The evolutionary significance of Tasmania's rainforests and associated vegetation types

FINAL REPORT – IVG 5C

Note: This report was prepared to inform the analysis of the World Heritage significance of the tall eucalypt/rainforest ecosystem discussed in Chapter 1 of IVG Report 5A, "Tall Eucalypt Forest as World Heritage".

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NRM Insights

Contents

Executive Summary

This topic of this review is the evolutionary significance of Tasmanian rainforests and their associated vegetation types. Rainforests in the state occur in a mosaic of vegetation types, ranging from button grass moorland to tall wet sclerophyll forests. For the purpose of the review the vegetation types that are covered in addition to rainforests are principally wet sclerophyll forests and mixed forests, where eucalypts are emergent over a rainforest understorey. Because of the limited time available to undertake the project, the review acts as an entry point into the diversity of topics that are relevant to such a broad subject area.

In order to set the scene for examining the evolutionary significance of Tasmanian rainforests and wet sclerophyll/mixed forests the review starts by examining the definition of rainforests within a national and state context. This includes an overview of the ongoing discussion about whether mixed forests should be classified as rainforests, as communities transitional to rainforest or as a separate vegetation community. All of these views are held in Tasmania, which is the focus of this report. Discussions held with experts as part of this review saw some support for mixed forests with a tall eucalypt overstorey to be classified as rainforests. This was based on the functional similarity of giant eucalypts to rainforest trees on the one hand, and the similarity of the species composition between rainforests and mixed forests on the other.

The distribution of rainforests and wet sclerophyll forests are described and illustrated where possible in the report, largely based on the widely used Tasmanian integrated mapping project TASVEG. This approach has some limitations as mixed forest communities are embedded within the broader wet eucalypt group. As a consequence, only three communities that can be identified as mixed forest (eucalypts over a rainforest understorey) are explicitly mapped – *Eucalyptus nitida*, *E. obliqua* and *E. delegatensis*. Even these three species have areas of mixed forest that are not explicitly mapped, being subsumed into broader wet eucalypt communities. The nature of the data available for mapping and analysing forest distributions has an impact on the ability to explore the extent and nature of the interactions between rainforest and wet sclerophyll/mixed forest and to calculate their reservation status. TASVEG does make it possible however to illustrate and describe the mosaic of rainforest and other vegetation types at a broad level.

A brief description is provided on the different communities and species that are found in Tasmanian rainforests and wet sclerophyll/mixed forests. Tasmania is a major centre of distribution for cool temperate *Nothofagus* rainforest in the world. In addition to this widespread species a number of other species, many of them long-lived and endemic, are found in Tasmanian rainforests. These include Huon pine *Lagarostrobos franklinii* (Huon pine) and *Athrotaxis selaginoides* (Pencil Pine). Rainforests and wet sclerophyll/mixed forests provide habitat for a number of endemic, rare and endangered plant and animal species. Bryophytes and fungi are abundant in wet sclerophyll and mixed forests, making a major contribution to the plant species diversity in these communities.

The evolutionary history of rainforest taxa and eucalypts are reviewed. Both ‘groups’ have a very long evolutionary history with Gondwanic origins. The rainforest taxa include both gymnosperms and angiosperms with a range of phylogenetic histories. It was not possible to address these separately in this review. Recent macro-fossil discoveries in South America and phylogenetic/molecular studies give considerable weight to a Gondwanic origin for eucalypts and a much earlier appearance of fire adapted biomes. Major environmental changes associated with tectonic plate movement over millions of years, and more recent glacial-interglacial cycles, has had a major impact on the evolution and current distribution of both rainforest and sclerophyllous species such as eucalypts. Fossil evidence shows the patchy nature of vegetation change in Australia depending on the location. Eucalypts and rainforest species have co-existed for at least 27 million years, in Victoria at least. The widespread radiation of sclerophyllous taxa appears to have occurred around 20 Ma, with wet eucalypt forest and mixed forest communities identified elsewhere around 10-15 Ma.

Eucalypts are thought to have been in Tasmania for around 20 million years. Based on the limited fossil evidence available, it is conjectured that eucalypts became established in south-western Tasmania around 2-3 Ma. Broadly similar dates are proposed using molecular data, with the divergence of two of the Tasmanian eucalypt lineages placed around 3.0-0.8 Ma. Recent changes in temperature, aridity and sea level associated with glacial and inter-glacial cycles (1.7 Ma to 17 ka) are considered to have had a major impact on the evolution of Tasmanian eucalypts. The associated changes in distribution pattern are thought to have enabled divergent species to come into contact and exchange genes through hybridisation (reticulate evolution). Although Tasmanian eucalypt species may be relatively 'new', the evolution of eucalypts in Tasmania is intimately related to the evolutionary history of eucalypts as a group overall. The links between earlier taxa and extant eucalypt species in Tasmania (17 taxa of which are endemic) would benefit from further exploration.

Understanding contemporary spatial and temporal dynamics of Tasmanian rainforests and associated sclerophyll/mixed forest is an important element in the story of their evolutionary significance. The model/s that are used to describe these dynamics reflect how people view the evolution of these systems and can have a major impact on their management. In turn, the way these ecosystems are managed will impact on their future evolution. The relay floristics model of succession is the model most widely applied to the dynamics of rainforests and associated vegetation in Tasmania. Early papers by Gilbert and Jackson were influential in this model being adopted. Five seral stages are generally described, ranging from buttongrass moorland to rainforest. The impact that fire regimes, soil characteristics and topography have on the ultimate expression of these seral stages has been the subject of many publications.

The alternative stable state model has recently been used to describe the dynamics of rainforests and associated vegetation in Tasmania and elsewhere. It is likely that different models will apply in different circumstances. It is recommended that a comprehensive review of the different vegetation models used in rainforests, wet sclerophyll forests and mixed forests in Tasmania be undertaken. Such a review would help determine the most appropriate models to describe and inform the dynamics and management of these ecosystems. Alternative approaches such as the State and Transition model could also be explored.

The review ends with an overview of the evolutionary significance of rainforests and associated wet sclerophyll/mixed forests drawing on the material presented in the rest of the report. A number of reviews of the outstanding values associated with these vegetation types have been undertaken, particularly in association with the listing of the Tasmanian Wilderness World Heritage Area on the World Heritage register. These reviews demonstrate a range of globally significant values for these vegetation types, many of which are related to their evolutionary significance. Some of the vegetation types examined in this review are under-represented in the reserve system with wet forests dominated by *Eucalyptus regnans* and *E. obliqua* having the lowest values (< 6%). The IUCN has consistently noted that there are areas of old growth *Eucalyptus* forest adjoining the Tasmanian Wilderness World Heritage Area which have the potential to be added to the property because of their outstanding values.

This review supports and provides additional material on the significance (evolutionary and other) and values of Tasmanian rainforests and associated vegetation types. Recent molecular and phylogenetic analysis of the eucalypts, as well as an important fossil discovery in South America, are leading to a reassessment of the timelines for the evolution of both the eucalypts and their ancestors and fire dependent communities. Plant species expansion, distribution and interactions during the glacial-interglacial cycles have been found to show different patterns compared to the northern hemisphere. Importantly, rainforests with an overstorey of giant eucalypts (>70 m in height) have been shown to be globally unique. This new information adds to the values already identified for these ecosystems, including their importance for carbon sequestration and storage. It also reinforces the importance of maintaining intact landscapes to support the evolutionary processes underpinning these ecosystems.

Acknowledgements

This report was written over the Christmas/New Year period of 2011-2012. The author gratefully acknowledges the time given by numerous experts on the ecology of rainforest and associated vegetation over this period when most people are on holidays! Tony Norton is also gratefully acknowledged for discussions about forest ecology in Tasmania and Virginia Young for her support during the project.

Cover photo: Rainforest vegetation along the Gordon River, west coast, Tasmania. All photos in the report are taken by Jann Williams.

Citing the Report

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Disclaimer

Literature review

Project scope

The Terms of Reference set the scope of this project. They are as follows:

> *Conduct a review of literature and other material sourced from the Australian Rainforest Conservation Society references and any other relevant material relating to the evolutionary significance of Tasmania's rainforests and associated vegetation types.*
>
> *Gather expert opinion from relevant scientists including Dr Aila Keto, Mr Peter Hitchcock, Professor Bill Laurence, Professor Dave Bowman, Professor Jamie Kirkpatrick and Professor Brendan Mackey.*

The report arising from the literature review and expert opinion is designed to form an important input to the heritage work being undertaken by Mr Peter Hitchcock. This in turn is being overseen by Professor Brendan Mackey of the Australian National University, a member of the Independent Verification Group.

The report highlights the key issues associated with the evolutionary significance of Tasmania's rainforests and associated vegetation types. It draws on the most recent and relevant literature, as well as the 'classics' where relevant. Where possible, review articles are cited as they provide an entrée into the rest of the literature. To undertake a more in-depth review would require considerably more time than was available.

Forest definitions

This report is designed to review the evolutionary significance of rainforest and associated vegetation types in Tasmania. The two associated vegetation types that have been identified as the most relevant to address are mixed forest and wet eucalypt forest. These vegetation types occur in mosaics with rainforest in eastern Australia, as well as Tasmania (Brown and Podger 1982, Lynch and Neldner 2000, Turton and Sexton 1996, Warman and Moles 2009). As will be illustrated below, these vegetation types have also been widely described as part of a successional sequence that ultimately leads to a mature ('climax') rainforest in Tasmania. The dynamics between mixed forests and rainforest has received particular attention in the literature and more broadly. As such, these interactions and the different ecological models used to describe them will be further explored in this report. This provides important context for the discussion of the evolutionary significance of these forest types.

As a starting point, the report addresses the definition of rainforest, mixed forest and wet eucalypt forest (also referred to as wet sclerophyll forest) at the national, state and regional level. As several authors have documented, the delimitation of rainforest and mixed forests from sclerophyll forests has led to considerable debate, especially between conservation and forestry groups (Lynch and Neldner 2000, Bowman 2000, Kirkpatrick and DellaSella 2011). These debates demonstrate that the definition of these vegetation types can have significant implications for the conservation and management of these systems.

The term rainforest was originally defined by the German botanist Schimper in 1903 (Schimper 1903). Since then, there have been a number of attempts to classify and define rainforest in the Australian context (e.g. Webb (1959), Webb *et al*. (1984), Adam (1992), Gell and Mercer (1992)). Lynch and Neldner (2000) and Bowman (2000) provide informative overviews of the history of classifying and defining rainforest, both focusing on Australia. These authors emphasise the variable nature of rainforest in Australia and the different purposes for which the classifications/definitions are used. These two publications also had different purposes, with Lynch and Neldner (2000) tackling the challenging issue of developing a national definition of rainforest for Australia (Box 1), while Bowman (2000) ended up adopting the definitions used in each study when incorporating them into his book on Australian rainforest ecology. From his review he concluded that despite the idiosyncratic definitions of rainforest he uncovered, they always fell within the broader class of vegetation that is intolerant of recurrent landscape fires (Bowman 2001).

Definition 1
Rainforest in Australia is a tree-dominated plant formation, where the tallest tree layer is usually closed (with a projective foliage cover of greater than 70%) and greater than 5 m in height. Rainforest also includes tree-dominated plant formations where the tallest tree layer is not closed (projective foliage cover of less than 70%) and the canopy is less than 5 m high, but the tallest trees are rainforest species. (**Additional qualifying criteria for Definitions 2 and 3). Rainforest plant species are adapted to regenerating in the low-light conditions experienced under the closed canopy or in localised gaps caused by recurring disturbances which are part of the natural rainforest ecosystem, and are not dependent on fire for successful regeneration. The closed-canopy mangrove communities are specially adapted to the intertidal zone, and should be considered a distinct formation.

Additional qualifying criteria for Definition 2
** The ecological definition of rainforest includes transitional (ecotonal) and seral (secondary or mixed) communities with a minimal (to be defined — somewhere between 5 and 50%) component of emergent non-rainforest species, where the community is of similar botanical composition to mature rainforests in which non-rainforest species are absent.

Additional qualifying criteria for Definition 3
** The ecological definition of rainforest includes the late successional stages of transitional (ecotonal) and seral (secondary or mixed) communities with emergent non-rainforest species in their older growth stages, where the community is of similar botanical composition to mature rainforests in which non-rainforest species are absent.

Box 1: A nationally applicable rainforest definition developed by Lynch and Neldner (2000) that is designed to apply across Australia. The first definition forms the basis for all three recommended definitions. The additional two definitions incorporate mixed forests.

The national definition proposed by Lynch and Neldner (2000) focuses on structural vegetation characteristics of vegetation, as well as the regeneration mode of rainforest species. While not explicit in the national definition, the amount of rainfall received at a site is also often used to help define rainforest. At the regional and state level, floristic characteristics are often used to define rainforest, in addition to structure and regeneration mode (e.g. Su *et al.* 2001). This is the case in Tasmania, where the definition developed by Jarman and Brown (1983) has been widely adopted (see Table 1). This definition defines rainforest using a relatively small number of dominant species that can regenerate without major disturbance, as well as using tree height as part of the definition. Bowman (2000) and Lynch and Neldner (2000) provide additional commentary on the definition developed by Jarman and Brown (1983).

Both Lynch and Neldner (2000) and Bowman (2000) address the issue of mixed forests (closed canopy vegetation beneath tall and open canopies of *Eucalyptus*), which Bowman (2000) states has 'bedevilled' the classification of rainforest in Australia. The term mixed forests was first used by Gilbert (1958) for Tasmanian cool temperate rainforest-eucalypt forest. These forests have a species composition characteristic of a recognised rainforest community, in additional to sclerophyllous emergents or dominants.

As noted by Lynch and Neldner (2000) policy for these mixed forests could take one of three options. These mixed-forest communities could be considered to be:

(*1*) non-rainforest;
(*2*) communities transitional to rainforest; or
(*3*) distinctive vegetation types/communities.

All three options have been used in differing circumstances in Australia, including in Tasmania. Lynch and Neldner (2000, 2001) concluded that the recognition of mixed forests as distinct vegetation types allows maximum flexibility in their management. In contrast, authors such as Kirkpatrick and DellaSella (2011) state that cool temperate mixed forests should be described as rainforests based on the similarity in species composition. Tng *et al.* (2012) focus on a sub-set of mixed forests, proposing that rainforests with a tall eucalypt overstorey (with eucalypts >70m in height) be classified as rainforest, with the eucalypts treated as pioneer rainforest species. The authors propose that if giant eucalypts are functionally seen as rainforest trees, the problems around the definition of rainforests will disappear.

Community	Definition/description	Publication/Source
Cool temperate rainforest	Vegetation dominated by species of *Nothofagus*, *Eucryphia*, *Atherosperma*, *Athrotaxis*, *Lagarostrobos*, *Phyllocladus* or *Diselma*. Comprises forest with trees greater than 8 m in height (Jarman *et al.* (1991) subsequently decreased the height threshold to 5 m).	Jarman and Brown (1983)
Tasmanian cool temperate rainforest	Vegetation dominated by species of *Nothofagus, Eucryphia, Anodopetalum, Atherosperma, Athrotaxis, Lagarostrobos, Phyllocladus* or *Diselma* and others that do not depend on exogenous disturbance for its perpetuation (*sensu* Jarman and Brown 1983).	Balmer *et al.* (2004)
Rainforest	Tasmanian rainforest is structurally and floristically variable and it is defined by the presence of any of the genera of *Nothofagus, Atherosperma, Lagarostrobos, Phyllocladus* or *Diselma* (p. 146) (*sensu* Jarman and Brown 1983).	Harris and Kitchener (2005)
Cool temperate rainforest	Forests in areas of high rainfall dominated by tree species such as myrtle (*Nothofagus cunninghamii*), sassafras (*Atherosperma moschatum*), celery-top pine (*Phyllocladus asplenifolius*), leatherwood (*Eucryphia lucida*), King Billy pine (*Athrotaxis selaginoides*), pencil pine (*Athrotaxis cupressoides*) and Huon pine (*Lagarostrobos franklinii*) and able to regenerate without a major disturbance. Eucalypts may be present at a density of less than 5 percent of the crown cover.	Forestry Tasmania (2007) Parks & Wildlife Service Tasmania (2011) has a similar definition. This publication states that the 5% threshold is arbitrary and emphasise the variability in Tasmanian rainforests.
Mixed forest	Wet eucalypt forest with an understorey of rainforest species (Glossary).	Harris and Kitchener (2005)
Mixed forest	Rainforest with greater than 5% cover of eucalypt species.	Parks & Wildlife Service Tasmania (2011)
Mixed forest	Eucalypt dominated forest with a rainforest understorey (sensu Gilbert 1958) (Glossary).	Balmer *et al*. (2004)

Table 1: Definitions/descriptions developed for Tasmanian rainforest and mixed forest.

Jarman and Brown (1983), whose definition of rainforest has been widely used in Tasmania (see Table 1), state that lowland mixed forests may be equally considered as mature eucalypt forest or as immature rainforest. In TASVEG, the integrated vegetation mapping program developed by the Tasmanian Government (Harris and Kitchener 2005), communities identified with a rainforest understorey and eucalypt overstorey are mapped as wet eucalypt forests. In this context, wet eucalypt communities are distinguished by the dominant eucalypt species or the eucalypt species in the canopy. These characteristics are sometimes used in combination with a description of the understorey type. TASVEG mapping is discussed in greater detail in the section on forest distribution.

Other definitions of wet eucalypt/sclerophyll communities in Tasmania include Balmer *et al.* (2004) who wrote a report on the floristic values of the Tasmanian Wilderness World Heritage Area. These authors define wet sclerophyll forest as vegetation dominated by *Eucalyptus* with an understorey characterised by a dense layer of mesophytic (broad-leaved) shrubs (*sensu* Beadle & Costin 1952).

Additional perspectives on the definition and significance of rainforest and associated vegetation will be provided in the following sections.

Forest distribution

Australian rainforests have been divided into four main types at a coarse level based on floristic composition: tropical, sub-tropical, monsoon and temperate (Beadle and Costin 1952). These types are still widely used to describe rainforests, with Tasmanian rainforests falling in the broad category of temperate rainforests. In Australasia, these rainforests are primarily restricted to coastal areas between latitudes 39.5 to 43.5 (Figure 1; Kirkpatrick and DellaSella 2011).

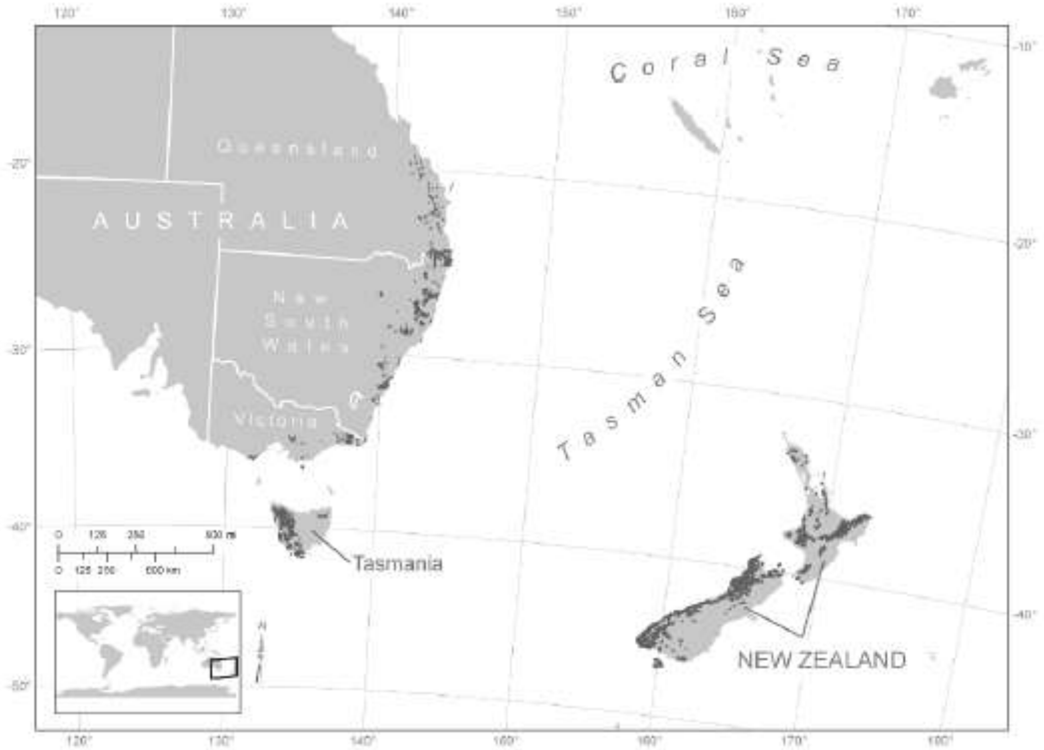

Figure 1: Distribution of temperate rainforest in Australasia as mapped by Kirkpatrick and DellaSella (2011).

Authors such as Adam (1992) further distinguish between warm and cool-temperate rainforest. Within the broad umbrella of cool temperate rainforest, four main structural/floristic types are recognised in Australasia: callidendrous (tall trees with an open, park-like understorey), thamnic (rainforest with shrubby understorey), implicate (short, tangled vegetation) and montane (Brown and Read 1996, Kirkpatrick and DellaSella 2011).Tasmania contains Australia's largest tracts of cool temperate rainforest, covering around 10% of the State (Figure 2a) (Parks & Wildlife Service Tasmania 2011). Rainforest is found throughout the western half of the State and in patches in the north-east highlands (Worth *et al*. 2009). The most extensive areas of callidendrous rainforests occur in Tasmania's north-west. Tiny patches of rainforest also survive in some east coast gullies where extra moisture from clouds or streams compensates for relatively low rainfall.

Wet sclerophyll and mixed forest communities dominated by eucalypt species principally occur in Australia (Groves 1994, Tng 2012). An exception is rainforest dominated by *Eucalyptus deglupta* which extends from Papua New Guinea, through the islands of Indonesia, to the southern Philippines.

Wet sclerophyll and mixed forests are predominantly found in the mesic zone of eastern and southern Australia (Byrne *et al.* 2011), including Tasmania. In this state, wet eucalypt forests are widespread, occurring in areas with fertile soil and reasonably good rainfall (Figure 2b)(Forest Education Foundation 2008). They can be distinguished by their overstorey of tall eucalypts with a dense understorey of small trees, broadleaved shrubs and ferns. The state-wide map of wet eucalypt forests in Tasmania (Figure 2b) incorporates mixed forests, as described further below. Mixed forest, accounts for approximately 20% (195,000 ha) of Tasmania's wet eucalypt forest (Tabor *et al.* 2007).

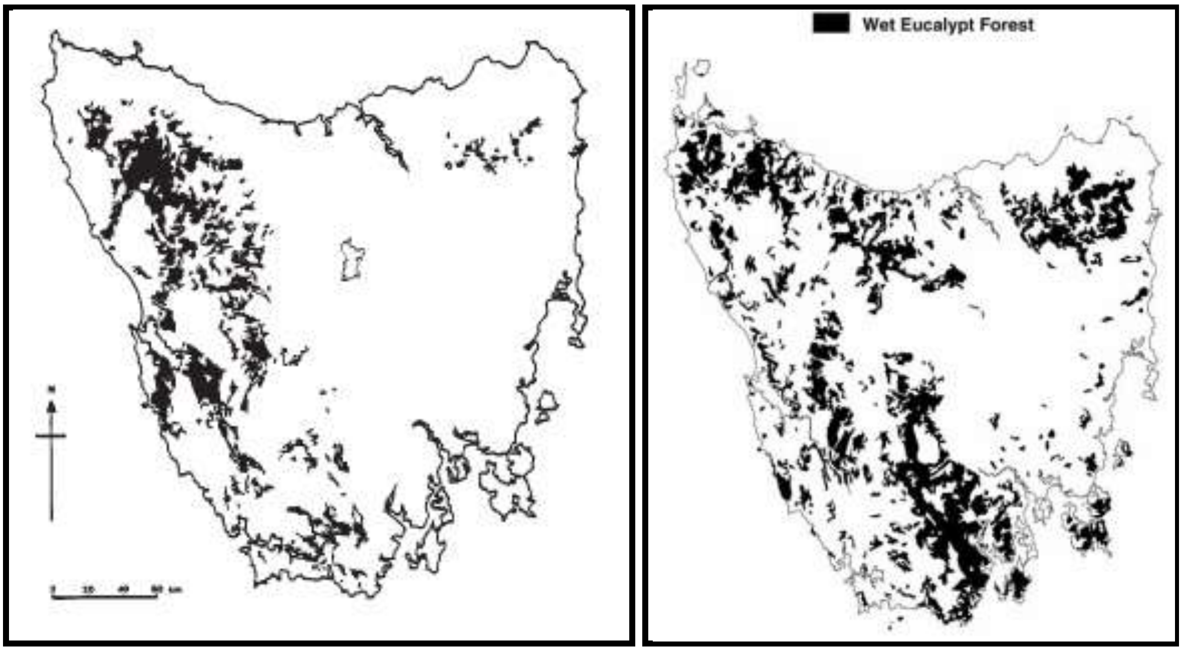

Figure 2: Distribution of a) cool temperate rainforest (left - Parks & Wildlife Service Tasmania 2011) and b) wet sclerophyll forest (right - Forest Education Foundation 2008) in Tasmania.

Cool temperate rainforests in Tasmania occur in a mosaic of vegetation types. The broad groups found in this mosaic have been identified as moorland, sclerophyll scrub, wet sclerophyll eucalypt forest, mixed forest and rainforest (Jackson 1968, Brown and Podger 1982, Balmer *et al*. 2004, Wood *et al*. 2011, Wood and Bowman 2012). The mix of vegetation types associated with rainforest in the mosaic can vary from place to place. For example, the mosaic studied by Wood *et al.* (2011) in south-western Tasmania consisted of moorland, sclerophyll scrub, wet sclerophyll forest and rainforest. As noted in the section on forest definitions, the focus of this report is on wet sclerophyll forests, mixed forest and rainforest. The forest mosaics of relevance are therefore where these three vegetation types co-occur, primarily in the west of the state.

Vegetation maps are a useful and widely used tool to illustrate and quantify the distribution of vegetation types. They are also often used as a basis for determining the conservation, management and reservation status of vegetation. In Tasmania, the TASVEG integrated vegetation map, has been developed by the Tasmanian Government (Harris and Kitchener 2005). This mapping data is publically available and is now widely used in the state to describe and map vegetation at different scales and vegetation types. Some brief background on TASVEG, including the different units used for vegetation mapping, is provided in Box 2.

The two most relevant broad TASVEG groups for this report are ‘Rainforest and related scrub’ (15 mapping units) and ‘Wet eucalypt forest and woodland’ (18 mapping units). Mixed forests sit within the second group. The dominant species in the 15 rainforest mapping units are *Athrotaxis* (*selaginoides* and *cupressoides*), *Lagarostrobos*, *Atherosperma*, *Phyllocladus, Leptospermum* and *Nothofagus*. As noted in the next section, several of these species are endemic to Tasmanian rainforests. The most widespread of these mapping units is *Nothofagus-Atherosperma* rainforest (RMT) which occurs in north-west, western and Southern Tasmania, around the north-eastern highlands and with small relict forests near the east coast (Harris and Kitchener 2005). This mapping unit is distinguished by the presence of a high continuous canopy of *Nothofagus* with or without *A. moscatum* or *Eucryphia lucida*. Communities such as *Lagarostrobus franklinii* rainforest and scrub

(RHP) are more restricted, in this instance occurring along many of the river systems of western and southern Tasmania between seas level and about 350m.

The TASVEG integrated vegetation map has been developed by the Tasmanian Government. Harris and Kitchener (2005) provide a comprehensive description of the first version of TASVEG and the vegetation that it maps. With the release of TASVEG Version 2.0, 165 mapping units have been mapped at 1:25,000 scale (Department of Primary Industries and Water 2009). Most of the mapping units are ecological communities, which are clustered in eleven broad groups.

In summary, TASVEG Version 2.0 (Department of Primary Industries and Water 2009) has:

** Eleven broad vegetation groups/categories;

** 165 mapping units (mostly ecological communities) spread across these groups. Each of these mapping units has a unique three letter code; and

** A variable number of floristic communities known to occur within each mapping unit, which are not separately mapped. These are limited to those covered by State-wide assessments of the respective vegetation type (as described in Harris and Kitchener 2005).

Vegetation maps are dependent on the underlying classification of vegetation types and the resolution and accuracy of the data. The TASVEG state-wide map is derived principally from three streams of mapping: the State's Regional Forest Agreement process (see Lynch and Neldner 2000), World Heritage Area mapping and the Tasmanian Vegetation Mapping Program mapping of primarily non-forest vegetation. A more detailed description of the characteristics of TASVEG, including the source and accuracy of the underlying data, can be found in Harris and Kitchener (2005) and Department of Primary Industries and Water (2009).

Box 2: Some brief background on TASVEG, the integrated vegetation mapping program developed by the State government and widely used in Tasmania.

Nine dominant eucalypts are described in the 'wet eucalypt forest and woodland' group in TASVEG (Harris and Kitchener 2005), which is used as the basis for the map in Figure 2b. Understorey species can be dominated by tea-trees (*Leptospermum* species), paperbarks, broad-leaved (soft-leaved) shrubs (e.g. *Bedfordia, Pomaderris, Olearia*) or rainforest species. Mixed forest types sit within the 'wet eucalypt forest and woodland' major group in TASVEG. Three of the 18 mapping units in this group explicitly map rainforest with a eucalypt overstorey: WDR – *Eucalyptus delegatensis* forest over rainforest; WOR - *E. obliqua* forest over rainforest; and WNR - *E. nitida* forest over rainforest. WDR is widespread and common, especially in the western half of the State, although it is largely absent from the far south west; WOR is widespread in the higher rainfall areas of Tasmania where fire frequency is low (with a stronghold in the south-west), and WNR is widespread in south-west and western Tasmania (Harris and Kitchener 2005). The distribution of *E. regnans* is restricted to the central south and north east of the state.

A number of other mixed forest communities, including *E. regnans*, are identified in Harris and Kitchener (2005). These are listed under different mapping units such as *E. obliqua* wet forest (undifferentiated) (WOU) and *E. regnans* forest (WRE) and are not explicitly mapped in TASVEG. For example, the description of WOR lists 8 floristic communities classified as mixed forest which are not mapped in TASVEG. As a consequence, TASVEG has most use for mapping the distribution of vegetation at a relatively broad scale for these wet eucalypt forests. Despite these constraints, TASVEG mapping can be used to illustrate the nature of the mosaic of rainforest and other vegetation. Two examples are provided here - in north-west (Figure 3) and south-west (Figure 4) Tasmania.

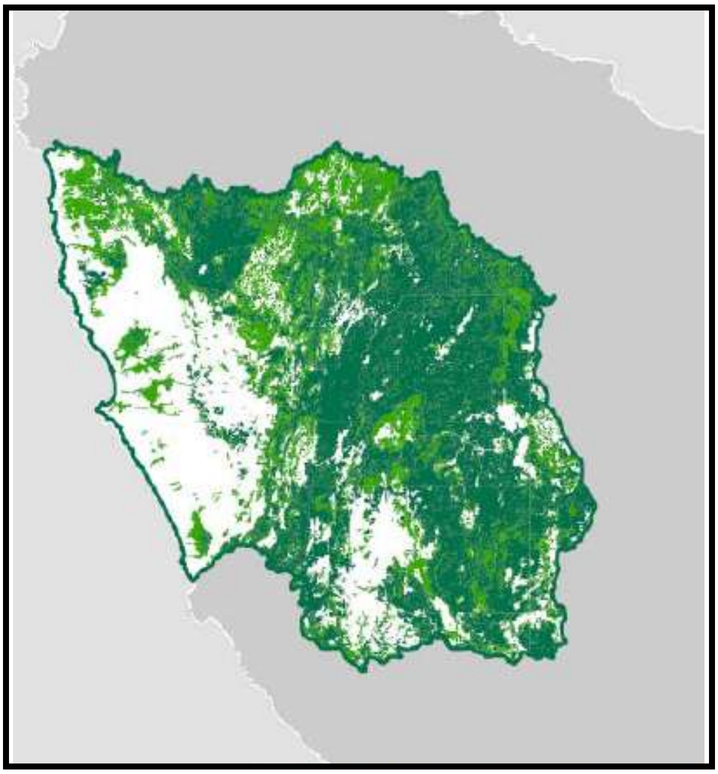

Figure 3: The mosaic of rainforest (light green) and eucalypt (dark green) forests in the Tarkine, north-western Tasmania. The Tarkine is approximately 4800 square km in area (~70 x 70 km). Source: Williams (2011).

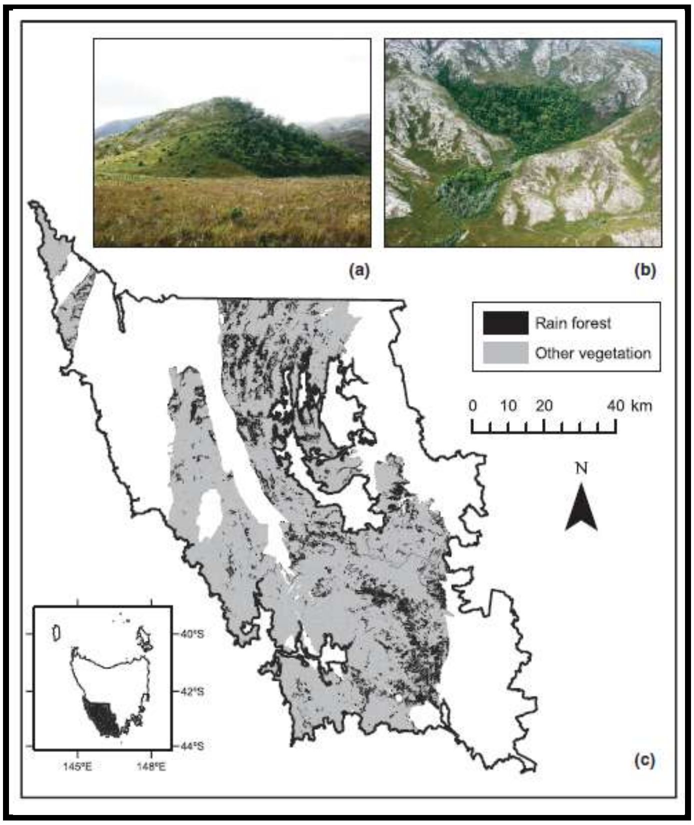

Figure 4: The mosaic of rainforest (black) and other vegetation (grey) in south-western Tasmania. a) and b) are images of topographically restricted rainforest and wet sclerophyll forest in the region. Source: Wood *et al*. (2011).

Community and species descriptions

Tasmanian cool temperate rainforests support a diverse range of vegetation types (see 'Forest distributions' above). The rainforest communities are characterised by their endemic animals (principally invertebrates) and plants (Kirkpatrick and DellaSella 2011). For example, both the thamnic and implicate rainforests of Tasmania are noted for their endemic podocarps and cypresses such as *Lagarostrobos franklinii* (Huon pine) and *Phyllocladus asplenifolius* (Celery top pine). The two species of *Athrotaxis* found in Tasmanian rainforests are the only living members of the tribe Athrotaxeae in Cupressaceae that diverged before the *Sequoia* group of genera (Gadek *et al.* 2000). As well as exhibiting high level of endemism and providing habitat for primitive relict genera of flora and fauna, the rainforests are rich in non-vascular plant species (Balmer *et al*. 2004).

Parks & Wildlife Service (2011) provide an overview of the animals that occur in rainforest communities in Tasmania. Mammals found include the endemic long-tailed mouse (*Pseudomys higginsii)*, ringtail possum (*Pseudocheirus peregrines*), pademelon (*Thylogale billardierii*), spotted-tailed quoll (*Dasyurus maculatus* ssp. *maculates*) and dusky antechinus (*Antechinus swainsonii*). Twenty-one species of native birds regularly visit rainforests, including the black currawong (*Strepera fuliginosa*), green rosella (*Platycercus caledonicus*)(endemic to Tasmania and Bass Straight islands), olive whistler (*Pachycephala olivacea*) and grey goshawk (*Accipter novaehollandiae*). As noted below, rainforest is one of several habitats used by many of these species. Of the reptiles, the endemic Tasmanian tree frog (*Litoria burrowsae*), tiger snake (*Notechis scutatus*) and brown skink are relatively common. Tasmanian rainforest also contains some of the most ancient and primitive invertebrates. These include the large land snail, Macleay's swallowtail butterfly (*Graphium macleayanum*), giant freshwater crayfish (*Astacopsis gouldi*) and the threatened peripatus, or velvet worm (*Tasmanipatus barretti*) (Balmer *et al*. 2004, Parks & Wildlife Service 2011). The Tasmanian giant freshwater crayfish is the largest freshwater invertebrate in the world. The species is only found in Tasmania and is listed as a vulnerable.

Turner *et al.* (2011) note that bryophytes constitute much of the plant biodiversity in Tasmanian mixed forests dominated by *Eucalyptus regnans* and *Eucalyptus obliqua*. These authors identified 236 bryophyte species (104 mosses, 132 liverworts) across three different age classes of eucalypt forest. The break down in each of the age classes are shown in Table 2. Packham *et al.* (2002) also demonstrated a high diversity of macro-fungi (242 taxa) in regrowth and old-growth mixed forests dominated by *Eucalyptus obliqua* and *E. delegatensis*. In this case, distinctly different macrofungal floras were found in regrowth and mature forest, with approximately 40% of the taxa in each forest type being restricted to that type of site.

Forest age class	**Age class (years since disturbance)**	**No. of moss species**	**No. of liverwort species**
Young	1-8	39	27
Middle	31-39	68	74
Old	>110	65	75

Table 2: Number of bryophytes identified in three age classes of eucalypt mixed forest in Tasmania. Source: Adapted from Turner *et al.* (2011).

Even though it is only a single species, some of the wet sclerophyll and mixed forests in Tasmania contain the largest flowering plant in the world - *Eucalyptus regnans* (Swamp Gum) (Kirkpatrick and DellaSella 2011, Tng *et al.* 2012). What the eucalypts lack in diversity they make up for in size and age. *E. regnans* can grow to over 100 metres in height and live to at least 500 years of age (Wood *et al*. 2010). The authors showed that the stem growth rates of *E. regnans* in the first 100 years were very rapid compared to the co-occurring rainforest understorey species *Phyllocladus aspleniifolius*, with over half of the stem diameter growth of *E. regnans* occurring in the first ninety years. Tng *et al.* (2012) propose that eucalypt species such as *E. regnans* should be considered pioneer rainforest species where they grow to over 70 m in height and have a rainforest understory. Read and Hill (1988) note that *P. aspleniifolius* has been recorded to 750 years of age and *Athrotaxis selaginoides* (Pencil Pine) to 2000 years. *Lagarostrobos franklinii* (Huon Pine) is another long-lived rainforest species with a known maximum age in excess of 2000 yr (Tasmanian Parks & Wildlife Service, http://www.parks.tas.gov.au/veg/pines.html).

Some of the faunal species found in wet eucalypt forests include the little pygmy possum (*Cercatetus nanus*), spotted tail quoll (*Dasyurus maculatus* ssp. *maculatus*), Tasmanian devil (*Sarcophilus* *harrisii*), long nosed potoroo (*Potorous tridactylus* ssp. *apicilus*), southern brown bandicoot (*Isodoon obesulus*), scrub tit (*Acanthornis magnus*) and yellow-tailed black cockatoo (*Calyptorhynchus funereus*) (Parks & Wildlife Service 2011). Tree hollows formed in large eucalypt species such as *E. regnans* are essential for species such as the yellow-tailed black cockatoo (Nelson and Morris 1994). Both wet and dry sclerophyll eucalypt forests (dominated by *Eucalyptus globulus*) provide important feeding areas for the endangered Swift Parrot (*Lathamus discolor*) on the species' annual migration to mainland Australia (Driessen and Mallick 2003, Balmer *et al*. 2004). Kirkpatrick and DellaSella (2011) note the large size of faunal species such as the endangered Wedgetail Eagle (*Aquila audax* ssp. *fleayi*) and the largest freshwater crustacean in the world (*Astacopsis gouldi*) that both frequent rainforests. While many of the species listed here utilise other vegetation types, both rainforest and/or associated wet sclerophyll forests are an important component of their habitat. Wet sclerophyll and mixed forest for example is part of the core habitat of the Grey Goshawk (*Accipter novaehollandiae*) along with blackwood swamps and riparian forest (Tasmanian and Australian Governments 2007).

Evolutionary history

The evolutionary history of Tasmanian rainforests spans tens of millions of year. Tasmanian cool temperate rainforest has affinities with rainforests in south-east Australia, New Zealand and the Andean region of southern Chile and Argentina (Harris and Kitchener 2005), reflecting the Gondwanic origin of many of the plant species (Balmer *et al.* 2004, Kirkpatrick and DellaSella 2011). As Australia finally split from Antarctica around 45 million years ago and drifted north, a drying climate - set against a background of nutrient-deficient soils - led to a transformation from extraordinarily diverse rainforest biomes across most of the continent through to predominantly desert biomes today (Hill 2004). Fire activity also increased over this period. Byrne (2011) argues that investigating the impacts of these and other processes on mesic zone biota (rainforests and open sclerophyllous forests) is critical to understanding the evolution of Australia's biodiversity.

Palaeobotanical studies have shown that the ancestors of most component taxa of Australian rainforests date back to the Cretaceous or early Tertiary (e.g. around 120 – 60 Ma), at least at the generic level (Lynch and Neldner 2000). The extant temperate rainforests of Tasmania contain several primitive gymnosperms and angiosperms (Lynch and Neldner 2000). Particularly ancient genera with fossil and pollen evidence to support their presence and evolution within Tasmania include *Agastachys, Athrotaxis, Anopterus, Archeria, Bellendena, Cenarrhenes, Dicksonia, Eucryphia, Phyllocladus, Microcachrys, Microstrobos, Nothofagus, Orites, Lomatia, Tasmannia* and *Telopea* (Parks & Wildlife Tasmania 2011). The rainforest taxa includes both gymnosperms and angiosperms with a range of phylogenetic histories. It was not possible to address these evolutionary histories separately in this review.

As the Australian continent moved north during the Tertiary new, more sclerophyllous plant characteristics evolved to cope with the new environmental conditions. Several rainforest genera are considered to have some affinity with the eucalypts. Wrigley and Fagg (2010) state that fossil evidence of eucalypts in Australia found at least far back as 45 Ma in South Australia. This reference to fossil eucalypt fruits is taken from Mary White's book, The Greening of Gondwana (White 1998). Rozefelds (1996) notes uncertainty around the dating of these fossils, placing them between around 32-42 Ma. Steart *et al*. (2005) dates the earliest reliable *Eucalyptus* leaf fossil locality to the Late Oligocene in Victoria (around 27 million years, see further discussion below). More recent eucalypt fossil examples include leaves and fruit from 20 million years ago and a tree stump dating 22 Ma in New South Wales (Wrigley and Fagg 2010). Byrne *et al*. (2011) compliment the fossil evidence by utilising molecular phylogenetic and phylogeographical data. Based on this evidence, these authors propose that the eucalypts and a range of other taxa had mesic zone origins at least 30 Ma or earlier. Taking this timeline back further, the Commonwealth of Australia (1999) postulated Gondwanic affinities for the ancestral eucalypts. This conclusion was strongly supported by the discovery of a eucalypt macrofossil, consisting of leaves and fruits, in Patagonia, South America (Gandolfo *et al.* 2011). Paleoecological data indicate that the Patagonian *Eucalyptus* dominated volcanically disturbed areas adjacent to standing rainforest surrounding an Eocene caldera lake, with the fossil deposit dated to 51.9 Ma.

The pollen record in Australia shows a radiation of sclerophyllous taxa such as eucalypts, with progressive transitions from rainforest to wet sclerophyll forest to dry sclerophyll vegetation - followed by a relatively sudden transition to open sclerophyll vegetation - during the period from the Mid Miocene (17 Ma) to the Late Pliocene/Pleistocene (about 2.2 Ma) (Commonwealth of Australia 1999, Kershaw *et al.* 2002). Recent molecular phylogenetic analysis (Crisp *et al.* 2004) overlap with these dates, showing rapid radiations in sclerophyll taxa such as *Banksia*, eucalypts, pea-flowered legumes and *Allocasuarina* during the Mid-Cenozoic (25-10 Ma). Hill (2004) proposes that vegetation changes during the Late Miocene (ca. 11–5 Ma) probably reflect wet sclerophyll communities, possibly with a myrtaceous canopy above an understorey including some rainforest taxa. These communities were thought to be similar to living vegetation (mixed forests) bordering north Queensland rainforests. Kershaw *et al*. (2002) places the appearance of wet sclerophyll forest with rainforest understorey in the Murray Basin at around the Mid Miocene, at 15 Ma. Steart *et al.* (2005) describe a fossil site at Berwick in Victoria with both eucalypt and *Nothofagus* present dating back to the Late Oligocene. Rozefelds (1996) placed this site around 27 Ma. Pole *et al.* (1993), who gave a younger date for the site (~22 Ma) were in little doubt that the flora at Berwick Quarry represents a mixture of rainforest and open forest taxa and that the vegetation was probably a mosaic of open and closed forest. The re-evaluation by Steart *et al.* (2005) proposed that *Nothofagus* did not dominate the original vegetation at Berwick Quarry and that *Eucalyptus* may have been more common than previously considered. A low altitude site in north-eastern Tasmania dated at around 22 Ma had no evidence of eucalypts, which may have indicated a wetter environment influenced by nearby mountains (Pole *et al.* 1993).

While our understanding of the evolution of eucalypt species continues to grow, especially given new analytical techniques, it is likely that wet eucalypt forests and mixed forests have existed widely in some form in Australia for at least 10-15 million years. Given that there is strong fossil evidence *Nothofagus* and eucalypts co-existed as long ago as 27 Ma (Steart *et al*. 2005), certain vegetation associations go back even further in some parts of Australia. The recent discovery of eucalypt macro-fossils associated with rainforest species in Patagonia, and new phylogenetic analyses (e.g. Crisp *et al*. 2011), raise many questions about the evolution and interaction of eucalypt and rainforest taxa. These and other studies point to a longer and more geographically diverse evolutionary history for eucalypts than previously thought. Crisp *et al*. (2011) for example concluded that their analysis probably pushes back the existence of fire dependent communities dominated by eucalypt progenitors to 60-62 million years ago – some 50 million years earlier than documented elsewhere.

Based on the pollen record, Rozefelds (1996) suggests that the eucalypts have been in Tasmania for at least the last 20 million years. Macphail (1996), for example, recorded eucalypt-type pollen in North-Western Tasmania in a site dated around 17 Ma. Well documented macro fossils of eucalypts, which can increase our understanding of their evolution, are rare occurrences - especially in Tasmania (Jordan and Hill 2002, Greg Jordan personal communication). Hill and MacPhail (1985), based on pollen fossils, proposed eucalypts may be become established in south-western Tasmania by the late Pliocene-early Pleistocene (around 2-3 Ma). McKinnon *et al*. (2001) propose broadly similar figures, stating that two of the Tasmanian eucalypt lineages appeared to have diverged between 3.0–0.8 Ma, although these dates were difficult to determine. Although Tasmanian eucalypt species may be relatively 'new', the evolution of eucalypts in Tasmania is intimately related to the evolutionary history of eucalypts as a group overall. Even though the link is considered to be weak (Greg Jordan, personal communication), the relationship between the earlier evidence of eucalypts in Tasmania and elsewhere and extant species in the state would benefit from further exploration,

Twenty nine species of eucalypt are currently found in the state (Williams and Potts 1996, Wiltshire and Potts 2007) with 16 species and one subspecies being endemic. Of the wet sclerophyll/mixed eucalypt species of relevance to this report, *Eucalyptus nitida* and *E. delegatensis* ssp. *tasmaniensis* are endemic. The latter taxon is closely related to *E. delegatensis* ssp. *delegatensis* which occurs in NSW and Victoria. *Eucalyptus obliqua* and *E. regnans* also have a south-eastern Australian distribution. Perhaps not unexpectedly, Nevill *et al.* (2010) found distinct genetic differences in *E. regnans* populations in Victoria and Tasmania using molecular data.

The Pleistocene (2.58 Ma to 11.7 ka) was subject to a number of glacial and inter-glacial cycles. These had a major impact on the distribution of rainforest and other vegetation in Tasmania, which was one of the few regions in Australia with glaciation (McKinnon *et al.* 2004). A range of studies have addressed the impact of glaciations on plant species in Tasmania when sea levels and air temperatures were much lower. These changes saw Tasmania linked to south-eastern Australia by a 'land-bridge' multiple times, acting as an inter-change for plant and animal species including humans (Figure 5). A study of the phylogeography of *Eucalyptus regnans* (Nevill *et al.* 2010) suggested a closer genetic link between north-west Tasmania and the mainland in the last glaciations than between north-east Tasmania and the mainland. Prior to relatively recent molecular studies such as this, the eastern link between Tasmania and continental Australia via what is now Flinders Island was seen as the most likely route for gene flow. McKinnon *et al.* (2004), analysing molecular variation in Tasmanian eucalypts, strongly support the fossil evidence that major redistributions of eucalypt forests occurred during the Quaternary glacial cycles. It is proposed that these changes in distribution pattern enabled divergent species to come into contact and exchange genes through hybridisation (reticulate evolution). Similar major changes in distribution have been identified for rainforest species with Worth *et al.* (2009) proposing that the topographically diverse western half of Tasmania provided long-term buffered climates for rainforest species throughout the Pleistocene, acting as an important reservoir of genetic diversity for a range of species including *Nothofagus cunninghamii*.

The assembly of modern vegetation communities in Australia commenced around 14 ka after the last glaciation ended. This saw the re-establishment of localized rain forests in parts of Tasmania and widespread sclerophyllous communities across remaining areas (Byrne *et al*. 2011). Fletcher and Thomas (2010) argue that at the landscape scale, the distribution of vegetation types in western Tasmania has remained remarkably stable through the most recent post-glacial period. These authors posit that open moorland has dominated the landscape since the Late Glacial, while rain forest expanded at that time into areas which it occupies today. It is proposed that moorland and rainforest was held in place by regular aboriginal burning and underlying edaphic features in the landscape (Fletcher and Thomas 2010). MacPhail (2010) treats this as only one of five models that might explain the origin and current extent of buttongrass moorland in south-western Tasmania during the current interglacial period, demonstrating the ongoing debate about the distribution and evolution of Tasmanian biota in both space and time.

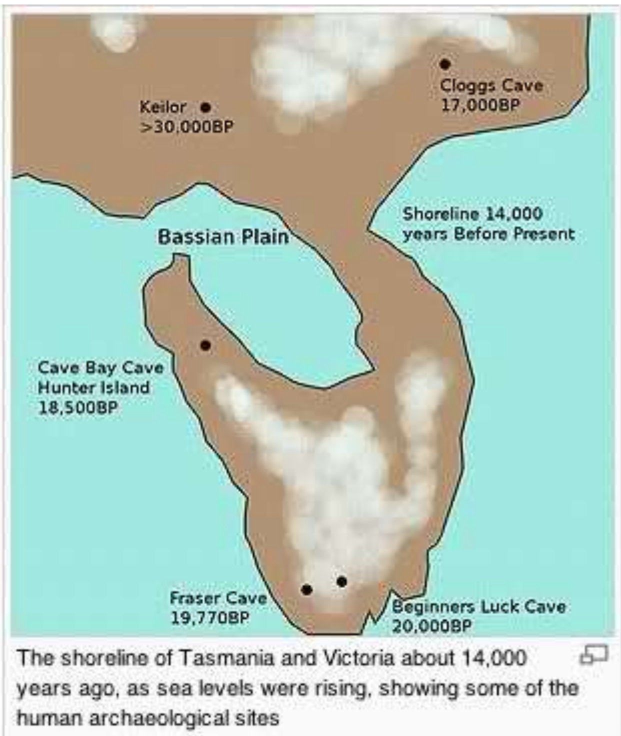

Figure 5: The shoreline showing the 'land bridge' between Victoria and Tasmania around 14 Ka. Source: en.wikipedia.org/wiki/Aboriginal_Tasmanians.

Driessen and Mallick (2003) have noted the impact of evolutionary processes such as continental drift and glacial cycles on the diversity and endemism of fauna in Tasmania. They report that vertebrate taxa well represented in western Tasmania that have clear Gondwanan links include the monotremes (the platypus *Ornithorhynchus anatinus* and short beaked echidna *Tachyglossus aculeatus*) and marsupials, the parrots (family Psittacidae), two families of frogs (Myobatrachidae and Hylidae; including the Tasmanian froglet *Ranidella tasmaniensis*, brown froglet *Ranidella signifera*, Tasmanian tree frog *Litoria burrowsi* and brown tree frog *Litoria ewingi*) and a freshwater fish family (Galaxiidae). As vegetation contracted during the glacial cycles, habitat for fauna was significantly reduced (Kirkpatrick and Fowler 1998). These changes contributed to complex faunal dynamics during glacial and inter-glacial cycles (Driessen and Mallick 2003, MacQueen *et al.* 2009). As reported by Macqueen *et al.* (2009) for example, gene flow appears to have been relatively unrestricted in the

Tasmanian pademelon (*Thylogale billardierii*) during glacial maxima in western Tasmania, while in the east there is evidence for historical expansion from at least one large glacial refuge and recolonization of Flinders Island. As noted by these authors, further studies of both sedentary, poorly dispersing fauna species and widespread, vagile species would help build a comprehensive picture of the effects of historical climate and sea level change on the biota of regions in the southern hemisphere such as Tasmania.

This section of the report demonstrates a complex series of changes in the distribution of rainforest and sclerophyll plant taxa and associated fauna in Tasmania in response to changes in, at least, rainfall, temperature, soil characteristics and fire regimes. These changes have been ongoing for tens of millions of years, with the last 14,000 years since the last glaciation being relatively stable climatically, even as human impacts have accelerated. As demonstrated, the evolution of the flora and fauna in the rainforests and wet sclerophyll forests of Tasmania are intimately tied to the environmental variability described above.

Spatial and temporal dynamics

Rainforest in Tasmania occurs in a dynamic mosaic with other vegetation types that have changed in space and time depending on the environmental conditions. The distribution of species and communities that has arisen since the last glacial is underpinned by complex processes associated with, at least, soil characteristics (including soil moisture and nutrient availability) and fire regimes. Future dynamics will see these and other factors interacting with the pervasive impact of climate change (Australian National University 2009). Current vegetation dynamics are the end result of the evolutionary history of the component plant and animal species and the landscapes they occupy. The type of vegetation model used to describe these dynamics reflects both the way people consider systems function as well as influencing the management approaches used. In turn, the way these ecosystems are managed will impact on their future evolution.

Ecologists have developed a number of models and tools to describe and understand changes in vegetation. The classic papers by Gilbert (1958) and Jackson (1968) have had a considerable influence on the models applied to rainforest/sclerophyll vegetation dynamics and the management of these vegetation types in Tasmania. Both papers were based on the Clementsian model of succession (Bowman 2000) with Jackson (1968) identifying five 'seral' stages in western Tasmania that would ultimately lead to 'climax' rainforest vegetation. While Jackson (1968) emphasised the role that fire frequency can have on modifying the successional sequence and lead to 'ecological drift', the concept of a progression of different vegetation communities on a site over time is now firmly embedded. As such, succession is the most widely used conceptual model used to describe the dynamics of rainforest and associated vegetation in Tasmania (Balmer *et al.* 2004, Harris and Kitchener 2005, Hingston and Grove 2010, Wood *et al*. 2010, Kirkpatrick and DellaSella 2011). Mount (1979) is one of the few earlier authors who presented a different model to Jackson's concept of succession, arguing instead that the interaction between fire and vegetation has led to the establishment of stable fire cycles.

Since the concept of succession was widely coined in the northern hemisphere nearly 100 years ago (Clements 1916), ecologists have argued about many aspects of the model – for example, whether succession proceeds in deterministic or indeterministic ways and the importance of stability versus change (Pickett *et al.* 2009). The role of seed banks in successional dynamics has also been debated. Authors such as Egler (1954), Connell and Slatyer (1977) and Noble and Slatyer (1981) proposed different models of succession that incorporate alternative pathways of change and multiple 'climax' states. The Alternative approaches such as state and transition models and alternative stable states have been proposed. These will be discussed further below. Ecologists have also recognised the importance of studying vegetation change at the landscape as well as the site scale, recognising that vegetation occurs in a mosaic in dynamic environments (e.g. Perestrello de Vasconcelos *et al*. 1993, Perry and Enright 2007). While the successional model is still recognised as applicable in some contexts, and has contributed some useful concepts to ecology and management, the term vegetation dynamics is becoming increasingly favoured (Pickett *et al.* 2009).

In Tasmania, the relay floristics model of succession (Figure 6) is the most widely promoted to explain the dynamics of rainforests and associated sclerophyll vegetation, although as noted elsewhere in the report there is debate about the most appropriate models to apply. The authors of the report on the floristic values of the Tasmanian Wilderness World Heritage Area (Balmer *et al*. 2004) emphasise the importance of (relay floristics) succession as an evolutionary process. The authors define succession as the gradual and orderly process of change in an ecosystem brought about by the progressive replacement of one community by another until a stable climax is established. This model is similar to the Clementsian model of succession (Clements 1916, Noble and Slatyer 1981), although with some refinements. While Kirkpatrick and DellaSella (2011) argue that the relay floristic model is the most appropriate for rainforests and mixed forests in Tasmania, they say it may not apply in all circumstances.

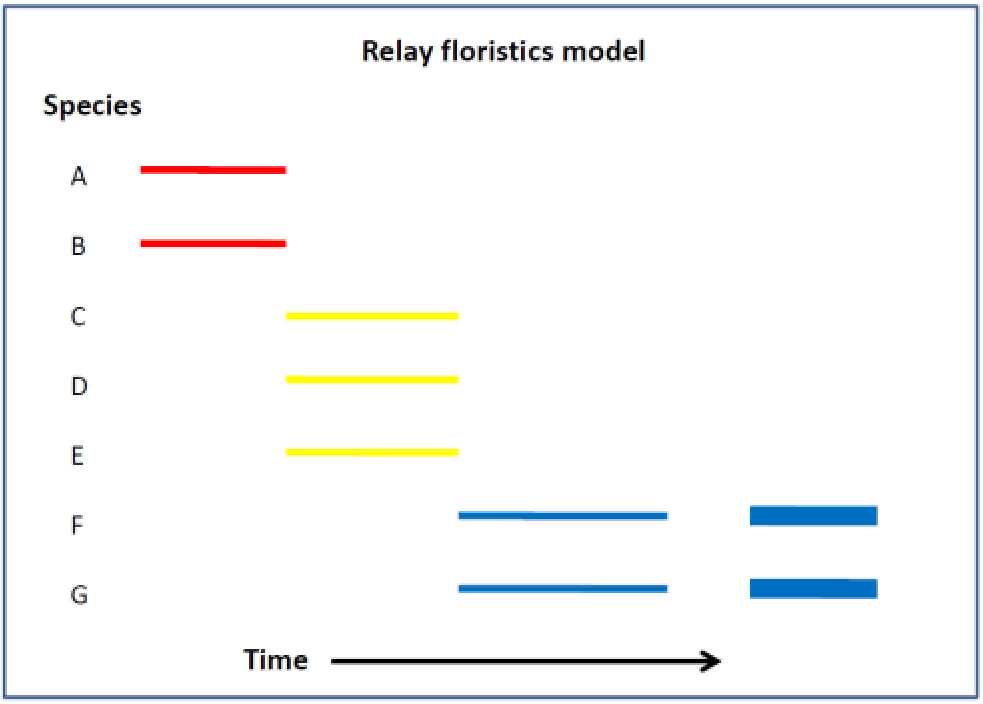

Figure 6: Diagram of Relay Floristics succession model. Red – pioneer/intolerant species; Yellow – intermediate species; Blue – climax/tolerant. Source: Adapted from the Forest Encyclopedia http://www.forestencyclopedia.net/p/p1/p1369/p1448/p1452

Balmer *et al.* (2004) further describe the vegetation succession process as follows:

> *These (succession processes) progress from the pyrogenic fire sere communities of buttongrass moorland through sclerophyll scrub, forests, mixed forest to climax cool temperate rainforest.*

This progression is illustrated in Figure 7. It is argued by Balmer *et al.* (2004) that the on-going natural processes of succession meet the Natural Criterion for inscription on the World Heritage register.

Figure 7: Successional model for cool temperate rainforest in Tasmania (based on Balmer *et al.* 2004).

The successional sequence described by Balmer *et al.* (2004) can take several hundred years. Even the process of succession from sclerophyll forests to rainforests, which is only part of the successional sequence, can take at least 500 years. The importance of the rainforest element increases within the community over time until the sclerophyll species in the understorey are replaced and a mixed forest is formed at around 110 years. Rainforest is not achieved until the disturbance requiring plant species have died out leaving only the plants able to grow and regenerate without catastrophic disturbance. This sequence means that mixed forest communities can occupy a site for several hundred years, as demonstrated by Wood *et al.* (2010) for old growth mixed forests dominated by *Eucalyptus regnans*. In this model, mixed forest is considered a successional stage from wet sclerophyll forest to 'climax' rainforest in the absence of stand replacing fires (Balmer *et al.* 2004, Harris and Kitchener 2005).

Jackson (1968) observed that different fire intervals influenced the ultimate expression of vegetation at a site, causing 'ecological drift' to different communities. As such, the successional sequence is disrupted with possible feedbacks related to soil characteristics and topography. The 'ecological drift' model has been reviewed and critiqued many times since it was formulated (e.g. Bowman 2000, Bowman and Wood 2009, Thomas *et al.* 2010, Wood and Bowman 2012). Thomas *et al*. (2010) concluded that the 'ecological drift' model best explained changes at decadal and centennial time scales, noting that scale dependency was paramount to studying these rainforest/sclerophyll systems. Wood and Bowman (2012) have re-labelled the 'ecological drift' model using the modern terminology of alternative stable states. These authors concluded that of the options explored, the alternative stable state model was the most appropriate as a framework for the vegetation mosaics in western Tasmania on nutrient poor substrates. This conclusion was based on an analysis of change from forest to non-forest using high resolution spatio-temporal data (Wood and Bowman 2012).

A significant amount of literature has been written about the alternative stable state model in the last ten years, much of it theoretical (Biesner *et al.* 2003, Van Nes and Scheffer 2004, Young *et al.* 2005, Carpenter *et al.* 2011, Marzloff *et al.* 2011, Fukami and Nakajima 2011). Broadly speaking, the alternative stable state model predicts that ecosystems can exist under multiple "states" with sets of unique biotic and abiotic conditions. When perturbed, ecosystems may transition from one stable state to another, in what is known as a state or regime shift. Due to ecological feedbacks, ecosystems display resilience to these shifts and therefore tend to remain in one state unless perturbations are large enough. It is argued that catastrophic disturbance such as fire may not be required to change states, with slower more subtle processes potentially operating over time (Biesner *et al.* 2003). A 'cup and ball' model is often used to visually represent the alternative stable states and the drivers that may underly a regime shift.

In the wet tropics, Warman and Moles (2009) have also proposed alternative stable states as a potentially useful model to describe rainforest dynamics. Taking this approach provides a different perspective on the stability/transience of mixed forests in both space and time. As noted by several authors, the alternative stable state model is not mutually exclusive to succession as it can form a framework for describing the transitions from one 'seral' state to another (Biesner *et al.* 2003, Walker and del Moral 2008, Cain *et al.* 2009).

The challenge has been raised to demonstrate the process of both succession and alternative stable states in the field. Like many ecological models, this is not as straight-forward as it may sound, especially in terrestrial landscapes with long lived species (Brown and Podger 1982, Schroder *et al.* 2005, Wood and Bowman 2012, Schooler *et al.* 2011). As with other ecological models, few studies are able to meet the criteria required to unambiguously demonstrate vegetation stability or persistence (Wood and Bowman 2012). Balmer *et al*. (2004) argue that evidence of successional dynamics in western Tasmania is provided by the spatial arrangement of each of the vegetation types in the landscape. Field studies have also been used to assess the nature of vegetation dynamics, usually aiming to test models such as Jackson (1968) or Mount (1979). Hill and Read (1984) for example supported Jackson's ecological drift model after documenting a change from rainforest to greater sclerophyll dominance after fire in mixed forest dominated by *Eucalyptus nitida*. Turner *et al.* (2011) propose that their state-wide study of bryophyte diversity in wet sclerophyll forest of different ages supports the relay floristics succession model.

A number of studies at the Warra Long-term Ecological Research site in southern Tasmania have explored the dynamics of wet eucalypt forests dominated by *Eucalyptus obliqua* (Brown *et al*. 2001; http://www.warra.com/warra/). Balmer *et al.* (2004) state that the global importance of Tasmania's successional processes was acknowledged with the establishment of the Warra long-term ecological monitoring site. Vegetation succession underpins the broad conceptual model developed for the Warra research site (Grove 2004), with many of the papers arising from the research focusing on successional dynamics (e.g. Hingston and Grove 2010). It is recommended that a comprehensive review of the different vegetation models used in rainforests, wet sclerophyll forests and mixed forests be undertaken. As noted above, there is a considerable body of research to draw on. Alternative models could also be explored. Such a review would help determine what the most appropriate models are to describe/inform their dynamics and management. Based on the literature and discussions with experts, different models are likely to apply to different circumstances.

Alternative frameworks such as the State and Transition model have been developed for systems such as the rangelands (Whalley 1994, Bestelmeyer *et al.* 2011, Schooler *et al.* 2011). Kanowski *et* *al*. (2009), in reviewing a number of vegetation models applied to primary and secondary tropical rainforest, note the widespread use of state and transition models to describe rainforest restoration. There is the potential that this could be a useful model to apply to mature rainforests and associated vegetation.

National and global significance

The significance of Tasmanian rainforests and associated vegetation communities has been recognised at the regional, national and international level (Lynch and Neldner 2000, Balmer *et al*. 2004, Kirkpatrick and DellaSella 2011). World Heritage listing was given to rainforests and associated vegetation in western Tasmania in 1982 and again in 1989. Modifications to the listing were also considered in 2010. The area that was listed for both its cultural and natural heritage is now called the Tasmanian Wilderness World Heritage Area (TWWHA) (Tasmanian Government 1999, 2007).

The criteria used to assess World Heritage significance of natural systems are listed in Box 3. A number of publications have been prepared that highlight the natural significance of the region, as well as additional values that could be considered (e.g. Driessen and Mallick 2003, Balmer *et al.* 2004, Law 2009). The determination made by the World Heritage committee, and subsequent reviews of the status of the listing, also provide insights into the significance of listing these forests (IUCN Evaluation report 2010, World Heritage Committee 2010).

World Heritage Convention - natural criteria (http://whc.unesco.org/en/criteria/)

* to contain superlative natural phenomena or areas of exceptional natural beauty and aesthetic importance;

* to be outstanding examples representing major stages of earth's history, including the record of life, significant on-going geological processes in the development of landforms, or significant geomorphic or physiographic features;

* to be outstanding examples representing significant on-going ecological and biological processes in the evolution and development of terrestrial, fresh water, coastal and marine ecosystems and communities of plants and animals;

* to contain the most important and significant natural habitats for in-situ conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of science or conservation.

The protection, management, authenticity and integrity of properties are also important considerations.

Box 3: Natural criteria to assess listing under the World Heritage Convention.

Balmer *et al.* (2004) reviewed the floristic values of the TWWHA as new information had come to hand and the criteria for listing had changed since the original nomination. The authors focused on values that were found to meet the World Heritage listing criteria or recognised as nationally important. The values they identified include those listed below. Some commentary is also provided against some of the values.

- Tasmania represents a major centre of distribution for cool temperate *Nothofagus* rainforest in the world.
- Tasmania's cool temperate rainforests provide habitat for primitive relict genera of flora and fauna flora;
- Cool temperate rainforests are rich in non-vascular species and exhibit high levels of endemism among seed plants, especially woody species;
- The importance of on-going natural processes of succession within the vegetation. The authors claim that the natural succession from moorland through sclerophyll forests to rainforests is considered an internationally significant example of seral succession. Considerable emphasis is placed on successional processes in the report;
- Tall open-forest communities provide visually majestic examples of mixed forest with eucalypts towering up to 86 m above a rainforest understorey. It is noted that most of the forests with immensely tall trees fall outside of the World Heritage area but also that there are forests in the TWWHA that have the potential to produce very tall trees;

- The best examples of mixed forest within a wilderness context are found within the TWWHA. These forests have the greatest species richness and highest levels of endemism of any mixed forest in Australia.

Kirkpatrick and DellaSella (2011) identified a number of globally significant attributes for Australasian temperate rainforests (incorporating mixed forests). The attributes that are relevant to Tasmania include:

- Ancient Gondwanan affinities shared with South African and Chilean temperate rainforests with many species remaining unchanged for millions of years;
- Large intact areas providing unimpaired ecosystem and evolutionary processes and high levels of ecological integrity;
- Trees up to 2000 years old, rivalling California redwoods and Chilean *alerce* forests, that provide specialist habitat and carbon-dense forests;
- Unusually large organisms such as eucalypts, the wedge-tail eagle and the giant freshwater crayfish (all found in Tasmania);
- A global "hotspot" for endemic taxa, including many vascular plants, invertebrates, amphibians, reptiles, birds and mammals; and
- Mixed forests, treeless moorlands and rainforest in close proximity, providing high levels of beta diversity (species turnover across environmental gradients).

Many of the attributes in these two lists overlap. For example, having large natural area for natural and evolutionary processes to occur is considered critical. To support such inventories, detailed work has been undertaken to identify, amongst other things, the significance of eucalypts in the context of the World Heritage Convention (Commonwealth of Australia 1999). Some of the factors identified as contributing to the outstanding universal value of the eucalypts are of relevance to the evolutionary significance of rainforest and associated sclerophyll forests:

- their ancient Gondwanan origins and their subsequent evolution which parallels the geological and ecological history of the Australian continent (also see Gandolfo *et al.* 2011, Crisp *et al*. 2011);
- their success in dominating the majority of woody ecosystems throughout an entire continent;
- the diversity of their growth forms which range from the tallest hardwood forests in the world to prostrate shrub forms;
- the wide diversity of the communities which they dominate; and
- their unique ecology.

A 'new' value that has gained considerable attention recently is the ability of rainforests and wet/mixed forests to capture and store carbon. This interest has been driven by emerging carbon markets as a response to mitigate some of the impacts of anthropogenic climate change. Kirkpatrick and DellaSella (2011) describe the major role that temperate rainforests (including mixed forests) play as a carbon store. Much of the rainforest of western Tasmania, for example, grows on 1–2 meters of red fibrous peat sitting on quartzite, with large amounts of carbon also trapped in individual giant eucalypts, their understory, litter, and soils. Accurately modelling carbon storage in systems such as these, both above and below ground, requires detailed information that is specific to different vegetation types (Smith 2010, Berry *et al.* 2010). Attempts to model above and below ground carbon storage in the eucalypt forests of south eastern Australia (Mackey *et al.* 2008) showed a large amount of variation in carbon stocks due to the influence of environmental variables, natural disturbance regimes and lack of field data. These and other reports can contribute to the growing discussion about how to accurately represent carbon sequestration and storage in these forests.

Because most of the data on tree biomass and growth is available for eucalypt species used in forestry, the majority of work on carbon stocks in mixed forest to date has been on species such as *Eucalyptus regnans*. Recent publications such as Keith *et al*. (2009) report that old-growth mixed forests of Australia and Tasmania, in particular, are among the world's most carbon-dense forests (on average 1,867 tonnes of carbon per hectare). The potential impacts of climate change and management practices on the carbon stocks of these forests are explored by authors such as Dean and Wardell-Johnson (2010) and Moroni *et al.* (2010). Some of the complexities of measuring carbon stocks in forests and the impact of management practices are demonstrated by the correspondence between Dean (2011) and Moroni *et al.* (2012).

Tall eucalypt forests with rainforest understoreys are one of unique associations that have evolved in response to the major environmental changes in Australia's past. Tng *et al.* (2012) suggest that gigantism has evolved at least seven times within *Eucalyptus* with all of these events occurring in the last 20 million years or potentially more recently. Authors such as Worth *et al*. (2009) and Byrne *et al*. (2011) have identified other unique evolutionary processes associated with rainforest and eucalypt dominated forests, such as the markedly different patterns of recolonisation of plant and animal species following glaciation in south-eastern Australia/Tasmania compared to the temperate biota of the northern hemisphere.

Reservation status

Balmer *et al.* (2004) give the following statistics for the reservation of tall eucalypt wet forest in the Tasmanian Wilderness World Heritage Area. These figures are based on TASVEG Version 1.0 mapping, which is described in the section on forest distributions.

- 67% of *Eucalyptus nitida* wet forest;
- 42% of other wet forest;
- 23% of *E. delegatensis* wet forest*;*
- 6% of *E. obliqua* wet forest*, and*
- Less than 5% of tall *Eucalyptus regnans* forest.

Turner *et al.* (2011) state that the reserved area of mixed forest dominated by *Eucalyptus regnans* forest and tall *Eucalyptus obliqua* may be inadequate to ensure the future of any biota dependent on the old growth stage of these two communities because of the high stochastic component in the incidence and area of fires. The IUCN (IUCN Technical Evaluation 2010) has consistently noted that there are areas of old growth *Eucalyptus* forest adjoining the Tasmanian Wilderness World Heritage Area which have the potential to be added to the property because of their outstanding values.

About 41% of Tasmania's rainforests are reserved in the Tasmanian Wilderness World Heritage Area (TWWHA) (Balmer *et al.* 2004, Parks & Wildlife Service Tasmania 2011). The best examples of implicate (short, tangled vegetation) and thamnic rainforests (shrubby understorey) which are richer in endemic species occur in the TWWHA. Another 25% of rainforests occur in other reserves around the state. Much of the rainforest of the north-west lies outside reserves (Figure 8). Of the rainforest outside of reserves, much occurs in the Tarkine, an area bound by the Arthur River and its tributaries to the north, the Pieman River to the south, the Murchison Highway to the east and the Southern Ocean to the west. The Tarkine crosses several catchments and, depending on the boundaries used, has an area of at least 477,000 hectares (approximately 4800 square kms). The Tarkine contains rainforest covering around 177,000 hectares making it the second largest area of cool temperate rainforest in the world and the largest in Australia. Figure 9 shows the Western Explorer Road that has increased access to the Tarkine. The building of this road was controversial due to concerns such as the potential impact of increased four wheel drive access and more frequent fires.

As with the TWWHA, the large and intact ecosystems found in the Tarkine (Figure 10, Michaels *et al*. 2010) play a significant role in maintaining ecosystem stability and resilience, providing habitat for a myriad of biota, and supporting the potential for natural selection and evolution (Williams *et al.* 2010). As noted in Figure 10, intact catchments are those with over 90% of native vegetation remaining. Eucalypt forest, cool temperate rainforest and sedgelands are the dominant communities in the Tarkine (Williams 2010). Over 400 plant species exist within the Tarkine, including a number of significant species and Threatened/priority wetlands. Despite its significance, relatively few scientific publications are available that examine the ecology of the region. The region also has highly significant Indigenous values and has been described by the Australian Heritage Commission as one of the world's great archaeological regions (Cradle Coast Authority 2008, 2009).

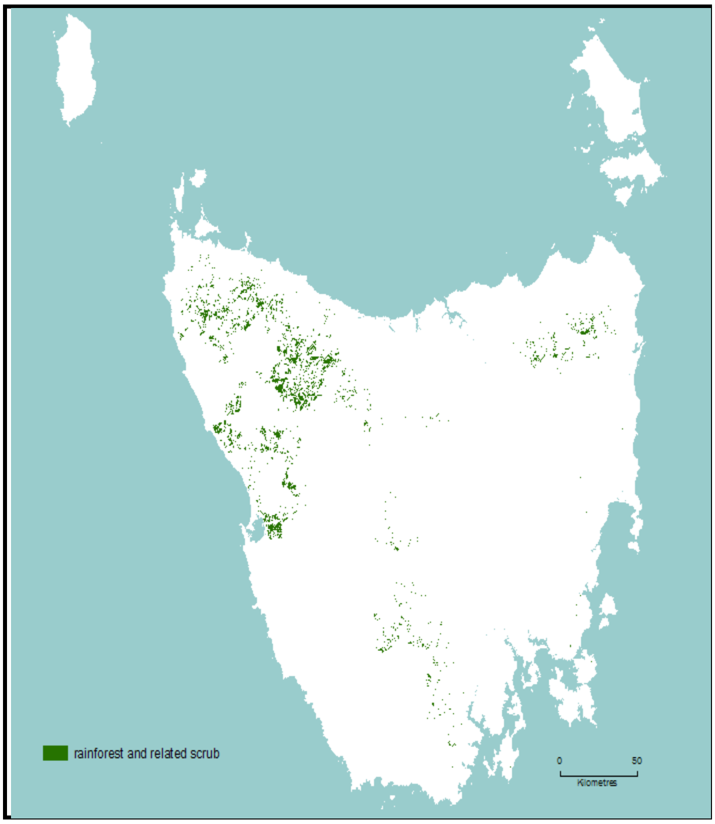

Figure 8: Non-reserved rainforest and related scrub in Tasmania. Source: Tasmanian Government (2009).

Figure 9: The Western Explorer Road running through the Tarkine, north west Tasmania.

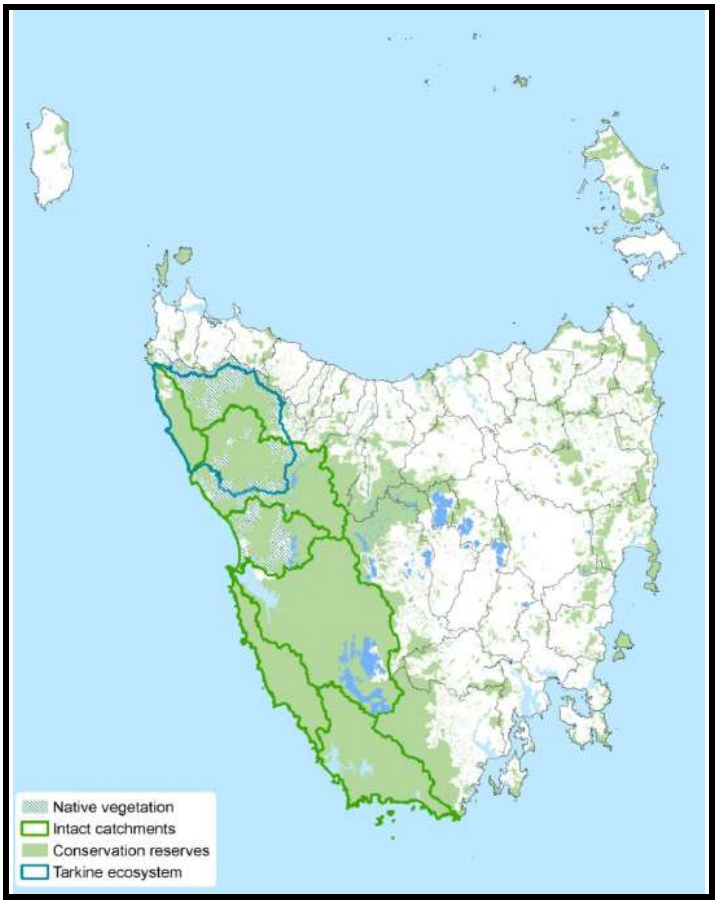

Figure 10: Tracts of large, natural and near-natural terrestrial ecosystems contiguous or near-contiguous in western Tasmania. The Tarkine boundary is shown in blue. Intact catchments represent >90% of native vegetation remaining. Base data theLIST © State of Tasmania. Source: Williams *et al.* (2010).

Most of the Tarkine's land area is managed by Forestry Tasmania or the Tasmanian Parks & Wildlife Service under State and Australian Government legislation, intergovernmental agreements and formal planning processes (Williams 2011). Parts of the Tarkine fall under the statutory planning authority of the Circular Head, Waratah-Wynyard and the West Coast councils. Significant natural areas in the Tarkine are protected to varying degrees in the Savage River National Park, Arthur Pieman Conservation Area, Pieman River and Hellyer Gorge State Reserves and Meredith Range Regional Reserve. Smaller areas are managed under a range of state, regional and forest reserves, conservation and recreation areas. In order to provide greater protection, nominations for Natural Heritage listing, National Park and World Heritage status are being promoted, assessed or developed ((The Tarkine National Coalition (http://www.tarkine.org/), Williams 2011). One of the issues of concern for the future conservation and management of the Tarkine is the presence of mineral leases over much of the area.

Conclusions

This review supports and provides additional material on the significance (evolutionary and other) and values of Tasmanian rainforests and associated vegetation types. Recent molecular and phylogenetic analysis of the eucalypts, as well as an important fossil discovery in South America, are leading to a reassessment of the timelines for the evolution of both the eucalypts and their ancestors and fire dependent communities. Plant species expansion, distribution and interactions during the glacial-interglacial cycles have been found to show different patterns compared to the northern hemisphere. Importantly, rainforests with an overstorey of giant eucalypts (>70 m in height) have been shown to be globally unique. This new information adds to the values already identified for these ecosystems, including their importance for carbon sequestration and storage. It also reinforces the importance of maintaining intact landscapes to support the evolutionary processes underpinning these ecosystems.

Summary of expert opinion

Appendix 1 lists the names and affiliations of a number of experts who were consulted about various aspects of this project. Their combined experience represented an in-depth understanding of the dynamics of rainforests and associated vegetation, both within and externally to Tasmania.

The ecology of vegetation with a tall eucalypt overstorey and rainforest understorey, and whether it should be defined as a separate community, was of particular interest to the experts. Three experts believed that at least some of these forests should be classified as rainforests: two stating that the tall eucalypts were functionally equivalent to pioneer rainforest species and the second that the similarity in species composition of the two forest types meant they should be included in the same community. There is broad agreement on the significance of rainforests and mixed forest, both evolutionary and ecologically. The point of debate is whether they should be treated as a separate vegetation community.

Opinions about the most appropriate model to describe the vegetation dynamics of these systems varied, mostly between the relay floristics model of succession and the alternative stable states model. The section in the report on ‘Spatial and temporal dynamics’ describes these two models in greater detail. These differences of opinion are common within the scientific community, as demonstrated by the large number of papers published on these topics in the scientific literature. Further testing of the most appropriate model under different circumstances is required using field data at a range of spatial and temporal scales. Whichever model is underpinning vegetation dynamics, it was agreed that large intact areas are required for these ecological processes to play out.

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Appendix 1: Record of discussions with relevant experts.

Name	Affiliation	Main discussion points
Professor Aila Keto	Australian Rainforest Conservation Society	Professor Keto believes that Clementsian succession is largely not relevant to rainforest and associated communities. Alternative stable states/regime shifts is the most appropriate conceptual framework including concepts such as thresholds and resilience; multiple drivers of change are involved; subtle changes can have major impacts over evolutionary time. She is interested to know if the rainforest with tall eucalypts represents a stable (rather than transitional) state, possibly reflecting an early transformation from ancestral rainforest and do they merit World Heritage status? Professor Keto supports the view that eucalypts emergent over rainforest are in many instances functionally similar to rainforest species and that these forests should be classified as rainforest.
Professor Brendan Mackey	Griffith University	Professor Mackey noted that rainforests with emergent eucalypts are found from Tasmania to northern Queensland. These were more common in the past, having been cleared and modified by logging in the last couple of hundred years. Sees the large eucalypts as a vital element of these systems.
Professor Dave Bowman	University of Tasmania	Professor Bowman stands by his book on rainforests published in 2000 – that the main characteristic defining them is that they are intolerant of recurrent landscape fires. He is co-authoring a paper on giant eucalypt forests, identifying them as globally unique. Comparable forests in the northern hemisphere are dominated by slow growing pines whereas species such as *E. regnans* put on most of size in the first 100 years. There may be an argument for convergent evolution of these giant forests in Tasmania, northern Queensland and south-west WA. He supports the alternative stable state model as the most appropriate for rainforest/ sclerophyll forest dynamics although notes other processes are also in play. Has not explored State and Transition models as a possible alternative as this has not widely been applied to rainforest/ sclerophyll forest systems. Professor Bowman said that many of his current ideas would be encapsulated in the paper on giant eucalypts which was provided on January 19th. This presented forests with a rainforest understorey and emergent 'giant' eucalypts (> 70 m) as globally unique and that the eucalypts were functionally equivalent to rainforest species (for

		further details see text).
Name	**Affiliation**	**Main discussion points**
Professor Jamie Kirkpatrick	University of Tasmania	Professor Kirkpatrick says that mixed forest should be classified as rainforest given the similarity in plant species composition. Does not feel that having large emergent eucalypts in a system, sometimes for hundreds of years, is enough to define mixed forests as a separate community. He believes that the relay floristic succession is the most appropriate model to describe rainforest dynamics in Tasmania, especially the transition of sclerophyll forests to rainforest. Evidence for succession is evident in the field, for example rainforest having downed large eucalypts. Large areas are required to conserve the range of successional stages. Professor Kirkpatrick believes that the alternative stable state model may apply to rainforests in other states, or to button grass moorlands, but not to rainforest in Tasmania. If the alternative stable state model did apply, the different forest types would be over-reserved as the vegetation communities would stay as they are.
Mr Peter Hitchcock	OC Consulting	Mr Hitchcock believes that tall eucalypt forests are globally significant due to their rarity, size, evolutionary history etc. Their conservation and management has been overshadowed to some degree by a focus on rainforests. Eucalypts are a much older lineage than many give credit to, going back to Gondwanan ancestry. Sees the setting aside of large areas to support natural processes is a key component of any conservation strategy.
Dr Greg Jordan	University of Tasmania	This discussion focused on the evolution of eucalypts. Dr Jordan thought that it was possible that eucalypt type species had been in Tasmania for at least 20 million years. A large gap in the fossil record between around 17-3 million years made it difficult to address this question. Even if we knew more about the ancestral eucalypt species on the island, the link with extant species is thought to be weak. For example, Dr Jordan thought that the endemic eucalypt species, which represent around half of the eucalypts in Tasmania, are only around 1 million years old. The impact of glaciations over the last 2 million years or so, and interactions with eucalypts on the 'mainland', appear to have had a major impact on the evolution of species in the state.