rugged and inaccessible nature of Wollemi National Park (the name 'Wollemi' comes from an Aboriginal word *wollumii* meaning, 'look around you', 'watch your step'; Jones *et al.*, 1995). The remote and precipitous terrain of the Wollemi Pine sites presents unique physical and logistical challenges for the recovery team who are often required to work in suspension from cliffs and helicopters to access, monitor and sample portions of the population.

4.4. *Fire response*

Fire scars on the trunks of most mature adults indicate that the groves have been impacted by, and survived, past wildfires (NSW Department of Environment and Conservation, 2006); however, the summer of 2019–2020 provided the first opportunity since the species' discovery to observe the response of wild individuals to fire. Most adult trees survived the fires with their upper canopies intact; however, juvenile trees ≥ 2 m tall sustained significant damage with two-thirds topkilled and only half of these resprouting to date (Mackenzie, Clarke and Auld, unpubl.). Up to 95 % of the pre-fire juvenile bank (plants < 2 m tall) is yet to resprout and has likely been eliminated; however, it is expected to re-establish over the next 20–30 years via ongoing annual seed production in adult trees. The population is being closely monitored and will need to be protected from fire for an extended period (50–100 years or more) to facilitate recovery of the juvenile bank and of plants that resprouted after the fires. This presents significant challenges for conservation managers in the current climate where wildfires are expected to increase in frequency and severity.

Further research is needed on the conditions required to promote the successful transition of seedlings and juveniles into adult trees, and the role of disturbance (e.g., canopy gap formation, fire) in recruitment (sexual and asexual) and population persistence. Data on the fire response of individuals in various size classes, and on survival, growth, and maturation rates of post-fire recruits (coppices and seedlings), is essential for effective fire management and determination of the minimum tolerable fire-return intervals to support long-term persistence, at least at low fire severity. The use of dendroecology and radiocarbon dating to better understand past growth dynamics would provide a valuable complement to existing ecological monitoring and inform ongoing conservation management.

5. *Ex situ* conservation program

5.1. *Ex situ living collection*

In situ research and management of the wild population is complemented by an active *ex situ* conservation program which centers around a living collection and seed bank maintained at the Australian Botanic Garden, Mount Annan, in NSW (Figure 2h). The bulk of the living collection consists of plants produced by vegetative propagation using material collected from wild individuals and currently captures 57 % of the total extant population (Table 1). The goal is to increase representation towards 100 %; however, many of the individuals yet to be sampled have only recently been discovered and/or accessed by field teams and are in a vulnerable state of post-fire recovery. Hence, it may be several years before it is safe to remove material from them.

5.2. *Global metacollection*

The living collection is one of the most important components of the Wollemi Pine conservation program, providing important insurance against loss of genetic diversity in the wild population, in addition to supporting a wide variety of *ex situ* research (Figure 1). However, just like the wild population, a single, concentrated collection is highly vulnerable to stochastic events. Hence, propagation is underway to support global distribution of genetically diverse, backup living collections under the Botanic Gardens Conservation International (BGCI) metacollections program (Griffith *et al.*, 2019) to safeguard this critical resource.

5.3. *Commercial cultivation for conservation*

Given the enormous public interest in the Wollemi Pine following revelations of its discovery and ancient lineage, commercialization and worldwide distribution of cultivated specimens was identified as a high priority to discourage illegal collection and exploitation of the wild population. The highly successful ‘cultivation for conservation’ project was launched in 2005 and *W. nobilis* is now widely cultivated in private and public gardens all over the world. Fifteen years later, a citizen science project called ‘I Spy a Wollemi’ (Offord and Zimmer, unpubl.) is gathering data on cultivated specimens from across the globe in a bid to characterize the species’ environmental tolerances and inform management of the wild populations under climate change, including the potential use of assisted migration.

5.4. *Translocation*

With so few individuals of *W. nobilis* remaining in the wild, and all of them concentrated in a single location, the risk of losing the entire population to a catastrophic event, such as a disease outbreak or severe wildfire, is high. Given the species’ dispersal and recruitment limitations, the only viable conservation strategy to reduce this risk is to use translocation to increase the population size and geographic distribution by creating additional wild populations at a distance from the original stands.

A semi-wild, pilot translocation was successfully conducted in the Blue Mountains in 2012 and demonstrated the importance of plant condition and plant size for establishment success (Zimmer *et al.*, 2016). Saplings that had been 'hardened off' (exposed to harsher conditions prior to outplanting, including less water and higher light levels) and smaller plants tended to have higher survival (Zimmer *et al.*, 2016). Mortality after the first two years was negligible until the site was impacted by fire in 2019–2020 (Figure 3a).

The success of this trial, coupled with increasing threats to the wild population, prompted the establishment of two remote-area translocated populations in Wollemi National Park in mid-2019. The selected sites occur in deep, steep-sided rainforest canyons that feature perennial watercourses and are located well within the species' (recent) putative historical range. These plantings incorporate knowledge gained from the earlier translocation study and have benefited from subsequent advances in propagation techniques and population genomics that have increased our capacity to produce large quantities of high-quality saplings that sample the known range of genetic diversity in *W. nobilis*. The trials have also been explicitly designed to address key knowledge gaps regarding the influence of contemporary disturbance regimes on the species' persistence niche (Bond and Midgley, 2001) and — once translocated populations reach maturity — its regeneration niche (Grubb, 1977).

As we are yet to observe a single wild seedling or juvenile transition into an adult tree, the best microsites to situate saplings within the canyons to ensure their long-term success —

especially in the context of recurrent disturbances such as fire and drought — remain unknown. Wild individuals only come of age and produce cones once they reach the sunlight above the rainforest canopy. Light (Offord *et al.*, 2014) and soil moisture are important for growth of young trees; however, the brightest planting locations in the canyons are often more exposed to frequent fire and drought (Figure 3b). Conversely, moister locations tend to have lower light availability. Hence, different locations within a site involve trade-offs between short- and long-term benefits and risks, and microsites that promote early survival and growth of Wollemi Pine may not be suitable for long-term persistence (Figure 3c).

An adaptive management framework was applied to the 2019 translocations to simultaneously evaluate competing planting strategies, thereby reducing the risk of failure and maximizing learning opportunities (Mackenzie and Keith, 2009). Saplings were positioned along natural environmental gradients from moist rainforest in the depths of the canyons to the eucalypt-dominated rocky ledges above. The consequences of variation in light, soil moisture and flammability/fire risk for growth, maturation and survival will be assessed over different timescales, enabling iterative refinement of the planting strategy during subsequent introductions or augmentations. This will also inform ongoing conservation and fire management of the wild and translocated populations.

All three translocated populations were impacted by the 2019–2020 bushfires with 0% and 3–30% plants escaping burning in the Blue Mountains and Wollemi National Park populations, respectively, demonstrating the efficacy of multiple large and widely-dispersed populations in spreading risk. The Blue Mountains population was well established at the time of fire impact compared to the Wollemi National Park populations. As of January 2021, 22 % (34) saplings in the Blue Mountains population had resprouted and survived (Figure 3a). Within the Wollemi National Park populations, 2 % (4) and 26 % (56) saplings, respectively —all unburnt (rather than post-fire resprouts) — were still alive in May 2021 when the populations were each augmented with c. 250 saplings (Figure 3a). Due to the slow growth and maturation of *W. nobilis* saplings in the wild (Zimmer *et al.*, 2014), it may be many decades before these translocated populations mature and even longer until they become self-sustaining and can be considered part of the wild population. Hence, protection and conservation of the original wild stands remains the highest priority.

7. Conclusions

The remarkable story of the discovery of the Wollemi Pine and the fight to save this ancient conifer from extinction highlights the incredible value of national parks and wilderness areas as refugia for biodiversity, as well as raising awareness of plant conservation and the plight of threatened species. The Wollemi Pine recovery program provides a world-class model for threatened species conservation and management and owes its success to strong interagency collaboration and forward planning via a dedicated recovery team and a well-developed and regularly updated species recovery plan. The synergy between *in situ* management, research, monitoring, *ex situ* conservation and commercial cultivation has made a significant contribution to reducing the species' risk of extinction, although there are many obstacles yet to overcome. Among these are the multidecadal timescales involved in delivering critical conservation outcomes such as long-term fire exclusion and the establishment of self-sustaining translocated populations. This requires intergenerational commitment and collaboration, with future generations of scientists and environmental stewards bringing the present work to fruition. An ongoing campaign of public engagement, science communication, and education has greatly enhanced public interest and support for the program. This continues to have direct benefits to conservation of the wild populations, from minimizing unauthorized site visitation through public understanding and co-operation, to influencing and attracting resourcing for important recovery actions.

However, the Wollemi Pine is but one of over 1,300 Australian plant species currently identified as nationally threatened with extinction — the vast majority of which do not have the benefit of a dedicated recovery team, recovery plan or funding to ensure their protection. These species are just as worthy of protecting and conserving for future generations and hopefully the efforts and strategies described here to conserve the Wollemi Pine can stimulate interest and raise awareness around the conservation issues faced by other rare and threatened plants.

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Conflicts of interest

None to declare.

Author contributions

BDEM wrote the manuscript and prepared the table and figures. BDEM, SWC and TDA provided data for Table 1. MTP and BDEM sourced images for Figure 2. HCZ, CAO, TDA, BDEM, SWC and DMC provided data for Figure 3a. All authors contributed to the drafts and gave final approval for publication.

References

Banks, J. C. G. (2002) Wollemi Pine: tree find of the 20th century, *in* John Dargavel, D. G. and B. L. (Ed.) *Australia's ever-changing forests V. Proceedings of the Fifth National Conference on Australian Forest History*. Centre for Resource and Environmental Studies, ANU, Canberra.

Benson, J. S. (1996) Threatened by discovery: research and management of the Wollemi Pine Wollemia nobilis Jones, Hill and Allen, pp. 105–109 *in* Stephens, S. and Maxwell, S. (Eds.) *Back from the Brink: Refining the Threatened Species Recovery Process*. Sydney, Surry Beatty & Sons.

Benson, J. S. and Allen, C. (2007) Vegetation associated with *Wollemia nobilis* (Araucariaceae). *Cunninghamia* **10**, 255–262.

Bond, W. J. and Midgley, J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* **16**, 45–51. doi:10.1016/S0169-5347(00)02033-4.

Bullock, S., Summerell, B. A. and Gunn, L. V (2000) Pathogens of the Wollemi pine, *Wollemia nobilis*. *Australasian Plant Pathology* **29**, 211–214.

Burrows, G. E., Offord, C. A., Meagher, P. F. and Ashton, K. (2003) Axillary meristems and the development of epicormic buds in Wollemi Pine (*Wollemia nobilis*). *Annals of Botany* **92**, 835–844. doi:10.1093/aob/mcg207.

de Bie, K., Currey, K., Woinarski, J., Wintle, B., Garnett, S. and Rumpff, L. (2021)

Protecting threatened species and ecological communities before and during bushfire: Learning from the 2019–20 fires. Brisbane.

Escapa, I. H. and Catalano, S. A. (2013) Phylogenetic analysis of Araucariaceae: Integrating molecules, morphology, and fossils. *International Journal of Plant Sciences* **174**, 1153–1170. doi:10.1086/672369.

Greenfield, A., McPherson, H., Auld, T. D., Delaney, S., Offord, C. A., Van Der Merwe, M., Yap, J. Y. S. and Rossetto, M. (2016) Whole-chloroplast analysis as an approach for fine-tuning the preservation of a highly charismatic but critically endangered species, *Wollemia nobilis* (Araucariaceae). *Australian Journal of Botany* **64**, 654–658. doi:10.1071/BT16105.

Griffith, P., Beckman, E., Callicrate, T., Clark, J., Clase, T., Deans, S., Dosmann, M., Fant, J., Gratacos, X., Havens, K., Hoban, S., Lobdell, M., Jiménez-Rodriguez, F., Kramer, A., Lacy, R., Magellan, T., Maschinski, J., Meerow, A. W., Meyer, A., Sanchez, V., Spence, E., Toribio, P., Walsh, S., Westwood, M. and Wood, J. (2019) *Toward the metacollection: Coordinating conservation collections to safeguard plant diversity*. San Marino, USA.

Grubb, P. J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**, 107–145.

Hill, K. D. (1997) Architecture of the Wollemi pine (*Wollemia nobilis*, Araucariaceae), a unique combination of model and reiteration. *Australian Journal of Botany* **45**, 817–826. doi:10.1071/BT96053.

IUCN Standards and Petitions Committee (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. IUCN Standards and Petitions Committee, 1–60.

Jones, W., Hill, K. D. and Allen, J. (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea* **6**, 173–176. doi:10.7751/telopea19953014.

Kershaw, P. and Wagstaff, B. (2001) The southern conifer family Araucariaceae: History, status, and value for paleoenvironmental reconstruction. *Annual Review of Ecology and Systematics* **32**, 397–414. doi:10.1146/annurev.ecolsys.32.081501.114059.

Kershaw, A. P., Clark, J. S., Gill, A. M. and D'Costa, D. M. (2002) A history of fire in Australia, pp. 3–25 *in* Bradstock, R. A., Gill, A. M., and Williams, R. J. (Eds.) *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. Cambridge, UK, Cambridge University Press.

Lewis, J. D., Phillips, N. G., Logan, B. A., Smith, R. A., Aranjuelo, I., Clarke, S. W., Offord, C. A., Frith, A., Barbour, M., Huxman, T. and Tissue, D. T. (2015) Rising temperature may negate the stimulatory effect of rising CO2 on growth and physiology of Wollemi pine (*Wollemia nobilis*). *Functional Plant Biology* **42**, 836–850.

Mackenzie, B. D. E. and Auld, T. D. (in press) *Wollemia nobilis*. *The IUCN Red List of Threatened Species 2021*. https://www.iucnredlist.org

Mackenzie, B. D. E. and Keith, D. A. (2009) Adaptive management in practice: Conservation of a threatened plant population. *Ecological Management and Restoration* **10**, S129–S135. doi:10.1111/j.1442-8903.2009.00462.x.

Macphail, M. K. and Carpenter, R. J. (2014) New potential nearest living relatives for Araucariaceae producing fossil Wollemi Pine-type pollen (*Dilwynites granulatus* W.K. Harris, 1965). *Alcheringa* **38**, 135–139. doi:10.1080/03115518.2014.843145.

McLoughlin, S. and Vajda, V. (2005) Ancient Wollemi Pines resurgent: Ten years after its discovery, a vanishingly rare tree from the Cretaceous Period is a scientific darling and may soon become a commercial success too. *American Scientist* **93**, 540–547.

NSW Department of Environment and Conservation (2006) *Wollemi Pine (Wollemia nobilis) Recovery Plan*. Hurstville, NSW, NSW Department of Environment and Conservation.

NSW Threatened Species Scientific Committee (2015) Final determination to list the Wollemi Pine, *Wollemia nobilis* W.G.Jones, K.D.Hill & J.M.Allen, as a critically endangered species under the Biodiversity Conservation Act 2016.

Offord, C. A. (2011) Pushed to the limit: Consequences of climate change for the Araucariaceae: A relictual rain forest family. *Annals of Botany* **108**, 347–357. doi:10.1093/aob/mcr135.

Offord, C. A., Porter, C. L., Meagher, P. F. and Errington, G. (1999) Sexual reproduction and early plant growth of the Wollemi Pine (*Wollemia nobilis*), a rare and threatened Australian conifer. *Annals of Botany* **84**, 1–9. doi:10.1006/anbo.1999.0882.

Offord, C. A., Meagher, P. F. and Zimmer, H. C. (2014) Growing up or growing out? How soil pH and light affect seedling growth of a relictual rainforest tree. *AoB PLANTS* **6**, plu011. doi:10.1093/aobpla/plu011.

Peakall, R., Ebert, D., Scott, L. J., Meagher, P. F. and Offord, C. A. (2003) Comparative genetic study confirms exceptionally low genetic variation in the ancient and endangered relictual conifer, *Wollemia nobilis* (Araucariaceae). *Molecular Ecology* **12**, 2331–2343. doi:10.1046/j.1365-294X.2003.01926.x.

Royal Botanic Garden Edinburgh (2021) *Threatened Conifers of the World* https://threatenedconifers.rbge.org.uk (accessed 20 September 2021).

Slippers, B., Summerell, B. A., Crous, P. W., Coutinho, T. A., Wingfield, B. D. and Wingfield, M. J. (2005) Preliminary studies on *Botryosphaeria* species from southern hemisphere conifers in Australasia and South Africa. *Australasian Plant Pathology* **34**, 213–220. doi:10.1071/AP05020.

Woodford, J. (2005) *The Wollemi Pine: the incredible discovery of a living fossil from the age of the dinosaurs*. Third editon. Melbourne, The Text Publishing Company.

Yap, J. Y. S., Rohner, T., Greenfield, A., Van Der Merwe, M., McPherson, H., Glenn,

W., Kornfeld, G., Marendy, E., Pan, A. Y. H., Wilton, A., Wilkins, M. R., Rossetto, M. and Delaney, S. K. (2015) Complete chloroplast genome of the Wollemi pine (*Wollemia nobilis*): Structure and evolution. *PLoS ONE* **10**, 1–15. doi:10.1371/journal.pone.0128126.

Zimmer, H. C., Auld, T. D., Benson, J. S. and Baker, P. J. (2014) Recruitment bottlenecks in the rare Australian conifer *Wollemia nobilis*. *Biodiversity and Conservation* **23**, 203–215. doi:10.1007/s10531-013-0593-2.

Zimmer, H. C., Brodribb, T. J., Delzon, S. and Baker, P. J. (2015) Drought avoidance and vulnerability in the Australian Araucariaceae. *Tree Physiology* **36**, 218–228. doi:10.1093/treephys/tpv111.

Zimmer, H. C., Offord, C. A., Auld, T. D. and Baker, P. J. (2016) Establishing a wild, ex situ population of a critically endangered shade-tolerant rainforest conifer: a translocation experiment. *PLoS ONE* **11**, e0157559. doi:10.1371/journal.pone.0157559.

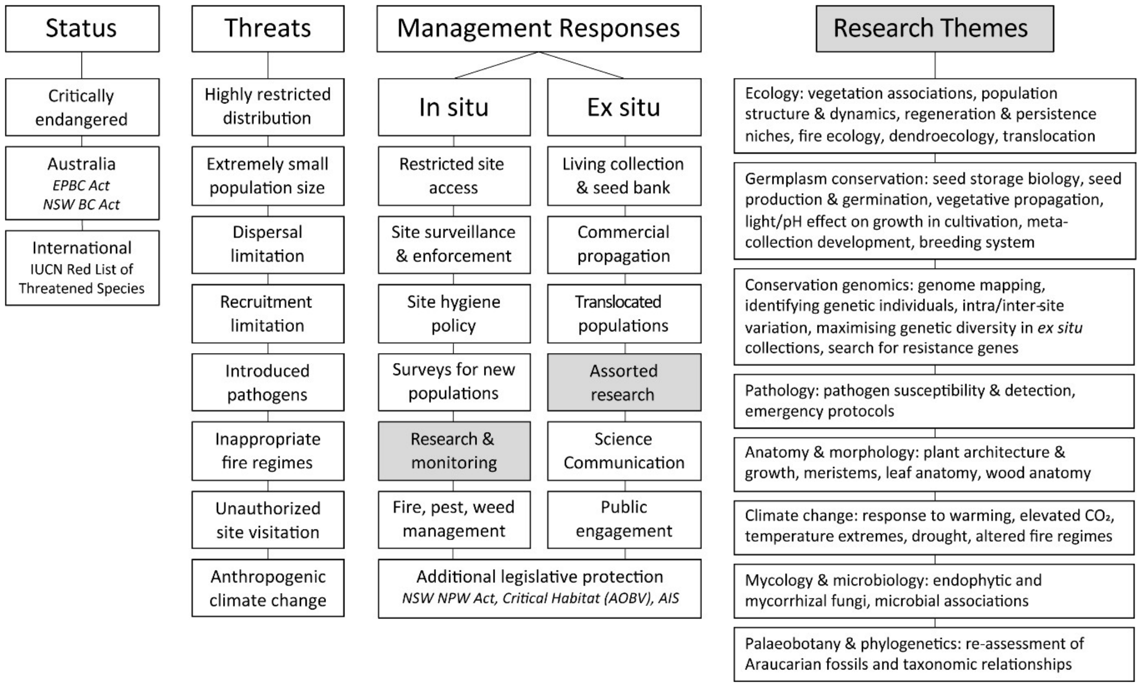

Figure 1. Conservation status, current threats, and key recovery actions for *Wollemia nobilis* (Wollemi Pine), including major *in situ* and *ex situ* research themes addressing knowledge gaps and enhancing ecological understanding. Italics refer to Australian legislative acts and related declarations: EPBC Act — Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*; NSW BC Act — New South Wales *Biodiversity and Conservation Act 2016,* including AOBV — Areas of Outstanding Biodiversity Value (Critical Habitat); NSW NPW Act — New South Wales *National Parks and Wildlife Act 1974*, including AIS — Assets of Intergenerational Significance.


(A)
(B)
(C)
(D)
(E)
(F)
(G)
(H)

Figure 2. Selected life history attributes of *Wollemia nobilis* (Wollemi Pine). **(A)** Mature Wollemi Pine *in situ*[1]; **(B)** male pollen cone (strobilus)[1]; **(C)** female seed cone (strobilus)[1]; **(D)** newly emerged seedling bearing two distinctive cotyledons[2]; **(E)** characteristic multi-stemmed habit[1]; **(F)** bark detail[1]; **(G)** prolific basal resprouting (coppicing) of a mature tree in response to the 2019–2020 bushfires[2]; **(H)** the *ex situ* living collection at the Australian Botanic Garden, Mount Annan[3]. Copyrights: [1]Jaime Plaza/New South Wales Royal Botanic Gardens and Domain Trust; [2]Berin Mackenzie/New South Wales Department of Planning, Industry and Environment; [3]Maureen Phelan/New South Wales Royal Botanic Gardens and Domain Trust.

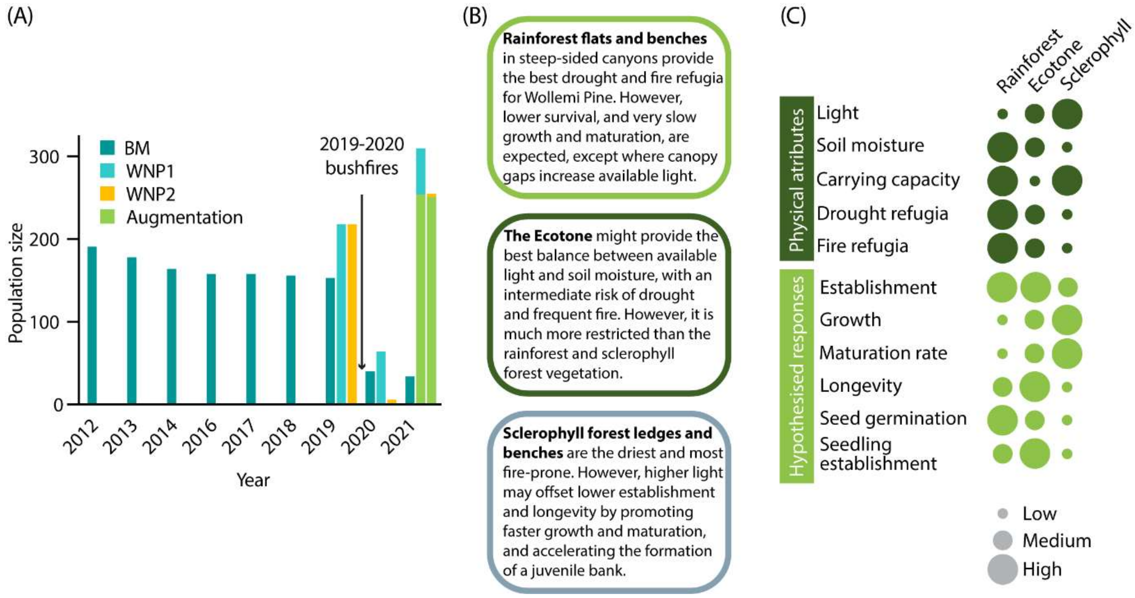

Figure 3. Aspects of the *Wollemia nobilis* (Wollemi Pine) translocation program. **(A)** Survival of translocated populations established in the Blue Mountains (BM) in 2012 (Zimmer *et al.* unpubl.) and in Wollemi National Park (WNP1, WNP2) in 2019 (Mackenzie *et al.* unpubl.). BM was not censused in 2015. WNP1 and WNP2 were each augmented with c. 250 saplings in 2021. **(B)** Summary of alternative planting strategies (positions along an environmental gradient) being experimentally evaluated in the two 2019 translocations in Wollemi National Park, and **(C)** the hypothesized benefits and risks of each strategy. Refer to Section 5.4 of main text for details.

Table 1. Structure of the wild *Wollemia nobilis* (Wollemi Pine) population as of mid-2021 (Mackenzie, Clarke and Auld, unpubl.). Adult trees are distinguished from juveniles (juv) by the presence of female seed cones (strobili), and functional juveniles (f.juv) are adult trees that have entered a secondary juvenile phase after loss of their mature trunks. Data presented are best estimates of putative individuals (discrete clumps of stems or trunks inferred to share a common base). Refer to Section 4.1 of main text and to Mackenzie and Auld (in press) for further details.

Site	**No. adults (% total)**	**No. f.juv (% total)**	**No. juv (% total)**
1	19 (41)	1 (9)	6 (19)
2	11 (24)	8 (73)	17 (53)
3	3 (7)	0 (0)	1 (3)
4	13 (28)	2 (18)	8 (25)
Total	46	11	32