Elaeocarpus carbinensis J.N.Gagul & Crayn (Elaeocarpaceae), a new species endemic to the Mt Carbine Tableland of northeast Queensland, Australia

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Summary

Gagul, J.N., Simpson, L. & Crayn, D.M. (2018). *Elaeocarpus carbinensis* J.N.Gagul & Crayn (Elaeocarpaceae), a new species endemic to the Mt Carbine Tableland of northeast Queensland, Australia. ***Austrobaileya* 10(2): 247–259.** *Elaeocarpus carbinensis* from montane areas of the Wet Tropics bioregion of northeast Queensland, Australia is described and compared with similar species. Notes on habitat, distribution, and relationships, and a key to allied large-fruited species is provided. The conservation outlook for the species was determined with environmental niche modelling analyses using a range of carbon dioxide emission scenarios. The results indicate that by the year 2080, suitable climate for the species will have disappeared from its current range. Thus, an IUCN Red List category of **Vulnerable** under criterion 'restricted distribution, and plausibility and immediacy of threat' is recommended.

Key Words: Elaeocarpaceae, *Elaeocarpus*, *Elaeocarpus carbinensis*, Australia flora, Queensland flora, Wet Tropics bioregion, taxonomy, new species, environmental niche modelling, identification key

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Introduction

Elaeocarpus L., the largest genus in Elaeocarpaceae, comprises more than 350 species with a mainly Indo-Pacific distribution (Coode 2004; Phoon 2015). New Guinea (*c*. 97 spp.) and Borneo (*c*. 70 spp.) have the highest species diversity (Coode 2004). Australia contains 34 taxa (30 endemic), the majority of which occur along the east coast with a few extending to the Northern Territory and one species (*E. costatus* M.Taylor) on Lord Howe Island (Baba & Crayn 2012). The genus is particularly diverse in the Wet Tropics bioregion of northeast Queensland where 23 species are found, 16 of which are endemic to the bioregion.

The Wet Tropics (**Fig. 1**) is a small bioregion of *c*. 20,000 ha (less than 0.3% of Australia's landmass) and includes extensive tropical mountain top habitat (*c*. 1000 ha, *c*. 5% of the bioregion, is above 1000 m elevation; Costion *et al*. 2015). This habitat is considered highly vulnerable to the effects of climate change (Murphy *et al*. 2012) because the warming signal in the tropics is amplified with elevation (Beniston *et al*. 1997) and the critical moisture provided by cloud cover is expected to decrease significantly with an upward shift in the elevation of cloud formation (Foster 2001; Still *et al*. 1999). Impacts of climate change including range shifts and species extinctions have already been observed on tropical mountain tops (Pounds *et al*. 1999, 2006). A recent study predicted similar impacts on the Wet Tropics bioregion – distribution modelling of endemic montane tree species under future climate scenarios predicted 86% of species included in the study would have no suitable climate in the bioregion by 2080 (Costion *et al*. 2015). Among the taxa modelled in that study was a putative new species of *Elaeocarpus* (*E*. sp. Mt Misery (L.J.Webb+ 10905) (Guymer 1997, 2017).

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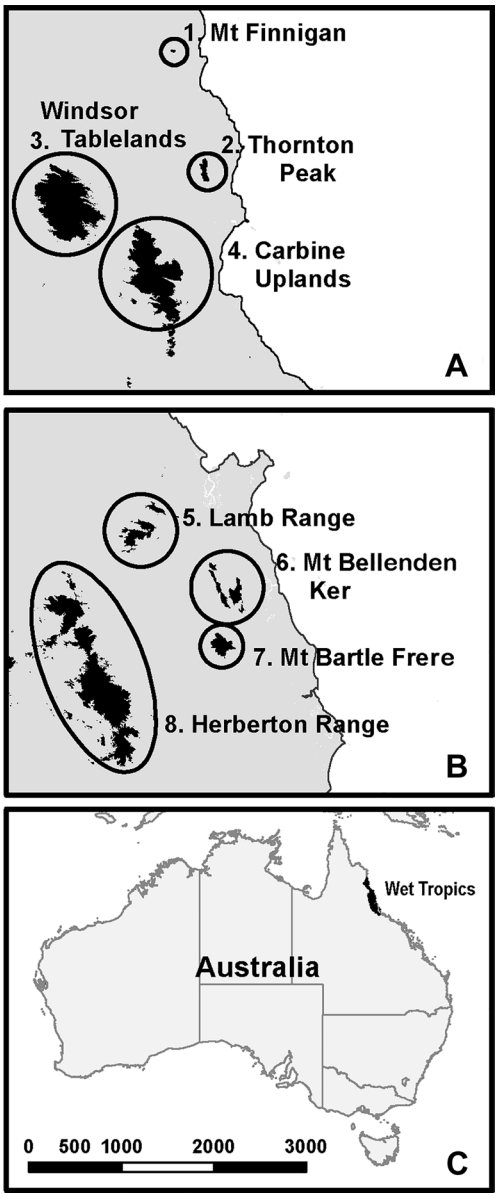

Fig. 1. Upland regions are shown for a) the northern Wet Tropics and b) the southern Wet Tropics, and the location of the Wet Tropics in Australia is shown in c).

Material of *Elaeocarpus* sp. Mt Misery (L.J.Webb+ 10905) was first collected by B. Hyland on 17 May 1973 from State Forest Reserve 143, North Mary Logging Area. The species is similar to *E. stellaris* L.S.Sm. but differs mainly in the mesocarp (equivalent to the fruit 'stone' and that is formed from the lignified inner mesocarp: Dettman & Clifford 2000) being smaller, with less pronounced flanges and less deeply grooved inter-flange valleys, and punctate abaxial leaf surfaces. This species is herein described as *E. carbinensis* J.N.Gagul & Crayn, and modelling of its environmental niche undertaken to inform a conservation status recommendation.

Materials and methods

Specimen preparation and examination

Observations were made using the naked eye and light microscopy on dried and spirit preserved (FAA or Bang mix) material held at CNS and BRI, and on living material in the field. Dried material was rehydrated by boiling with water and a small amount of detergent. Measurements were made with a ruler or microscope eyepiece graticule. Information on plant growth habit and size, colour of fresh floral parts and fruit, habitat and locality were taken from the collector's notes recorded on the herbarium label and from field observations by the authors.

Specimens originally deposited in the C.S.I.R.O. QRS herbarium at Atherton are now incorporated in CNS at the Australian Tropical Herbarium in Cairns.

Species distribution modelling

Environmental niche modelling (ENM) was utilised to predict the potential distribution of *E. carbinensis* under contemporary and future climates. Species distribution models were produced in MaxEnt v. 3.3.3 (Phillips *et al*. 2006).

The distribution models used in the previous ENM study (Costion *et al*. 2015) omitted several point records of this species. To ensure the species' full distribution was represented in the present analysis, Australia's Virtual Herbarium (AVH 2016) was queried for all known synonyms, returning 13 unique locational records. All specimens used in the modelling analysis have been seen and verified by the authors and are cited below*.

Climate layers were sourced from the Australian Wet Tropics Decadal Climate Change Predictions dataset sourced from the James Cook University Tropical Data Hub (VanDerWal 2011), and consisted of bioclimatic variables mapped at ~250 m resolution across the Wet Tropics bioregion. These layers had previously been created using the "climates" package in R (VanDerWal *et al*. 2011) using baseline climate surfaces from ANUCLIM 6.1 software with a climate baseline of 1975–2005 (Hutchinson *et al*. 2000). Four uncorrelated bioclimatic variables were used, previously selected from 19 bioclimatic variables using a jackknife test for importance (Costion *et al*. 2015): Temperature Seasonality, Maximum Temperature of Warmest Month, Mean Temperature of Wettest Quarter and Annual Precipitation. Suitable climate is defined as an area or areas providing a climate niche that the species currently occupies. This was used as a surrogate for habitat suitability following VanDerWal *et al*. (2009) and is referred to throughout the text as suitable habitat.

Habitat suitability was modelled with 10 replicates using the cross-validation option with linear, quadratic, product and hinge features enabled. To model habitat suitability under future climates, models were run for the years 2040, 2060 and 2080 under the intermediate (A1b), extreme (A2) and best case (B1) emission scenarios of Nakićenović *et al*. (2000).

Abbreviations

LA (Logging Area), NP (National Park), SF/SFR (State Forest/State Forest Reserve)

Taxonomy

Elaeocarpus carbinensis J.N.Gagul & Crayn **sp. nov.** Similar to *E. stellaris* L.S.Sm. but differs in having smaller fruits (50–55 × 35–50 mm versus 43–65 × 50–60 mm) with thinner mesocarp flanges (3–5 mm versus 5–10 mm) that are more closely spaced (15–20 mm versus 20–25 mm), less deeply grooved inter-flange valleys, punctate abaxial leaf surfaces, longer petals (35–40 mm versus 20–25 mm) and filaments (10–15 mm versus 6–8 mm), and petals hairy outside only (both sides in *E. stellaris*). **Typus:** Queensland. Cook District. SFR 143, Kanawarra, Carbine LA, 25 January 1995, *B. Gray 5938** (holo: CNS [2 sheets]; iso: B, BO, BRI, CANB, E, K, L, MEL, MO, NY, NSW, SING *distribuendi*).

Elaeocarpus sp. (=RFK/2907); Hyland (1982: 139).

Elaeocarpus sp. Mt Lewis (B.P.Hyland RFK2907); Thomas & McDonald (1987: 24).

Elaeocarpus sp. Mt Misery (L.J.Webb+ 10905); Guymer (1997: 67; 2017).

Elaeocarpus sp. (Mt Spurgeon BH 2907RFK); Hyland *et al*. (1999: 63).

Elaeocarpus sp. (Mt Spurgeon); Cooper & Cooper (2004: 162).

Elaeocarpus sp. 'Mount Spurgeon'; Crayn & Kupsch (2006).

Elaeocarpus sp. Mt Spurgeon (B.Hyland 2907RFK); Hyland *et al*. (2010).

Trees to 30 m tall, buttressed, outer bark blaze yellow, white, cream or brown, speckled markedly with longitudinal stripes; stipules ± triangular, *c*. 2 mm long, caducous; branchlets covered in short, white, appressed hairs <0.5 mm long. **Leaves** simple, alternate, crowded toward the branchlet tips; petiole (15–)20–45(–58) mm long, ± glabrous, usually with pulvinus at both ends, more pronounced at distal end; lamina obovate, oblanceolate or elliptic, 45–180 mm long, 19–80 mm wide, abaxial surface punctate, densely covered with small dark dots (? glands) visible (barely) to the naked eye, base cuneate, apex obtuse or slightly retuse; domatia present in secondary vein axils, 2–8(–10) per leaf, foveolate, glabrous; margins entire or crenate; venation reticulate, ± flush with adaxial leaf surface when fresh (slightly raised in dried material), prominent abaxially, ± glabrous. **Inflorescences** 2–5-flowered, usually arising behind leaves, occasionally axillary, racemose but appearing ± umbellate; peduncle 12–15 mm long, pubescent, hairs <0.5 mm, appressed. **Flowers** white or cream; pedicels 10–18 mm long, pubescent, hairs 0.5–1 mm, spreading; calyx cream or greenish cream

to brown, lobes narrowly triangular, 24–26 mm long, 5–6 mm wide at base, apex acute, densely pubescent to velvety outside, hairs 0.5–1 mm long, spreading to erect, golden-brown when dried, sericeous inside, hairs 2–3 mm long, appressed; petals 5, free, 35–40 mm long, *c*. 10 mm wide, apex 2–3 lobed, lobes *c*. 5 mm long, rounded to acuminate or acute, with dense hairs on the outside, glabrous or with very few scattered hairs on the inside, indumentum extending across middle half, and along 3/4 of the length of the petal, hairs appressed, 2–3 mm long, margins entire, glabrous; ovary hairy, globular, 5-locular, *c*. 10 ovules per locule, sericeous, hairs *c*. 2 mm long, erect to appressed; style 18–22 mm long, tapering to ovary, sericeous over the lower 2/3, hairs similar to ovary, stigma not expanded; stamens numerous (*c*. 55), filaments very slender, 10–15 mm long, sericeous, anthers tubular, *c*. 8 mm long, with very short ascending hairs, longer (to *c*. 1 mm) along midline on back, awned, posterior tooth longer (*c*. 1.5 mm), backward-tilted. **Fruits** drupaceous, broadly ovoid to ellipsoid, 50–55 mm long, 35–50 mm wide, dark blue, or slatey to brownish grey, glabrous, shrinking and cracking irregularly upon drying; pedicel 15–25 mm long; outer mesocarp 1.7–2.2 mm thick, detaching cleanly from inner mesocarp (stone). **Mesocarps** ovoid-ellipsoid, 30–45 mm long, 32–40 mm wide, robust, woody; sutures 5, forming grooves on prominent longitudinal ridges (flanges), grooves becoming shallower basally; flanges 3–4 mm high, 3–5 mm thick (mesocarp appearing 5-angled in transverse section, wall *c*. 11 mm thick), base attenuate, apex rounded to slightly pointed; surface punctate. **Seeds** 1–3 per fruit, ellipsoid, 18–20 mm long, 8–10 mm wide; embryo straight, endosperm entire. **Figs. 2 & 3A.**

***Additional specimens examined*: Queensland.** Cook District: TR 140 Cow LA, Jan 1975, *Hyland 7971** (BRI); Along the main path, *c*. 400 m from Mr Cooper's Camp, Mt Spurgeon NP, May 2010, *Baba 426 et al.** (BRI, CNS); Mt Misery E of Mt Spurgeon 15.4 km NNE of Mt Carbine, Nov 1988, *Jessup GJM919** (BRI); Mt Spurgeon, Jun 1990, *Gray 5196** (CNS), *5197* (BRI, CNS); TR 143, Zarda LA, near Zarda clearing, Sep 1973, *Hyland 2907RFK** (CNS), *2908RFK* (BRI, CANB, CNS); Mt Misery, Mt Carbine Tableland, Nov 1972, *Webb 10905** (BRI); SFR 143, Kanawarra, Carbine LA, Nov 1994, *Gray 5825* (CNS); *ibid*, Mar 1991, *Gray 5294* (BRI, CNS); *ibid*, Jul 1990, *Hyland 25789RFK** (CNS); *ibid*, Nov 1990, *Hyland 14087** (BRI, CNS); SFR 143, North Mary LA, May 1973, *Hyland 6731** (BRI); 32.5 km along Mt Lewis Road from Mossman – Mt Molloy Road, Dec 1989, *Jessup GJD3364** (BRI); Daintree NP, NW of Black Mountain, May 1998, *Forster PIF22897 et al.* (BRI); Cultivated Tolga, ex-Mt Lewis area beyond hut, May 2005, *Ford 4312 & Sankowsky* (CNS).

Key to large-fruited *Elaeocarpus* species allied to *E. carbinensis*

1 Leaf domatia present; mesocarps with flanges **2**
1. Leaf domatia absent; mesocarps without flanges **3**

2 Mesocarp 30–45 mm long, 32–40 mm wide; flanges 3–5 mm thick, distance between flanges 15–20 mm, valley between flanges shallow, weakly grooved; abaxial leaf surface with small dark dots; elevational range 940–1260 m, NE QLD . . . . . **E. carbinensis**
2. Mesocarp 41–50 mm long, 35–42 mm wide; flanges 5–10 mm thick, distance between flanges 20–25 mm, valley between flanges deeply grooved; abaxial leaf surface without dots; elevational range 50–500 m, NE QLD . . . . . **E. stellaris**

3 Fruits blackish, dark blue or dark green, 40–75 mm long, 30–50 mm wide; fibres permanently attached to mesocarp surface; anther awns present; elevational range 25–2500 m, New Guinea, Papuan Islands and the Moluccas . . . . . **E. womersleyi**
3. Fruits dull greenish-blue to khaki, 40–55 mm long, 33–40 mm wide; fibres detaching cleanly from mesocarp surface, ornamentation punctate and pitted with irregularly scattered pits; anther awns absent; elevational range near sea level–1200 m, NE QLD . . . . . **E. bancroftii**

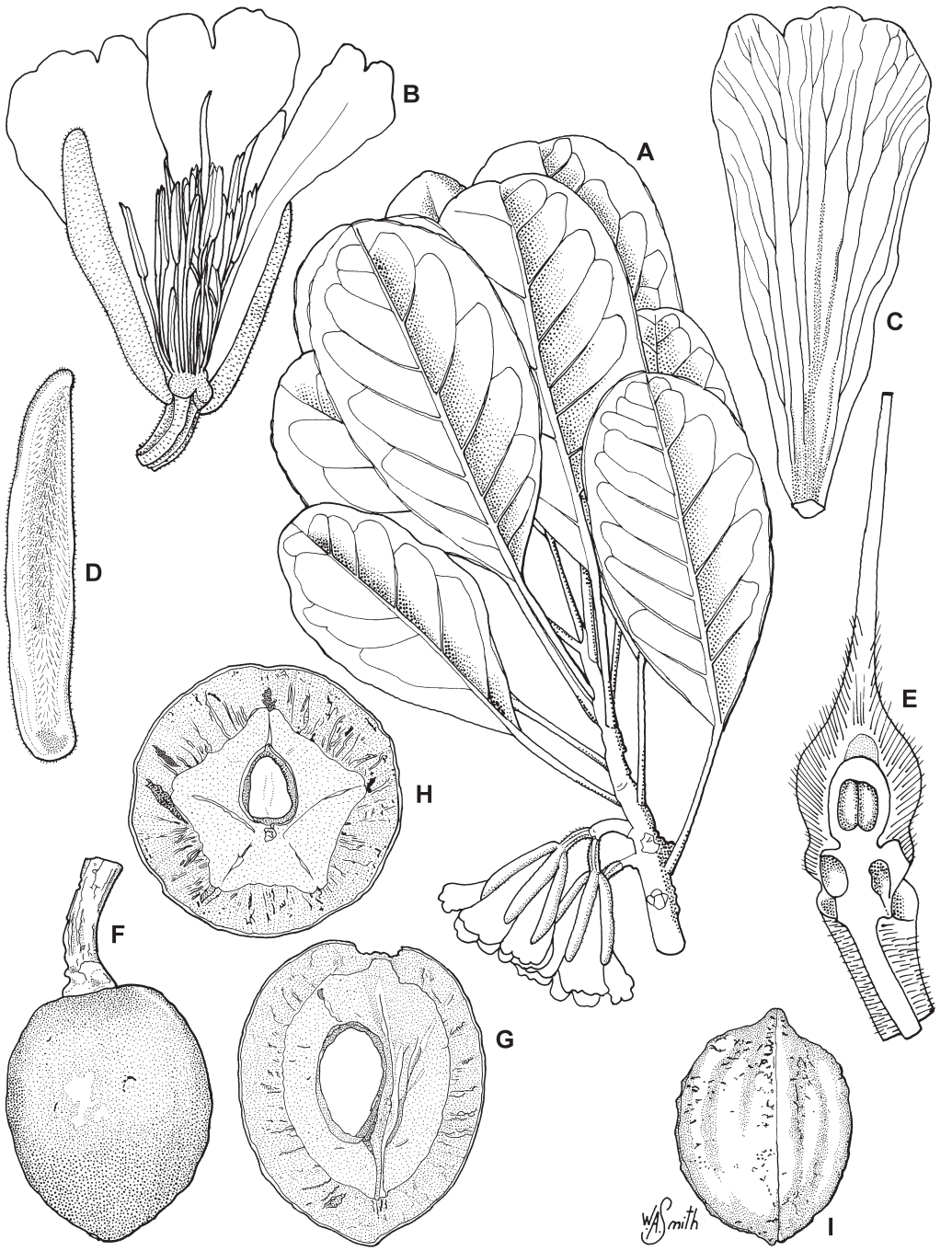

Fig. 2. ***Elaeocarpus carbinensis.*** A. leafy twig with flowers ×0.5. B. mature flower with two petals and sepals removed ×1.5. C. petal showing adaxial surface ×2. D. sepal showing abaxial surface ×2. E. pistil (ovary and pedicel partly sectioned longitudinally) ×3. F. lateral view of fruit ×0.8. G. lateral section of fruit ×1. H. transverse section of fruit showing 5-angled mesocarp ×1. I. lateral view of whole mesocarp with flesh removed ×1. A–E from *Gray 5938* (BRI, isotype); F from *Hyland 14087* (BRI); G–I from *Gray 5294* (CNS). Del. W. Smith.

Fig. 3. Mesocarps of ***Elaeocarpus carbinensis*** and similar species. A. ***E. carbinensis*** (*Gray 5197*, CNS). B. ***E. stellaris*** (*Stocker 1774*, CNS). C. ***E. bancroftii*** (*Gray 2328*, CNS). D. ***E. womersleyi*** (*Gagul 039*, CNS). Photos: Nick Rockett.

***Affinities*:** On the basis of similarities in mesocarp morphology (Gagul *et al.* unpublished; Rozefelds & Christophel 2002) and its close molecular phylogenetic relationship with *Elaeocarpus bancroftii* F.Muell. & F.M.Bailey and *E. stellaris* (Baba 2014; Phoon 2015), *E. carbinensis* seems best placed in Group VI, Subgroup B (Coode 1978, 1984) which comprises *E. bancroftii*, *E. stellaris* and *E. womersleyi* Wiebel (**Table 1**). The three Australian species *E. bancroftii*, *E. carbinensis* and *E. stellaris* are distinguished from the New Guinea species *E. womersleyi* by outer mesocarp fibres, which detach cleanly from the mesocarps (persistent and permanently attached in *E. womersleyi*, Coode 1984, **Fig. 3**). *E. womersleyi* has not been included in any molecular phylogenetic study to date so its evolutionary relationships remain unclear.

A fossil mesocarp (*Elaeocarpus peteri* Rozefelds & Christophel) from late Oligocene-early Miocene (Rozefelds 1990) deposits at Glencoe in central Queensland resembles *E. carbinensis* and *E. stellaris* in having pronounced ridges and punctate ornamentation (Rozefelds & Christophel 1996), but its precise relationships to extant lineages is unknown.

***Distribution and habitat*:** *Elaeocarpus carbinensis* is restricted to the Carbine Tableland west of Mossman and has been recorded on Mt Spurgeon, Mt Lewis and Mt Misery at elevations ranging from 940–1260 m. It occurs in notophyll vine forest and mixed mesophyll vine forest on soils derived from granite or a mixture of granite and basic volcanic rocks. Across the recorded localities mean annual temperature ranges between 19–20 °C, mean minimum and maximum temperatures of the coldest and warmest months range between 11–12 °C and 27–28 °C respectively, mean annual rainfall ranges between 1942–2319 mm and the mean rainfall of the driest month ranges between 123–161 mm.

Predicted future distribution

Environmental Niche Modelling (ENM) under contemporary climatic conditions predicts that suitable climate for *E. carbinensis* exists across several upland regions in the northern Wet Tropics including the Windsor and Carbine Tablelands, Thornton Peak and Mt Finnigan (**Fig. 4**). Herbarium records, however, indicate the realised distribution of the species includes only the Carbine Tableland. Explanations for the apparent failure of the species to fully occupy its predicted climate niche were not investigated in this study but may include a range of biotic and abiotic factors such as competitive exclusion, predation, disease, unsuitable geology/soil, or failure to recolonise after past extinction.

ENM models under future climates predict a complete loss of highly and moderately suitable habitat by 2040 and of all suitable habitat by 2080 across the Wet Tropics bioregion (**Figs. 4 & 5**). Although this study did not examine whether suitable habitat is predicted in other bioregions, the closest area of substantial upland rainforest outside the Wet Tropics is the Eungella region of central Queensland, located *c*. 250 km to the south east. Lowland tropical savanna and cleared land separates the Wet Tropics and Eungella therefore dispersal of the large fruits of this species, which is probably achieved only by rodents (which predate the seeds) and cassowaries, to suitable habitat elsewhere (should it exist) is highly unlikely.

***Phenology*:** Data from herbarium specimens indicate that flowering occurs in January and fruiting in March.

***Conservation status*:** All known wild plants of *Elaeocarpus carbinensis* are restricted to 940–1620 m altitude, and occur within protected areas (Daintree NP, Mt Lewis NP and Mt Spurgeon NP), but complete loss of suitable habitat by 2080 is predicted by the environmental niche modelling analysis. Assessment against the IUCN red list guidelines suggests this species should be recognised as **Vulnerable** under criterion **D2** (restricted distribution, and plausibility and immediacy of threat) due to climate change (IUCN 2012).

If the model predictions are realised then the survival of the species *in situ* will depend on rapid evolutionary change and/or inherent physiological plasticity to tolerate novel climates and the novel ecological communities that differential extinction and migration will bring about. The population demographics of the species have not been studied in detail but field observations indicate all known plants are large, old trees; to date no seedlings or juveniles have been located. This suggests that generation length is likely measured

Fig. 4. Potential distribution of ***Elaeocarpus carbinensis*** for contemporary and future climates under an intermediate emission scenario: a) MAXENT species distribution models of *Elaeocarpus carbinensis* mapping habitat suitability in the Wet Tropics under current conditions and years 2040, 2060 and 2080 under an intermediate emission scenario. Highly suitable habitat is mapped in black, moderately suitable habitat in dark grey, lowly suitable habitat in light grey and unsuitable habitat in the lightest grey.

in decades and that the potential for rapid evolutionary change is limited. Published studies on the physiology of the species are lacking therefore its capacity to tolerate novel climates is unknown.

Currently, the species is known from only 13 unique locational records on the Mt Carbine Tableland. Further studies are urgently required to increase knowledge of its realised distribution, population demographics, physiology and ecology to enable a revised assessment of conservation status. In the meantime application of the precautionary principle justifies the establishment of an *ex situ* conservation program including both germplasm banking and cultivation of living plants.

***Etymology*:** The specific epithet *carbinensis* refers to the Carbine Tableland in northeast Queensland, the area to which the species is restricted.

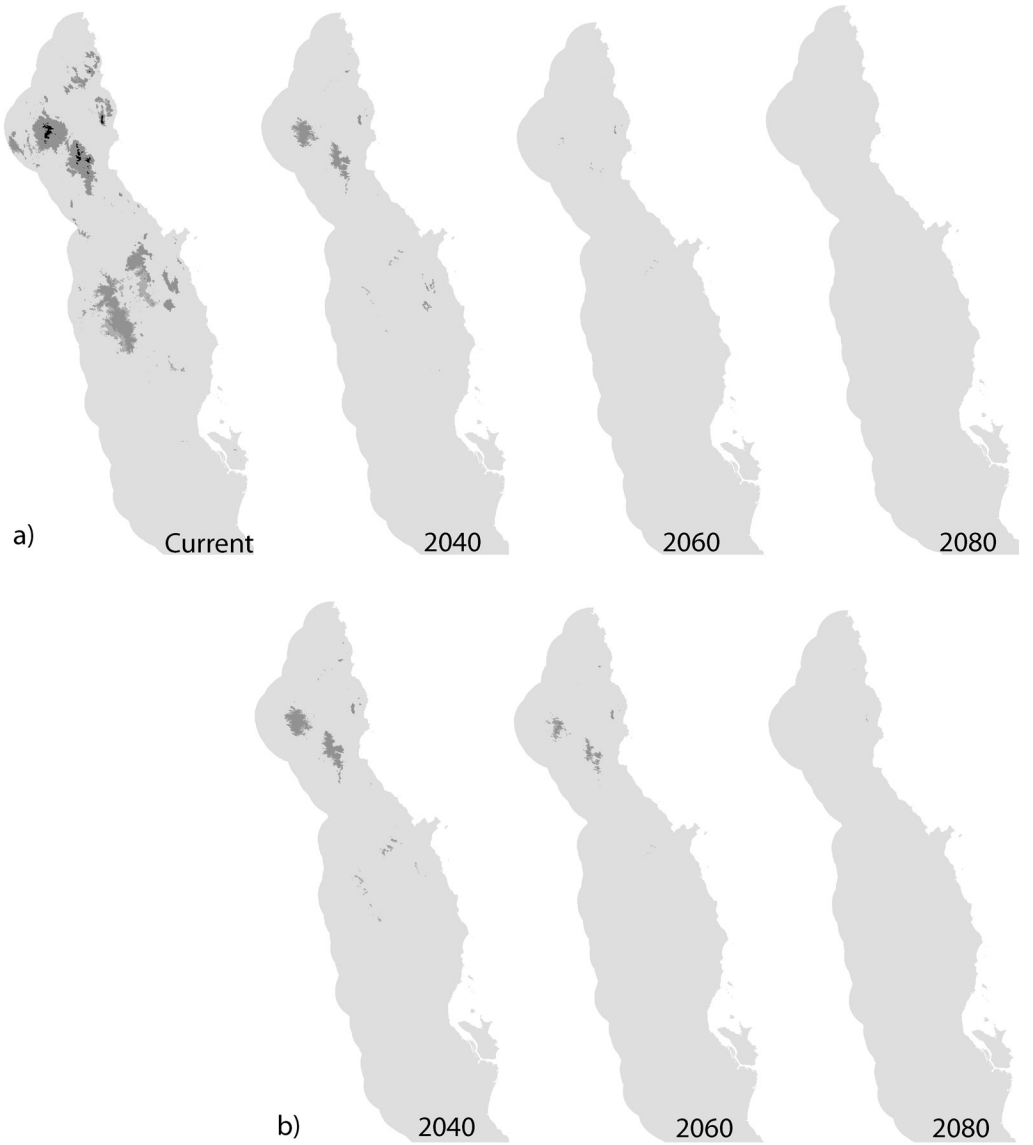

Fig. 5. Potential distribution of ***Elaeocarpus carbinensis*** for contemporary and future climates under extreme and best-case emission scenarios: a) MAXENT species distribution models of *Elaeocarpus carbinensis* mapping habitat suitability in the Wet Tropics under current conditions and years 2040, 2060 and 2080 under an extreme emission scenario. b) Habitat suitability modelled for the years 2040, 2060 and 2080 under a best-case emission scenario. Highly suitable habitat is mapped in black, moderately suitable habitat in dark grey, lowly suitable habitat in light grey and unsuitable habitat in the lightest grey.

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Table 1. Comparison of features of *Elaeocarpus carbinensis* and similar species

	E. carbinensis	***E. stellaris***	***E. bancroftii***	***E. womersleyi***
Distribution	940–1260 m, Mt. Spurgeon – Mt. Lewis – Mt. Misery area on Carbine Tableland.	50–500 m, Alexandra Creek – McDowall Range to Innisfail.	0–1200 m, Cooktown to Innisfail.	25–2500 m, New Guinea, Papuan Islands, Moluccas.
Habit	tree to 30 m, buttressed	tree to 25 m, may be buttressed	tree to over 30 m, buttressed, flanged or fluted	tree to 45 m, may be buttressed
Leaf margin	entire or crenate	entire or crenate	entire or sinuate	entire to slightly dentate, or sinuate
Leaf surfaces	glabrous or sparsely hairy (hairs visible with a lens), densely covered with small, barely visible, dark dots (? glands) below	glabrous above, sparsely hairy below	glabrous above, sparsely hairy below (hairs visible with a lens)	glabrous on both sides
Leaf dimensions	45–180 × 19–80 mm	80–180 × 40–90 mm	50–180 × 25–50 mm	100–150 × 40–80 mm
Petiole	(15–) 20–45 (–58) mm long; pulvinus at both ends, more pronounced at distal end	20–55 mm long; pronounced pulvinus at both ends	10–45 mm long; pulvinus at base, apex, or both	10–30 mm long; pulvinus generally absent, sometimes weakly present at base, apex or both
Stipules	*c.* 2 mm long, caducous	*c.* 2 mm long, caducous	1–2 mm long, deciduous	1–2 mm long, deciduous, sometimes caducous
Leaf domatia	present as foveoles in secondary vein axils, glabrous, 2–8(–10) per leaf	present as foveoles in secondary vein axils, glabrous, (–5)10–17 per leaf	absent	absent
Petals	5, white or cream, obovate, 35–40 mm long and 10 mm wide, with dense hairs on the outside, glabrous or with very few scattered hairs on the inside, divided at apex into 2–3 lobes, lobes *c.* 5 mm long	5, white or cream, obovate, 20–25 mm long and 10 mm wide, with dense hairs on both sides, divided at the apex into 3 lobes, lobes *c.* 3 mm long	4, white, obovate, 20–24 mm long and 10–18 mm wide, with sparse hairs on the outside, glabrous or with very few scattered hairs on keel on the inside, divided at apex into *c.* 3(–5) lobes, lobes *c.* 3 mm long	4, white or cream, obovate, 30–40 mm long and 15–20 mm wide, with hairs on the inside of basal half, divided at apex into 3–5 lobes, lobe length unknown
Anther awns	1–1.5 mm long	present, *c.* 1 mm long	absent	present, *c.* 2 mm long
Stamens	*c.* 55	50–60	30–50	*c.* 40
Filaments	10–15 mm long, with long appressed or slightly ascending hairs	6–8 mm long, with long ascending or appressed hairs	5–9 mm long, with long scattered ascending hairs	6–13 mm long, hairs unknown
Fruit colour	dark blue, or slatey to brownish grey	blue, shiny	dull greenish-blue to khaki	blackish, dark blue or dark green

	E. carbinensis	*E. stellaris*	*E. bancroftii*	*E. womersleyi*
Fruit shape & dimensions	broad ovoid to ellipsoid, 50–55 × 35–50 mm	globose to ellipsoid, 43–65 × 50–60 mm	globose to ellipsoid, 40–55 × 33–40 mm	globose or obovoid, 40–75 × 30–50 mm
Pedicel	15–25 mm long	23–25 mm long	10–35 mm long	9–26 mm long
Mesocarp dimensions	30–45 × 32–40 mm	41–50 × 35–42 mm	30–80 × 20–70 mm	40–55 × 30–50 mm
Mesocarp fibres	detach cleanly from mesocarp	detach cleanly from mesocarp	detach cleanly from mesocarp	persistent and permanently attached to mesocarp
Mesocarp flanges	5, 3–5 mm thick, distance between flanges 15–20 mm, valley between flanges shallow	5, 5–10 mm thick, distance between flanges 20–25 mm, valley between flanges deeply grooved	absent	absent
Mesocarp ornamentation	punctate	punctate	punctate and pitted with irregularly scattered pits	fibres permanently attached
Sutures	5, prominent on flanges, becoming less grooved distally	5, prominent on flanges grooved	4 (–5), grooved, sometimes on weak ridges distally	difficult to see due to persistent fibres permanently attached to surface, but mesocarp 4–partite in TS
Locules	5	5	(2–) 4 (–5)	4 (–5)
Ovules	*c*. 10 per locule	4–8 per locule	9–10 per locule	6 per locule
Seeds	1–3 per fruit	1–3 per fruit	1–2 per fruit	1–2 per fruit

Where necessary, information was also taken from other sources (Coode 1978, 1984; Dettman & Clifford 2000; Rozefelds & Christophel 2002; Cooper & Cooper 2004; Phoon 2015). Mesocarp characters for each species are illustrated in **Fig. 3**.