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Effect of landscape fires on the demography of the endangered New Caledonian conifer *Callitris sulcata*

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ABSTRACT

New Caledonia is a global biodiversity hotspot and an epicentre for Gondwanan conifers, many of which are threatened by mining and by altered fire regimes. We studied the distribution, abundance and demography of the endangered *Callitris sulcata*. The largest populations are restricted to one river system in the south-east of the island, with satellite populations in adjoining rivers. The local distribution is controlled by the fire protection afforded by terrain features such as scree slopes, creeklines and small cliffs. Adult trees, which have comparatively thick bark, are able to tolerate and recover from infrequent surface fires, but severe fires kill trees and the seeds they store, a pattern similar to that in many Australian *Callitris* species. Radiocarbon dating revealed the species is slower growing than Australian *Callitris* species, possibly due to the extreme infertility of the ultramafic soils. The species is of high cultural value to the indigenous population who also prizes the durable and aromatic timber, and harvests have been traditionally regulated. Illegal cutting of trees has become a problem, but uncontrolled fires, which have caused substantial population declines, dwarf this threat. Given these threats, conservation of the species hinges on ensuring some populations remain remote and rarely visited by humans.

1. Introduction

New Caledonia, an archipelago located 1300 km east of Australia, is a biodiversity hotspot (Myers et al., 2000; Mittermeier et al., 2004). It contains 3371 indigenous vascular species, of which 74.7% are endemic, one of the highest endemism rates in the world (Morat et al., 2012). New Caledonia is renowned for its rich endemic conifer flora, with 45 species in the families Taxaceae, Podocarpaceae, Araucariaceae and Cupressaceae (Morat et al., 2012). The New Caledonian Cupressaceae include two species of *Callitris* (*Callitris sulcata* & *Callitris neocaledonica*) and the closely allied *Neocallitropsis pancheri*, the only extra-Australian members of the otherwise endemic Australian clade. The genus includes some remarkably drought resilient trees (Jaffré, 1995; Piggin and Bruhl, 2010; Brodribb et al., 2014). The New Caledonian *Callitris* species are of special importance to understanding the radiation of Gondwanan conifers in general and the *Callitris* clade in particular, as well as the evolution of drought tolerance.

The origin of the New Caledonian flora is hotly debated. The diversity of the current fauna and flora has been attributed to adaptive radiation following long distance dispersal and vicariant speciation by species originating from Australia, Melanesia and New Zealand (Murienne et al., 2005; Smith et al., 2007; Pascal et al., 2008; Grandcolas et al., 2008; Morat et al., 2012). This widely accepted view is based on the assumption that all terrestrial life on New Caledonia was eliminated between submersion of the landmass in the Paleocene (66–56 Ma ago), and re-emergence during the Oligocene, 35–40 Ma ago (Grandcolas et al., 2008; Richer de Forges and Pascal, 2008). However, some researchers posit that the species assemblage is truly relictual, evolving from meta-populations on transient islands that persisted during the tectonic upheavals of this micro-continental fragment of Gondwana (Ladiges and Cantrill, 2007; Heads, 2010). Humans colonised New Caledonia 3350 years ago, causing the loss of more than half its natural vegetation, and extinction of many vertebrates due to overhunting, landscape burning and shifting agriculture (Jaffré et al., 1998; Sand et al., 2005; White et al., 2010). Anthropogenic impacts intensified following European colonisation in the 19th century, resulting in land clearance for agriculture and mining. New Caledonia is currently one of the biggest nickel producers in the world, and this economic development has been accompanied by further habitat loss and fragmentation (Kettle et al., 2007; Pascal et al., 2008; Jaffré et al., 2010), wildfire

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(McCoy et al, 1999; Ibanez et al,., 2013a), urbanization and human population growth, and the introduction of invasive species (Gargominy et al., 1996; Meyer et al., 2006; Pascal et al., 2006), which all act synergistically to threaten the endemic flora and fauna.

C. sulcata is an exemplar of the issues that surround the conservation of the New Caledonia endemic flora. This species is restricted to about 226 km^2 of the South Province of New Caledonia. Its distribution is centred on the Mt Humboldt massif, between 15 and 300 m above sea level (Laubenfels, 1972; Jaffré, 1995) and has been estimated to cover a total area of 20 km^2 (IUCN Red List, Thomas, 2010). Like most New Caledonian conifers, *C. sulcata* grows on soils derived from ultramafic rock, which are characterised by deficiencies in nitrogen, phosphorus, potassium and calcium, and can have excessive amounts of magnesium, nickel and manganese (Jaffré, 1995). Growth rates and recruitment are thought to be very slow, although there are no data on the demography of *C. sulcata*, and little is known of its ecology, distribution and response to fire. It is threatened by mining activity, increasingly frequent wildfires and timber harvesting (Cabalion et al., 2003; Jaffré et al., 2010; Haverkamp, 2012). *C. sulcata* is currently listed by the IUCN as endangered (Thomas, 2010), but it has been suggested that its status should be upgraded to critically endangered (Cabalion et al., 2003; Haverkamp et al., 2013). Although *C. sulcata* is a protected species, and hence it is now illegal to collect any part of the plant according to the South Province environmental code, it is not currently represented in New Caledonia's network of protected areas (Jaffré et al., 2010).

Known as Comboui Fir-tree or "Nié" in Xârâguré (Borendi district vernacular language), *C. sulcata* is esteemed by the local population as much for its totemic value as its exceptional qualities in traditional and ceremonial building (Haverkamp et al., 2013). Indeed, *C. sulcata* is exceptionally durable (Compton, 1922) and because of the essential oils it contains (Hnawia et al., 2008) it is resistant to decay, termites and fungal attack (Cabalion et al., 2003). Traditionally, the Borendi district tribes closely regulated the harvest of *C. sulcata* trees, but illegal harvesting has recently occurred (Haverkamp et al., 2013). A tripartite partnership was established between the local Thio Council, Noé Conservation and the New Caledonian Agronomic Institute (IAC) to undertake an action plan to improve the management and conservation of *C. sulcata* by increasing knowledge about the ecology and biology of the species, as well as a socio-anthropologic study. Here, we present the results of a study originating from the action plan, which focused on the distribution and demography of *C. sulcata*, and aimed to quantify the threats to its populations. Specifically, we aimed to determine the current distribution of the species, analyse stand structures and relate these to past logging and fire activity, and investigate the reproductive biology of the species to understand the capacity of the species to recover from fire disturbance. We contextualised the biology and ecology of *C. sulcata* by comparing it with some of the better-studied Australian *Callitris* species, some of which are threatened by changed fire regimes. Finally, we discuss the findings of our study in relation to the conservation and management of this endangered conifer.

2. Material and methods

2.1. Distribution

C. sulcata is known to occur along the Comboui, Dumbéa and Tontouta Rivers and their tributaries, so detailed mapping of *C. sulcata* populations was undertaken along these rivers, and along the nearby Ngoi and Néfacia Rivers, where indigenous testimony had indicated that some individuals were present. Our mapping combined field checking with binoculars from a helicopter in river valleys surrounding the known distribution, and a foot traverse of the lower 6 km of the Comboui River (Fig. 1; Appendix Aa and b). We used a polygon drawn in a GIS to estimate stand area. All *C. sulcata* populations were mapped (1:50 000) according to three density classes: *high density*, where *C. sulcata* dominated forest stands; *medium density* for mixed stands of *C. sulcata* and other species; and *low density* for stands with scattered *C. sulcata* trees. Corresponding densities of trees with diameter at breast height (DBH) ≥5 cm were: > 300, 150 to 300 and <150 trees ha^{-1} respectively for high, medium and low densities respectively.

2.2. Stand structure

The region where *C. sulcata* occurs is remote, rugged and largely inaccessible, so we restricted demographic analyses to the lower Comboui River. Because wildfire is known to be a threat to *C. sulcata* populations, we selected stands with three fire histories: (i) Unburnt — no evidence of fire, i.e., no visible fire scars to the lower trunk; (ii) Old burnt — evidence of fire scars on weathered wood, with no visible new fire scars on trunk; (iii) Recently burnt by a wildfire (in 2011). We recorded in 2012 stand structure data from 20 m × 20 m, plots. The plots were representative of the target population and centred on a large tree so as to capture as many seedlings and juveniles as possible. Five plots were established in unburnt stands, and four plots each in old burnt and recently burnt stands (a total of 13 plots). Aspect, elevation, slope, presence of boulders and stand density were recorded for each plot (Appendix B).

All *C. sulcata* individuals, including dead trees and cut stumps, which persist for many years given the durable timber, were identified in each plot. Height was measured for all plants, and DBH for those >1.5 m tall, which were considered 'trees'. 'Seedlings' had germinated in the current year and could be distinguished by the presence of cotyledons and a pale green main stem (Appendix Ac). 'Juveniles' were defined as plants that germinated before the current year but with only juvenile foliage, and 'saplings' were plants < 1.5 m tall but with some adult foliage (Appendix Ad). 'Small mature trees' were >1.5 m tall and with a DBH < 5 cm. 'Medium mature trees' were classed as those between 5 and 20 cm DBH, and 'large mature trees' were those ≥20 cm DBH (Appendix Ae). Presence of male or female cones, fire scars, and % of crown burnt were also recorded.

2.3. Bark thickness

Because bark thickness is a key determinant of a tree's resistance to surface fires (Lawes et al., 2011), it was measured with a bark thickness gauge at three points in each of 31 *C. sulcata* trees growing at one site along the Dumbéa River (Fig. 1). The measured trees ranged from 2–51 cm diameter at 10–30 cm height for saplings and 1.3 m (breast height) for trees.

2.4. Tree ages and growth rates

Stem sections were collected from seven stumps that were illegally felled in 2011, for growth ring analysis and accelerator mass spectrometry (AMS) ^{14}C dating. Sections were sanded with sandpaper, and then sections were scanned and growth rings counted and measured using WinDendro (Regent Instruments Inc., Quebec City, Canada). Because sections are not perfectly circular, rings were counted and measured along 3–7 radii, according to size (Appendix C), and the maximum number of rings was recorded (Waring and O'Hara, 2006). The *C. sulcata* growth rings were exceptionally narrow. A sample of wood from the pith of Tree 46 and five samples of wood from along a growth radius of Tree 66 were used for radiocarbon analysis (Appendix C). It is important to note that these wood samples were small (<3 mm width) but unavoidably included several growth rings. The wood samples were pre-treated to extract alpha-cellulose using the method described in Hua et al. (2004). Alpha-cellulose was then combusted to CO_2 and reduced to graphite (Hua et al., 2001) for ^{14}C analyses using the STAR accelerator mass spectrometry (AMS) facility at the Australian Nuclear Science and Technology Organisation (ANSTO; Fink et al., 2004).

Age calibration was performed using OxCal 4.2 (Bronk Ramsey, 2009) with bomb radiocarbon data for the Southern Hemisphere Zone

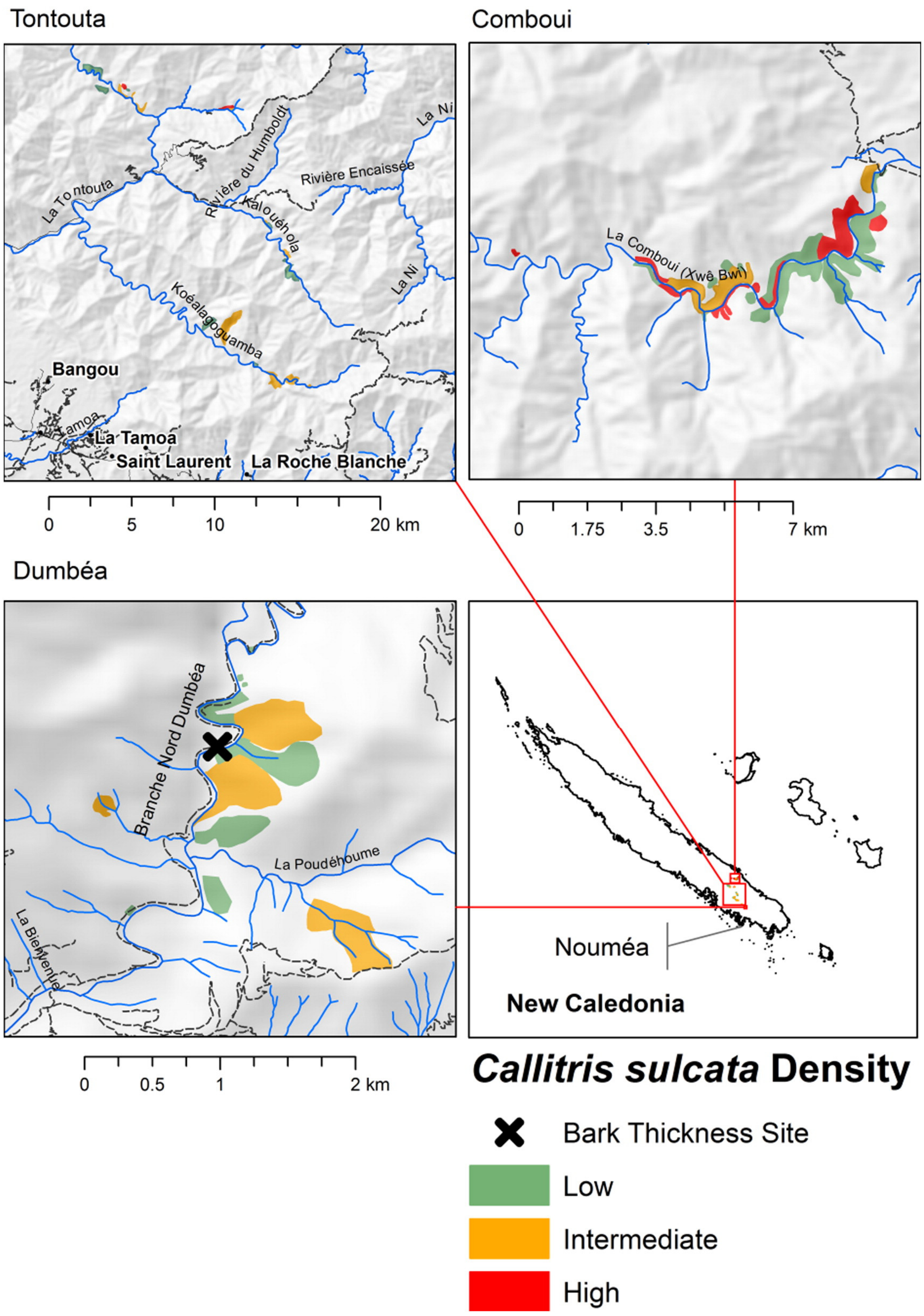

Fig. 1. Maps showing distribution of *C. sulcata* populations along the Tontouta, Domboui and Dumbéa Rivers. Rivers are shown in blue and dashed lines are minor roads. The location of sampling for bark thickness is also shown.

1–2 (Hua et al., 2013) extended back in time using SHCal13 data (Hogg et al., 2013). We employed the "Simple Sequence" deposition model of the OxCal calibration programme (Bronk Ramsey, 2008) for chronological reconstruction of Tree 66 using the chronological ordering constraint (outer samples are younger than inner samples). The same calibration data, used for unmodelled calendar ages, were also used for modelled calendar ages.

Growth rates of Trees 46 and 66 were calculated from section radii (under bark) using (1) the mean AMS ^{14}C dates, and (2) assuming annual growth rings (see discussion in Section 3.5). Growth rates, assuming annual growth rings, were also calculated for each of the seven trees subjected to ring counts.

2.5. Seed germination

We collected more than 1000 seeds during several periods (from July 2012 to May 2013) from natural populations to test whether seed viability and/or germination is a major constraint on regeneration. To assess seed viability, seeds were germinated under favourable laboratory conditions, using two light and temperature regimes: (i) continuous light and 25 °C (7 petri dishes of 25 seeds each) and (ii) cycles of 12 h dark at 20 °C/12 h light at 30 °C (4 petri dishes of 25 seeds each). Germination was monitored every 2–6 days for a total of 100 days.

2.6. Statistical analyses

All analyses were performed using the software package R (R Core team, 2014). Model selection was based on AICc, a form of Akaike's information criterion modified for small sample size (Burnham and Anderson, 2002). Counts of seedlings, juveniles, saplings, medium mature trees, large mature trees, dead trees, cut stumps and the percentage of dead trees in each plot were all over-dispersed, so we used negative binomial models in the package MASS (Venables and Ripley, 2002). For each response variable, the model containing fire history was compared to the one without.

There were too few trees to meaningfully analyse stand structures at an individual plot level, so stand structures on a regional scale were compared among the fire histories by binning counts of live trees into 10-cm diameter bins, up to the largest diameter class for that fire history. The data were over-dispersed so we used negative binomial modelling in the package glmmADMB (Skaug et al., 2014). Plot was used as a random effect to account for the spatial correlation in the data. Preliminary modelling showed that the slopes of the log(count) vs diameter relationship varied among fire histories, so we fitted a separate log(count) vs diameter model for each fire history to test conformity to the negative exponential distribution (Prior et al., 2011).

The proportion of dead trees was modelled as a function of fire history and tree size, with plot as a random effect. The binomial generalised linear model including the interaction was compared to the one without the interaction, using the package lme4 (Bates et al., 2014). Similarly, the proportion of trees with male cones was modelled as a function of tree size using a binomial model. This model was compared to the corresponding null model.

3. Results

3.1. Distribution

Our study confirmed the occurrence of *C. sulcata* in the Comboui, Dumbéa and Tontouta Valleys, but failed to detect additional populations along the Ngoi and Néfacia Rivers. All populations are below 300 m elevation, The main population, totaling 509 ha, is along the Comboui River. There are many high density stands along non-permanent tributaries, as well as along the Comboui River itself. Some stands are isolated, with one small stand located 3.5 km upstream of its nearest neighbour at between 220 m and 300 m elevation.

We found that *C. sulcata* currently occupies a total area of 992 ha, much less than the previous IUCN estimate (Thomas, 2010). High, medium and low density stands occupy 154, 380 and 458 ha respectively. In the Comboui Valley, there are 134 ha of high density stands, 94 ha of medium density stands, and low density stands occupy 281 ha, mainly lower down the valley.

3.2. Demography and the effects of fire

Stand structures of the unburnt and old burnt fire histories approximately conformed to negative exponential distributions (Fig. 2), which explained 39% and 45% respectively of the deviance in the data. The recently burnt site clearly did not conform to this distribution (2% deviance explained) due to a paucity of small live trees (Fig. 2), which were presumably killed by the recent fire.

Fire history affected the numbers of seedlings, juveniles and saplings (Table 1), demonstrated by w_i for the fire history model of 0.94, 1.00 and 1.00 respectively. There were many more seedlings in the recently burnt plots than in the old burnt or unburnt plots (1925 ha^{-1} compared with 125 and 50 ha^{-1} respectively) (Table 1). The pattern was very different for juveniles, where numbers were highest in old burnt plots, intermediate in unburnt and lowest in recently burnt plots (13,025 ha^{-1} compared with 1575 and 12.5 ha^{-1} respectively). Similarly, sapling numbers were higher in old burnt and lower in unburnt plots (800 compared with 275 ha^{-1}), and none were found in recently burnt plots. Collectively, these results indicate *C. sulcata* shows weak pulse recruitment following fire disturbance.

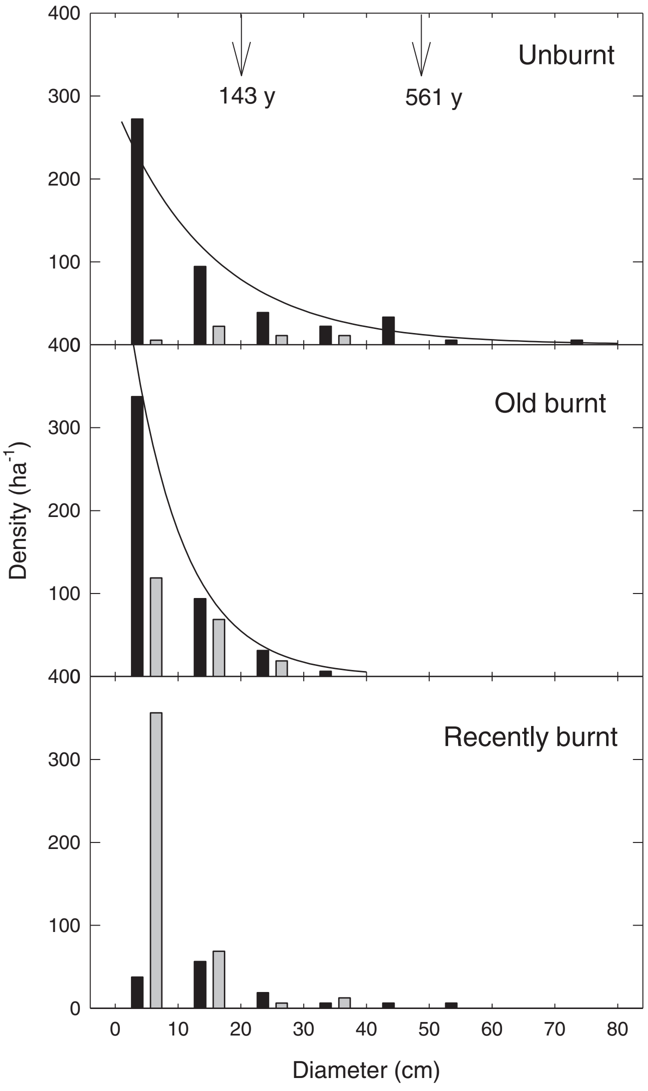

Fig. 2. Density of live trees (black bars) and dead trees (grey bars) as a function of diameter. Trees were binned into 10-cm diameter classes. The numbers of live trees in the unburnt and old burnt fire histories conformed approximately to a negative exponential distribution, shown by the solid lines. AMS dates corresponding to the diameters of the two analysed (unburnt) trees are shown by the arrows.

Table 1
Counts per plot of live seedlings, juveniles, saplings, and small, medium and large mature trees, and dead mature trees, by fire history and plot. 'Trees' were considered to be individuals >1.5 m tall. Percent dead trees are the percent (dead/live mature trees), and did not include cut stumps. Plots were 400 m^2. The Akaike weight (w_i) of the model containing fire history, which indicates the statistical support for this model relative to the null model, is also listed; values > 0.73 show strong support. Thus there was strong statistical support for an effect of fire history on densities of seedlings, juveniles and saplings and the percentage of dead trees.

Plot	Seedlings	Juveniles	Saplings	Small mature trees	Medium mature trees	Large mature trees	Live mature trees — total	Dead trees	Cut stumps	% dead trees
Unburnt										
Plot 1	0	65	3	3	2	1	6	0	1	0
Plot 3	1	24	4	0	3	3	6	1	0	14
Plot 4	1	9	3	8	7	6	21	1	5	5
Plot 11	4	136	32	16	16	8	40	4	0	9
Plot 12	3	82	11	9	16	3	28	5	4	15
Mean	1.8	63	10.6	7.2	8.8	4.2	20.2	2.2	2.0	9
SE	0.7	22	5.6	2.7	3.1	1.2	6.5	1.0	1.0	3
Old burnt										
Plot 8	4	479	38	3	10	1	14	2	0	13
Plot 9	14	307	39	13	18	1	32	9	1	22
Plot 10	0	633	26	6	7	4	17	14	1	45
Plot 13	1	665	23	6	6	0	12	8	0	40
Mean	4.8	521	31.5	7	10.2	1.5	18.8	8.2	0.5	30
SE	3.2	82	4.1	2.1	2.7	0.9	4.5	2.5	0.3	8
Recently burnt										
Plot 2	26	1	0	0	0	2	2	6	0	75
Plot 5	1	0	0	0	1	0	1	5	0	83
Plot 6	106	1	0	0	0	4	4	9	7	69
Plot 7	176	0	0	3	11	0	14	51	3	78
Mean	77.2	0.5	0	0.8	3	1.5	5.2	17.8	2.5	77
SE	39.8	0.3	0.0	0.8	2.7	1.0	3.0	11.1	1.7	3
w_i	0.94	1.00	1.00	0.47	0.10	0.14	0.35	0.38	0.06	0.99

Recently burnt plots had fewer live mature trees, and more dead mature trees, than the other fire histories (Table 1). These differences in counts of live and dead trees were not statistically important, but there was a statistically supported effect of fire history on the percentage of dead trees in each plot (Table 1). The percentage of dead trees (>1.5 m tall) was highest in the recently burnt plots: 77%, compared with 30% in the old burnt plots and 9% in the unburnt plots (Table 1). This was even more pronounced for small trees: 90% of trees <10 cm DBH were dead in the recently burnt plots, compared with 26% in the old burnt plots and 2% in the unburnt plots (Table 1; Appendix D). Indeed, the binomial models analysing the proportion of individual trees that were dead showed strong support for both a fire history effect and a tree size by fire history interaction (Appendix D).

Assuming the difference in the percentage of dead trees in recently burnt plots compared with unburnt plots was due to fire, this equates to an overall mortality due to fire of 67%, or 48 trees in the recently burnt plots, and 21% or 7 trees in the old burnt plots. By comparison with these estimated 55 trees killed by fire, there was a total of 22 cut stumps in these burnt and unburnt sample plots as a consequence of illegal logging in 2011 (Table 1). Thus in our plots, which were relatively accessible by road, there was evidence of more trees killed by fires than by logging.

3.3. Bark thickness

Bark thickness increased with tree diameter to a maximum at DBH of about 15 cm (Fig. 3). Average bark thickness for trees ≥ 15 cm DBH was 10 mm.

3.4. Reproductive biology

C. sulcata is monoecious, and female cones require more than one year to mature. Female cones were present on all except 3 of the 168 mature trees (Fig. 4); thus analyses were not performed on these data. By contrast, 51 trees lacked male cones. There was a strong relationship between tree size and presence of male cones (w_i for this model = 1.00), with trees less than 5 cm DBH having <50% chance of bearing male cones (Fig. 4).

Germination tests confirm that the populations produce viable seeds, but with high variability among batches. Overall germination of all seed collected was 11% (120 of 1095 seeds germinated). The highest germination was recorded for the batch collected in February (23% in the continuous light/25 °C treatment, and 17% in the dark/light, 20–30 °C treatment: the difference between the two germination conditions was not significant (Appendix E)).

3.5. Growth rates and tree ages

The ^{14}C results indicate that the large cut tree (Tree 46; 51 cm diameter) started growing in AD 1450 ± 14 (1σ), and was therefore 561 ± 14 years old when cut. This ^{14}C-based age is slightly higher than the maximum ring count of this tree (500 rings), giving an estimated average of 0.89 rings produced per year. The smaller Tree 66 (21 cm diameter) started growing in AD 1868 ± 40 (1σ) and its growth spans 143 ± 40 (1σ) years (Appendix C). This ^{14}C-based age overlaps with the ring count of this tree (172 rings) within 1σ uncertainty associated

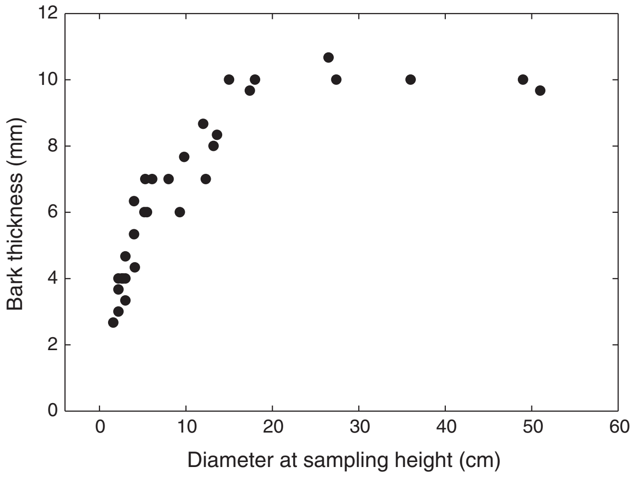

Fig. 3. Relationship between bark thickness and tree diameter at sampling height.

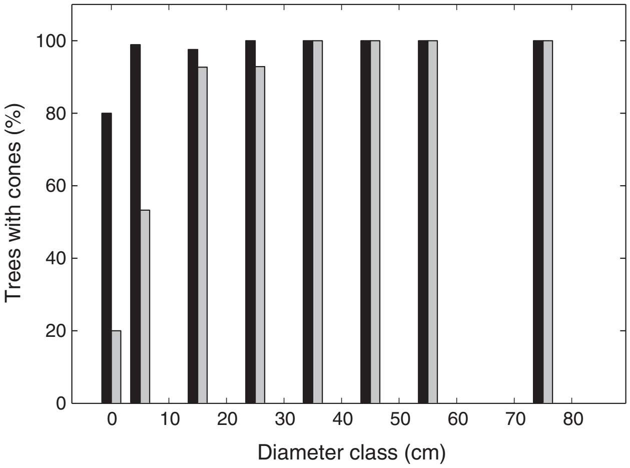

Fig. 4. Percentages of trees with female cones (black bars) and male cones (grey bars) by tree diameter. Trees are binned into 10-cm diameter classes for presentation.

with the ^{14}C measurement, giving an estimated average of 1.20 rings produced per year (range 0.94–1.67 rings per year within 1σ uncertainty). Combining results from both trees suggests that on average, ring production is close to annual.

Based on the ^{14}C dates, the diameter growth rates of Tree 46 and Tree 66 averaged 0.90 and 1.49 mm y^{-1}, respectively. Alternatively, assuming annual growth rings yields values of 1.01 and 1.24 mm y^{-1}, respectively. Ring counts of the seven illegally cut stumps (including Trees 46 and 66) ranged from 90 to 500 years, and diameters ranged from 11 to 51 cm. Based on these ring counts, and assuming annual growth rings, mean diameter growth was 0.97 ± 0.15 mm y^{-1} (±S.E.). The largest tree we recorded was in an unburnt plot and had a DBH of 79.5 cm. This would correspond to an age for this largest tree of 821 years, assuming the overall average growth rate of 0.97 mm y^{-1}.

4. Discussion

C. sulcata is a highly restricted, slow growing conifer that shares many similarities with Australian *Callitris* species. It is currently undergoing range contraction and population declines. The primary threatening process is canopy-defoliating fire, although the species has the capacity to tolerate surface fires and regenerate following infrequent fire events. Other endemic conifers in New Caledonia face the same threats, as outlined below.

4.1. Distribution

We found that *C. sulcata* occupied 9.92 km^2, which is about half the 20 km^2 cited by the IUCN Red List (Thomas, 2010). Thus the species could be more vulnerable than previously thought, warranting a re-assessment of its conservation status. While we cannot rule out the possibility that relictual populations exist in a few inaccessible valleys (Grignon et al., 2006), these are very likely to be small. The largest population of *C. sulcata* was found on the Comboui River, but within this area its presence and density are apparently highly variable and topographically related. It is most abundant, and is the dominant tree species, on steep slopes, where there are many fallen rocks and long periods of shade during the day, and along non-permanent creeks, where rocks provide some protection from insolation and fire. These patterns are similar to the landscape positions of many Australian *Callitris* species, which are strongly correlated with topographic protection from wildfire (Stocker, 1966; Bowman and Wightman, 1985; Bowman et al., 1988; Harris and Kirkpatrick, 1991; Bowman and Latz, 1993; Hahs et al, 1999; Prior et al, 2010, 2011). Extensive mining and associated roads have rendered some of these redoubts, particularly on the western side of the island, vulnerable to fire. It is possible that the species was more widespread prior to human colonisation, but was subsequently eliminated from all but the remote valleys in the infertile south of the island. This biogeographic hypothesis could be tested by undertaking genetic analyses of the populations, as has been done for the *Callitris glaucophylla* complex across Australia (Sakaguchi et al., 2013).

4.2. Stand structure and fire impact

At the regional scale, stand structures of both the unburnt and old burnt areas conformed to a negative exponential distribution, consistent with frequent recruitment and reasonably constant mortality and growth rates (Rubin et al., 2006; Prior et al., 2011). This is consistent with *C. sulcata* being a light demanding species that can tolerate moderate shade in the juvenile stage (Jaffré, 1995). Frequent recruitment has also been demonstrated for several Australian *Callitris* species growing in the absence of major disturbance (Clayton-Greene and Ashton, 1990; Harris and Kirkpatrick, 1991; Bowman et al, 1988; Prior et al., 2011). By contrast, there was a clear deficit of live small trees in the recently burnt plots. The high proportion of dead trees, especially in the small size classes, recorded in the recently burnt plots is strong evidence for fire being a major cause of mortality for *C. sulcata*. This is also the case for many Australian *Callitris* species (Bowman and Panton, 1993; Bradstock and Cohn, 2002; O'Donnell et al., 2010; Prior et al., 2010; Cohn et al., 2011).

The radiocarbon dating showed that *C. sulcata* trees can live for many hundreds of years, and suggests that the largest trees could be over 800 years old. It also demonstrated that these trees grow very slowly, in the order 0.9 to 1.5 mm y^{-1}, which is about half the rate found in an Australian *Callitris* species growing at the most arid extreme of its range (Bowman et al., 2011). Such slow growth is presumably a result of the ultramafic soils on which it grows (Jaffré, 1995). Diameter growth rates of 0.5 to 2.5 (mean 1.6) mm y^{-1} have been reported for 15 rainforest species growing on ultramafic soils in New Caledonia (Read et al., 2011) and growth rates of 0.2to 0.4 mm y^{-1}, among the slowest for any tree species, have been recorded for *Araucaria muelleri* and *Araucaria laubenfelsii*, two other New Caledonian conifers that grow on ultramafic soils (Rigg et al., 2010; Enright et al., 2014). The presence of large, fire-sensitive and slow-growing trees suggests that past fire events must have been very infrequent, as indicated by the palynological evidence (Stevenson and Hope, 2005). Fire free intervals of at least 200 years would be required to allow *C. sulcata* trees to grow to 30 cm diameter. Clearly, contemporary disturbances such as logging or fire will have long lasting effects on population structures, given that recovery will be very slow.

The presence of female cones on almost all trees, and reasonably high seed viability, suggest that availability of fertile seed is not a major constraint on *C. sulcata* wild populations. This contrasts to the very low proportion (~5%) of fertile seed for *C. sulcata* reported by Ladd et al. (2013), who suggested this may have been because it was collected from an isolated, and hence self pollinating, tree in an arboretum. However, we cannot rule out seed supply as a constraint on *C. sulcata* populations given that even viable seed can be inbred, compromising survival of seedlings under field conditions that are far harsher than those in laboratory assessments of seed viability (Kettle et al., 2008).

4.3. Fire recovery and regeneration strategies

C. sulcata does not have aerial (serotiny) nor soil seedbanks but can tolerate surface fires that do not completely defoliate the canopy and destroy mature cones. For instance, we observed that trees that were completely scorched died, and no seedlings germinated beneath them (Table 1). We know from previous studies in the genus that the buds are killed by fire and that the damage is permanent, and if the trees are entirely defoliated they are killed (Bowman et al., 2014). In the other recently burnt plots, some trees that escaped complete canopy scorch survived, and many more seedlings established. Even a juvenile 15 cm high survived after its foliage was only partially scorched. Our measurements suggest that while the recent fire killed most juveniles and saplings, it stimulated the germination of new seedlings. This is consistent with earlier fires stimulating a pulse of regeneration in the old burnt plots, evident in relatively high numbers of juveniles and saplings in these plots. In the unburnt plots, current year seedling densities were very low, but there were moderate densities of juveniles and saplings, demonstrating that fire is not necessary for seed germination. However, any new seedlings stimulated by fire are extremely vulnerable to subsequent fires.

No Australian *Callitris* species have soil seedbanks, and they range from serotinous obligate seeders dependent on fire for seedling establishment (*Callitris verrucosa* (Bradstock and Cohn, 2002) and *Callitris preissii* (O'Donnell et al., 2010)) to non-serotinous species with establishment controlled by periods of good rainfall coinciding with release of viable seed, often produced in mast cycles (*C. glaucophylla* and *Callitris intratropica*; Stocker, 1966; Read, 1995; Lawes et al., 2013). Selection pressure by crown fire regimes may have given rise to serotiny in the *Callitris* clade (Ladd et al., 2013) because they are extremely vulnerable to canopy defoliation by fire, given a very limited epicormic response. Many Australian species, however, have highly insulating bark that protects the cambium from high temperatures (Lawes et al., 2011; Bowman et al., 2014), consistent with adaptation to surface fire regime (Keeley, 2012). Although a previous study reported that *C. sulcata* has thin bark, which renders it vulnerable to fire (Ladd et al., 2013), we found that bark thickness of *C. sulcata* trees reached a plateau of 10 mm at a diameter of around 15 cm. Although this is substantially thinner than bark of *C. intratropica* trees (15 mm for trees with mean DBH of 21 cm), which grow in north Australian savannas subject to frequent surface fires (Bowman et al., 2014), it is thicker than that of *Callitris macleayana* (4.4 mm for trees with mean DBH of 20 cm), which grows in infrequently burnt Queensland rainforest (Lawes et al., 2011). It is therefore possible *C. sulcata* has evolved to tolerate infrequent surface fires.

In summary, *C. sulcata*'s fire regeneration strategies most resemble those of the Australian species *Callitris rhomboidea* because: (a) its establishment appears to be promoted by fire, but is not reliant on it (Harris and Kirkpatrick, 1991), (b) both species have sufficiently thick bark for many adults to survive ground fires, and yet (c) they both are vulnerable to population collapse following crown fires because of the lack of aerial seedbanks (serotiny) (Ladd et al., 2013).

4.4. Management implications

The *Callitris* clade presents an interesting counterpoint to northern hemisphere conifers, and particularly *Pinus* species, which have better developed fire tolerating mechanisms (branch shedding, thick bark, basal sprouting and serotiny) (Kershaw and McGlone, 1995; Gauthier et al., 1996; Schwilk and Ackerley, 2001; Ne'eman et al., 2004; He et al., 2012). Despite tolerating seasonal dryness and soil infertility (Brodribb et al., 2014), environmental factors which are often associated with flammable foliage (Bowman et al., 2014), the limited development of fire recovery traits may reflect the low frequency of ignitions prior to prehistoric and historic human colonisation. There was very little landscape fire in New Caledonia in the 47,000 years prior to the arrival of humans 3000 years ago (Stevenson and Hope, 2005). This has rendered the New Caledonian vegetation, including *C. sulcata*, particularly vulnerable to frequent and extensive burning by human colonists (McCoy et al., 1999; Perry and Enright, 2002; Ibanez et al., 2013a). The increased incidence and severity of fire following European colonisation poses a major threat to many of New Caledonia's endangered species (Bouchet et al., 1995; Pascal et al., 2008; Jaffré et al., 2010; Wulff et al., 2013). Indeed, Jaffré et al. (1998) consider fire to be the most important threat to the survival of the biota of New Caledonia. Species on ultramafic substrates are particularly vulnerable because numerous tracks and activity associated with mining and forestry have led to repeated wildfires, and forest cover has been reduced to less than 20% of its original extent (Jaffré et al., 2010). Forty-one endemic conifer species occur on ultramafic substrates, and 17 species (including *C. sulcata*) occur in the maquis (Jaffré et al., 2010), which is especially fire-prone (Perry and Enright, 2002). However, the dense forests that host many iconic *Araucaria* and Podocarp species are also susceptible to fire during drought (Ibanez et al., 2013b), which could become increasingly frequent and severe with climate change (IPCC, 2001).

Fire regimes prior to European colonisation allowed *C. sulcata* to persist in its current range, although it is unclear whether the first wave of human colonisation caused ranged contractions to the remote valleys and fire-protected landscape settings that form the current domain of the species. The apparent loss of *C. sulcata* trees from the Néfacia and Ngoi rivers suggests that since European colonisation, fire regimes have become more hostile for the species. The continuing decline of *C. sulcata* demonstrates that legal protection on its own is not sufficient to maintain populations of threatened plants in New Caledonia. Our findings support the contention that fire is the most important threat to *C. sulcata*, given we estimated there were 2.5 times as many trees killed by fire than were logged in our sample plots, which were relatively close to roads and therefore especially vulnerable to harvest. Importantly, both fire and logging are facilitated by road access, so effective protection of *C. sulcata* can be best achieved by ensuring some populations remain in remote and inaccessible locations rarely visited by people. In more accessible locations, construction of fire-breaks, suppression of wildfire and reseeding or replanting burnt areas could also help maintain populations (Jaffré et al., 1998). Finally, while our findings suggest that the current extent of illegal logging is less threatening than fires to *C. sulcata* populations, it is important to minimise any additional pressures, such as logging, on the species, given its extremely slow growth rates.

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Appendix A. Supplementary data

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References

Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2014. lme4: linear mixed-effects models using Eigen and S4. R package version. 1 pp. 1–7.

Bouchet, P., Jaffre, T., Veillon, J.M., 1995. Plant extinction in New Caledonia — protection of sclerophyll forests urgently needed. Biodivers. Conserv. 4, 415–428.

Bowman, D.M.J.S., Latz, P.K., 1993. Ecology of *Callitris glaucophylla* (Cupressaceae) on the MacDonnell Ranges, central Australia. Aust. J. Bot. 41, 217–225.

Bowman, D.M.J.S., Panton, W.J., 1993. Decline of *Callitris intratropica* R.T. Baker & H.G. Smith in the Northern Territory: implications for pre- and post-European colonization fire regimes. J. Biogeogr. 20, 373–381.

Bowman, D.M.J.S., Wightman, G.M., 1985. Small scale vegetation pattern associated with a deeply incised gully, Gunn Point, Northern Australia. Proc. R. Soc. Queensland 96, 63–73.

Bowman, D.M.J.S., Wilson, B.A., Davis, G.W., 1988. Response of *Callitris intratropica* R.T. Baker and H.G. Smith to fire protection, Murgenella, Northern Australia. Aust. J. Ecol. 13, 147–159.

Bowman, D.M.J.S., Prior, L.D., Tng, D.Y.P., Hua, Q., Brodribb, T.J., 2011. Continental-scale climatic drivers of growth ring variability in an Australian conifer. Trees — Struct. Funct. 25, 925–934.

Bowman, D.M.J.S., MacDermott, H.J., Nichols, S.C., Murphy, B.P., 2014. A grass-fire cycle eliminates an obligate-seeding tree in a tropical savanna. Ecol. Evol. 4, 4185–4194.

Bradstock, R.A., Cohn, J.S., 2002. Demographic characteristics of mallee pine (*Callitris verrucosa*) in fire-prone mallee communities of central New South Wales. Aust. J. Bot. 50, 653–665.

Brodribb, T.J., McAdam, S.A.M., Jordan, G.J., Martins, S.C.V., 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. PNAS 111, 14489–14493.

Bronk Ramsey, C., 2008. Deposition models for chronological records. Quat. Sci. Rev. 27, 42–60.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Practical Information-theoretic Approach. 2nd edn. Springer, New York.

Cabalion, P., Hnawia, E., Menut, C., Waikedre, J., Patissou, J., 2003. Protection Needed for *Callitris sulcata*, an Endemic but Very Threatened Resource From Southern New Caledonia. In Preservation and Restoration in Tropical Mining Environments. IRD Centre, Nouméa.

Clayton-Greene, K.A., Ashton, D.A., 1990. The dynamics of *Callitris columellaris*/*Eucalyptus albens* communities along the Snowy River and its tributaries in South-eastern Australia. Aust. J. Bot. 38, 403–432.

Cohn, J.S., Lunt, I.D., Ross, K.A., Bradstock, R.A., 2011. How do slow-growing, fire-sensitive conifers survive in flammable eucalypt woodlands? J. Veg. Sci. 22, 425–435.

Compton, R.H., 1922. A systematic account of the plants collected in New Caledonia and the Isle of Pines by Mr. R. H. Compton, M.A., in 1914. Part II. Gymnosperms and cryptogams. Bot. J. Linn. Soc. 45, 421–466.

Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Enright, N.J., Miller, B.P., Perry, G.L.W., Goldblum, D., Jaffré, T., 2014. Stress-tolerator leaf traits determine population dynamics in the endangered New Caledonian conifer *Araucaria muelleri*. Austral Ecol. 39, 60–71.

Fink, D., Hotchkis, M., Hua, Q., Jacobsen, G., Smith, A.M., Zoppi, U., Child, D., Mifsud, C., van der Gaast, H., Williams, A., Williams, M., 2004. The ANTARES AMS facility at ANSTO. Nucl. Instrum. Meth. B 223–224, 109–115.

Gargominy, O., Bouchet, P., Pascal, M., Jaffre, T., Tourneur, J.C., 1996. Consequences for biodiversity of plant and animal species introductions in New Caledonia. Revue D Ecologie-La Terre Et La Vie 51, 375–402.

Gauthier, S., Bergeron, Y., Simon, J.P., 1996. Effects of fire regime on the serotiny level of jack pine. J. Ecol. 84, 539–548.

Grandcolas, P., Murienne, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E., Deharveng, L., 2008. New Caledonia: a very old Darwinian island? Philos. Trans. R. Soc., B 363, 3309–3317.

Grignon, C., Chambrey, C., Rigault, F., Munzinger, J., 2006. Recensement du patrimoine botanique des aires protegées terrestres de la Province Sud - synthese de l'étude - caracterisation et cartographie des formation végétales des 24 aires protegées terrestres de la Province Sud. Rapport de Contrat de Développement Etat/Province Sud/IRD (Convention n°C.193/07-CD2006/10). Institut de recherche pour le développement, Nouméa.

Hahs, A., Enright, N.J., Thomas, I., 1999. Plant communities, species richness and their environmental correlates in the sandy heaths of Little Desert National Park, Victoria. Aust. J. Ecol. 24, 249–257.

Harris, S., Kirkpatrick, J.B., 1991. The distributions, dynamics and ecological differentiation of *Callitris* species in Tasmania. Aust. J. Bot. 39, 187–202.

Haverkamp, C., 2012. Vers un plan de gestion de *Callitris sulcata*. Distribution, structure et ecologie des populations. Université de Lorraine, Metz (Master Thesis).

Haverkamp, C., Anquez, M., Wulff, A.S., Grochain, S., L'Huillier, L., Fogliani, B., 2013. Etude conservatoire du conifère *Callitris sulcata* (Sapin de Comboui) sur la commune de Thio. Rapport final, Novembre 2013. IAC, Nouméa.

He, T.H., Pausas, J.G., Belcher, C.M., Schwilk, D.W., Lamont, B.B., 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. New Phytol. 194, 751–759.

Heads, M., 2010. Biogeographical affinities of the New Caledonian biota: a puzzle with 24 pieces. J. Biogeogr. 37, 1179–1201.

Hnawia, E., Menut, C., Agrebi, A., Cabalion, P., 2008. Wood essential oils of two endemic trees from New Caledonia : *Callitris sulcata* (Parl.) Schltr. and *Callitris neocaledonia* Dummer. Biochem. Syst. Ecol. 36, 859–866.

Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.M., Turney, C.S.M., Zimmerman, S.R.H., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 cal yr BP. Radiocarbon 55, 1889–1903.

Hua, Q., Jacobsen, G.E., Zoppi, U., Lawson, E.M., Williams, A.A., Smith, A.M., McGann, M.J., 2001. Progress in radiocarbon target preparation at the ANTARES AMS Centre. Radiocarbon 43, 275–282.

Hua, Q., Barbetti, M., Zoppi, U., Fink, D., Watanasak, M., Jacobsen, G.E., 2004. Radiocarbon in tropical tree rings during the Little Ice Age. Nucl. Instrum. Meth. B 223–224, 489–494.

Hua, Q., Barbetti, M., Rakowski, A.Z., 2013. Atmospheric radiocarbon for the period 1950–2010. Radiocarbon 55, 2059–2072.

Ibanez, T., Curt, T., Hely, C., 2013a. Low tolerance of New Caledonian secondary forest species to savanna fires. J. Veg. Sci. 24, 177–188.

Ibanez, T., Hely, C., Gaucherel, C., 2013b. Sharp transitions in microclimatic conditions between savanna and forest in New Caledonia: insights into the vulnerability of forest edges to fire. Austral Ecol. 38, 680–687.

IPCC, 2001. In: McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.), Small Island States. In Climate Change 2001: Impacts, Adaptation, and Vulnerability. Cambridge University Press, Cambridge, U.K., pp. 843–876.

Jaffré, T., 1995. Distribution and ecology of the conifers of New Caledonia. In: Enright, N.J., Hill, R.S. (Eds.), Ecology of the Southern Conifers. Melbourne University Press, Melbourne, pp. 171–196.

Jaffre, T., Bouchet, P., Veillon, J.M., 1998. Threatened plants of New Caledonia: is the system of protected areas adequate? Biodivers. Conserv. 7, 109–135.

Jaffre, T., Munzinger, J., Lowry, P.P., 2010. Threats to the conifer species found on New Caledonia's ultramafic massifs and proposals for urgently needed measures to improve their protection. Biodivers. Conserv. 19, 1485–1502.

Keeley, J.E., 2012. Ecology and evolution of pine life histories. Ann. For. Sci. 69, 445–453.

Kershaw, A.P., McGlone, M.S., 1995. The Quaternary history of the southern conifers. In: Enright, N.J., Hill, R.S. (Eds.), Ecology of the Southern Conifers. Melbourne University Press, Melbourne, pp. 30–63.

Kettle, C.J., Hollingsworth, P.M., Jaffre, T., Moran, B., Ennos, R.A., 2007. Identifying the early genetic consequences of habitat degradation in a highly threatened tropical conifer, *Araucaria nemorosa* Laubenfels. Mol. Ecol. 16, 3581–3591.

Kettle, C.J., Ennos, R.A., Jaffre, T., Gardner, M., Hollingsworth, P.M., 2008. Cryptic genetic bottlenecks during restoration of an endangered tropical conifer. Biol. Conserv. 141, 1953–1961.

Ladd, P.G., Midgley, J.J., Nield, A.P., 2013. Serotiny in southern hemisphere conifers. Aust. J. Bot. 61, 486–496.

Ladiges, P.Y., Cantrill, D., 2007. New Caledonia-Australian connections: biogeographic patterns and geology. Aust. Syst. Bot. 20, 383–389.

Laubenfels, D.J., 1972. Flore de la Nouvelle-Caledonie et Dependances 4. Gymnospermes. Mus. Nat. Hist. Nat, Paris.

Lawes, M.J., Adie, H., Russell-Smith, J., Murphy, B., Midgley, J.J., 2011. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. Ecosphere (volume 2, article 42).

Lawes, M.J., Taplin, P., Bellairs, S.M., Franklin, D.C., 2013. A trade-off in stand size effects in the reproductive biology of a declining tropical conifer *Callitris intratropica*. Plant Ecol. 214, 169–174.

McCoy, S., Jaffre, T., Rigault, F., Ash, J.E., 1999. Fire and succession in the ultramafic maquis of New Caledonia. J. Biogeogr. 26, 579–594.

Meyer, J.-Y., Loope, L.L., Sheppard, A., Munzinger, J., Jaffré, T., 2006. Les plantes envahissantes et potentiellement envahissantes dans l'archipel néo-caledonien: première évaluation et recommandations de gestion. Les espèces envahissantes dans l'archipel néo-calédonien. IRD Éditions, Nouméa, pp. 115–150.

Mittermeier, R.A., Robles-Gil, P., Hoffmann, M., Pilgrim, J.D., Brooks, T.B., Mittermeier, C.G., Lamoreux, J.L., Fonseca, G.A.B., 2004. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions. CEMEX, Mexico City, Mexico (390 pp.).

Morat, P., Jaffre, T., Tronchet, F., Munzinger, J., Pillon, Y., Veillon, J.M., Chalopin, M., Birnbaum, P., Rigault, F., Dagostini, G., Tinel, J., 2012. The taxonomic reference base Florical and characteristics of the native vascular flora of New Caledonia. Adansonia 34, 179–221.

Murienne, J., Grandcolas, P., Piulachs, M.D., Belles, X., D'Haese, C., Legendre, F., Pellens, R., Guilbert, E., 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? Cladistics 21, 2–7.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Ne'eman, G., Goubitz, S., Nathan, R., 2004. Reproductive traits of *Pinus halepensis* in the light of fire — a critical review. Plant Ecol. 171, 69–79.

O'Donnell, A.J., Cullen, L.E., McCaw, W.L., Boer, M.M., Grierson, P.F., 2010. Dendroecological potential of *Callitris preissii* for dating historical fires in semi-arid shrublands of southern Western Australia. Dendrochronologia 28, 37–48.

Pascal, M., Barré, N., de Garince-Wichatitsky, M., Lorvelec, O., Frétey, T., Brescia, F., Jourdan, H., 2006. Les peuplements néo-calédoniens de vertébrés: invasions, disparitions. In: Beauvais, M.-L., Coléno, A., Jourdan, H. (Eds.), Les espèces envahissantes dans l'archipel néo-calédonien. IRD Éditions, Nouméa, pp. 111–162.

Pascal, M., Richer de Forges, B., Le Guyader, H., Simberloff, D., 2008. Mining and other threats to the New Caledonia biodiversity hotspot. Conserv. Biol. 22, 498–499.

Perry, G.L.W., Enright, N.J., 2002. Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. J. Biogeogr. 29, 1143–1158.

Piggin, J., Bruhl, J.J., 2010. Phylogeny reconstruction of *Callitris* Vent. (Cupressaceae) and its allies leads to inclusion of *Actinostrobus* within *Callitris*. Aust. Syst. Bot. 23, 69–93.

Prior, L.D., Lee, Z., Brock, C., Williamson, G.J., Bowman, D.M.J.S., 2010. What limits the distribution and abundance of the native conifer *Callitris glaucophylla* (Cupressaceae) in the West MacDonnell Ranges, central Australia? Aust. J. Bot. 58, 554–564.

Prior, L.D., McCaw, W.L., Grierson, P.F., Murphy, B.P., Bowman, D.M.J.S., 2011. Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change. For. Ecol. Manag. 262, 252–262.

Read, J., 1995. Recruitment characteristics of the white cypress pine (*Callitris glaucophylla*) in arid South Australia. Rangel. J. 17, 228–240.

Read, J., Evans, R., Sanson, G.D., Kerr, S., Jaffre, T., 2011. Wood properties and trunk allometry of co-occurring rainforest canopy trees in a cyclone-prone environment. Am. J. Bot. 98, 1762–1772.

Richer De Forges, B., Pascal, M., 2008. La Nouvelle-Calédonie, un "point chaud" de la biodiversité mondiale gravement menacé par l'exploitation minière. Le Journal de la Société des Océanistes 126–127, 95–112.

Rigg, L.S., Enright, N.J., Jaffré, T., Perry, G.L.W., 2010. Contrasting population dynamics of the endemic New Caledonian conifer *Araucaria laubenfelsii* in maquis and rain forest. Biotropica 42, 479–487.

Rubin, B.D., Manion, P.D., Faber-Langendoen, D., 2006. Diameter distributions and structural sustainability in forests. For. Ecol. Manag. 222, 427–438.

Sakaguchi, S., Bowman, D.M.J.S., Prior, L.D., Crisp, M.D., Linde, C.C., Tsumura, Y., Isagi, Y., 2013. Climate, not Aboriginal landscape burning, controlled the historical demography and distribution of fire-sensitive conifer populations across Australia. Proc. R. Soc. B Biol. Sci. 280 (article 20132182).

Sand, C., Bole, J., Ouetcho, A., 2005. Alterations to and development of Pacific Island environments by humanity in prehistoric times: from regional characteristics to specific features in New Caledonia. In: Mokaddem, H. (Ed.), Eleven Approaches to Culture and Nature in the South Pacific. Secretariat of the Pacific Community, Nouméa, pp. 103–116.

Schwilk, D.W., Ackerly, D.D., 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94, 326–336.

Skaug, H.G., Fournier, D.A., Bolker, B.M., Magnusson, A., Nielsen, A., 2014. Generalized linear mixed models using AD model builder. R package version 0.8.0.

Smith, S.A., Sadlier, R.A., Bauer, A.M., Austin, C.C., Jackman, T., 2007. Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. Mol. Phylogenet. Evol. 43, 1151–1166.

Stevenson, J., Hope, G., 2005. A comparison of late Quaternary forest changes in New Caledonia and northeastern Australia. Quat. Res. 64, 372–383.

Stocker, G.C., 1966. Aspects of the seeding habits of *Callitris intratropica*. Forestry and Timber Bureau Leaflet No. 97. Department of National Development, Canberra.

Thomas, P., 2010. The IUCN Red List of Threatened Species. *Callitris sulcata*. Version 2014.2. www.iucnredlist.org (Accessed on 27 October 2014).

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics With S. Fourth ed. Springer, New York.

Waring, K.M., O'Hara, K.L., 2006. Estimating relative error in growth ring analyses of second-growth coast redwood (*Sequoia sempervirens*). Can. J. For. Res.-Rev. Can. Rech. For. 36, 2216–2222.

White, A.W., Worthy, T.H., Hawkins, S., Bedford, S., Spriggs, M., 2010. Megafaunal meiolaniid horned turtles survived until early human settlement in Vanuatu, Southwest Pacific. PNAS 107, 15512–15516.

Wulff, A.S., Hollingsworth, P.M., Ahrends, A., Jaffre, T., Veillon, J.M., L'Huillier, L., Fogliani, B., 2013. Conservation priorities in a biodiversity hotspot: analysis of narrow endemic plant species in New Caledonia. PLoS ONE 8 (9), e73371.