

THE AMPHIBIAN FAUNA OF EUNGELLA AND THEIR IMPORTANT ROLE IN UNRAVELLING THE EVOLUTIONARY HISTORY OF THE AUSTRALIAN EAST COAST CLOSED FOREST BIOTA

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The species diversity and endemism of the amphibians of the closed forest habitats at Eungella are assessed in the context of surrounding bioregions. The Central Mackay Coast bioregion in which Eungella occurs has a relatively high diversity of frogs, with 24 species from three native families: 5 species of Limnodynastidae, 7 Myobatrachidae, and 12 Pelodyadidae. The closed forest communities support a high level of phylogenetic endemism, with representatives of three ancient lineages of myobatrachids: one species of *Rheobatrachus*, two *Taudactylus*, and a disjunct population of a species of *Mixophyes*. In addition, it supports disjunct populations of several species of the genus *Litoria*. This high level of endemism is indicative of the importance of the upland rainforests of Eungella as a cool and moist refuge that has persisted over many millions of years.

Keywords: Eungella, Amphibia

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INTRODUCTION

Eungella, and the Clarke Range in which it occurs in mid-eastern Queensland, holds a special place in understanding the evolution of Australia's amphibian fauna due to its high phylogenetic endemism and species diversity. Unravelling and telling that story requires that we quantify its significance and place it into the larger context of the evolutionary history of the biota of eastern Australia. The aim of this study is to consider the amphibian fauna of Eungella National Park (Clarke Range) in broad biogeographic and evolutionary contexts, which together will lead to a deeper appreciation of why further research of its importance and intrinsic value is required. The outcome also serves to strengthen the conservation significance of the area.

For many decades Australian biologists have focused attention on species richness and endemism in the arc of rainforest that occurs as a series of disjunct blocks associated with the Great Dividing Range and eastern uplands of Australia. Attention is drawn to two important biogeographic features. First is that the mesic biome, which encompasses rainforest elements, was the ancestral vegetation of Australia; and, second, that expansion of drier-adapted sclerophyllous flora occurred as the climate dried and became warmer as the Australian continent drifted northwards over the past 30 to 50 Myr (Crisp *et al.*, 2001; Hill, 2004). Consequently, mesic communities contracted to near

coastal mountains that receive high annual rainfall and now function as refugia (Crisp *et al.*, 2001). To reflect their historical connection and the process of climate warming and drying, these have been termed climate relicts (Hampe & Jump, 2011; Rosauer *et al.*, 2015). While most emphasis has been placed on identifying the location and biotic composition of these refugia, there has also been a focus on the role of the geographic barriers or gaps that separate them (Byrne *et al.*, 2008, 2011; Bryant & Krosch, 2016). More recently, the investigation of biotic composition has involved testing of specific evolutionary hypotheses based on the comparative phylogenetic pattern of taxa (species and populations) that have disjunct distributions in the refugia (Joseph & Moritz, 1994; Joseph *et al.*, 1995; Stuart-Fox *et al.*, 2001; Mahony *et al.*, 2006; Catullo & Keogh, 2014). These studies have uncovered common phylogeographic patterns, but they also demonstrate that different taxa show different responses to past environmental changes. Missing from these studies, which have included anurans, is the inclusion of taxa that have a deep evolutionary antiquity and which are represented in only a small number of the refugia. Inclusion of such taxa in comparisons is likely to be valuable since, because of their antiquity, the refugia are often disproportionately important for the conservation of the genetic diversity and phylogenetic history they represent (Rosauer *et al.*, 2009; Hampe & Jump, 2011).

To address this issue, this study focuses on the taxa of deeper genetic antiquity which form the endemic component of the amphibian fauna of Eungella National Park (NP). By necessity this analysis includes information on amphibian species richness and range limits among refugia.

METHODS

The focus of this study is on the biogeography of the anuran fauna of the closed forest vegetation communities at Eungella. The category 'closed forest' is used to maintain consistency with the terminology used in several reviews of the biogeography of eastern Australia (Byrne *et al.*, 2011; Bryant & Krosch, 2016). This category is equivalent to 'wet-forest' used in other descriptions such as that applied by Meyer *et al.* (this volume).

The analysis of anuran distribution is undertaken at the scale of the larger bioregional landscape unit (Thackway & Cresswell, 1995). The Eungella uplands are within the Central Mackay Coastal (CMC) bioregion. The largest areas of upland closed forests within this bioregion occur in Eungella NP. To assess the biogeographic context of the closed forest refugia for amphibians, a process of classifying species by taxonomy, distribution, forest preference and breeding biology has been adopted so that the analysis was biologically meaningful and tractable. Accordingly, the geographic analysis was restricted to all presence records for amphibians from the *Atlas of Living Australia* (ALA), for the bioregions (Thackway & Cresswell, 1995) that include the Central Mackay Coast (CMC) and the two adjacent bioregions to the north, south and west based on IBRA7 mapping (<https://www.environment.gov.au/land/nrs/science/ibra>).

The data-set was therefore restricted to the Central Mackay Coast (CMC), the Brigalow Belt North (BBN) (that surrounds the CMC on its north, south and west), Southern Eastern Queensland (SEQ) (further south), Brigalow Belt South (BBS) (further south-west), Wet Tropics (WT) (further north), Einasleigh Upland (EU) (further north-west), and Desert Upland (DU) (further west) bioregions (Figure 1). Some reference is also made to an isolated closed forest refugium at Kroombit Tops, which is to the south-east of Eungella and is within the SEQ bioregion.

Throughout, reference is made to the names of barriers of low-lying country that separate the closed forest refugia (see Bryant & Krosch, 2016), including the 'Burdekin Gap' between the CMC and the WT

bioregions, which corresponds to the lower Burdekin River drainage, and the 'St Lawrence Gap' between the CMC and SEQ bioregions that corresponds to the lower Fitzroy River drainage. For the quantitative assessment, the refugia and gaps are considered at the landscape scale using the bioregional approach.

There is considerable debate surrounding the higher taxonomic nomenclature among the Australian ground frogs and tree frogs (Frost *et al.*, 2006; Duellman *et al.*, 2016). For the ground frogs, although all are recognised as belonging to a southern hemisphere clade of Gondwanan origin (superfamily Myobatrachoidea), several familial and subfamilial classifications have been proposed (Heyer & Liem, 1976; Farris *et al.*, 1982; Frost *et al.*, 2006). Because there is instability in usage, I have chosen to adopt a conservative approach and follow the taxonomy described by Frost *et al.* (2006). The ground frogs are placed into two families, the Limnodynastidae (8 genera) and Myobatrachidae (13 genera), with *Mixophyes* and *Rheobatrachus* (formerly Rheobatrachidae of Heyer & Liem, 1976) placed in the Myobatrachidae. The phylogenetic analysis of Frost *et al.* (2006) placed these two genera as a sister lineage to all myobatrachid frogs. Read *et al.* (2001) provided a phylogenetic study of myobatrachid frogs that assumed monophyly of the group and used only *Limnodynastes* to root the tree and, therefore, did not consider the relationships of *Mixophyes* and *Rheobatrachus*. Their analysis provided strong support for the position that *Taudactylus* was the sister lineage to all the other myobatrachid frogs they tested. The important point for this study is that, whatever classification is adopted, the ground frogs are old endemics with a long evolutionary history in Australia. Furthermore, in phylogenetic analyses several of the important Eungella taxa are shown to be basal in the topology of the family tree and have long evolutionary lineages.

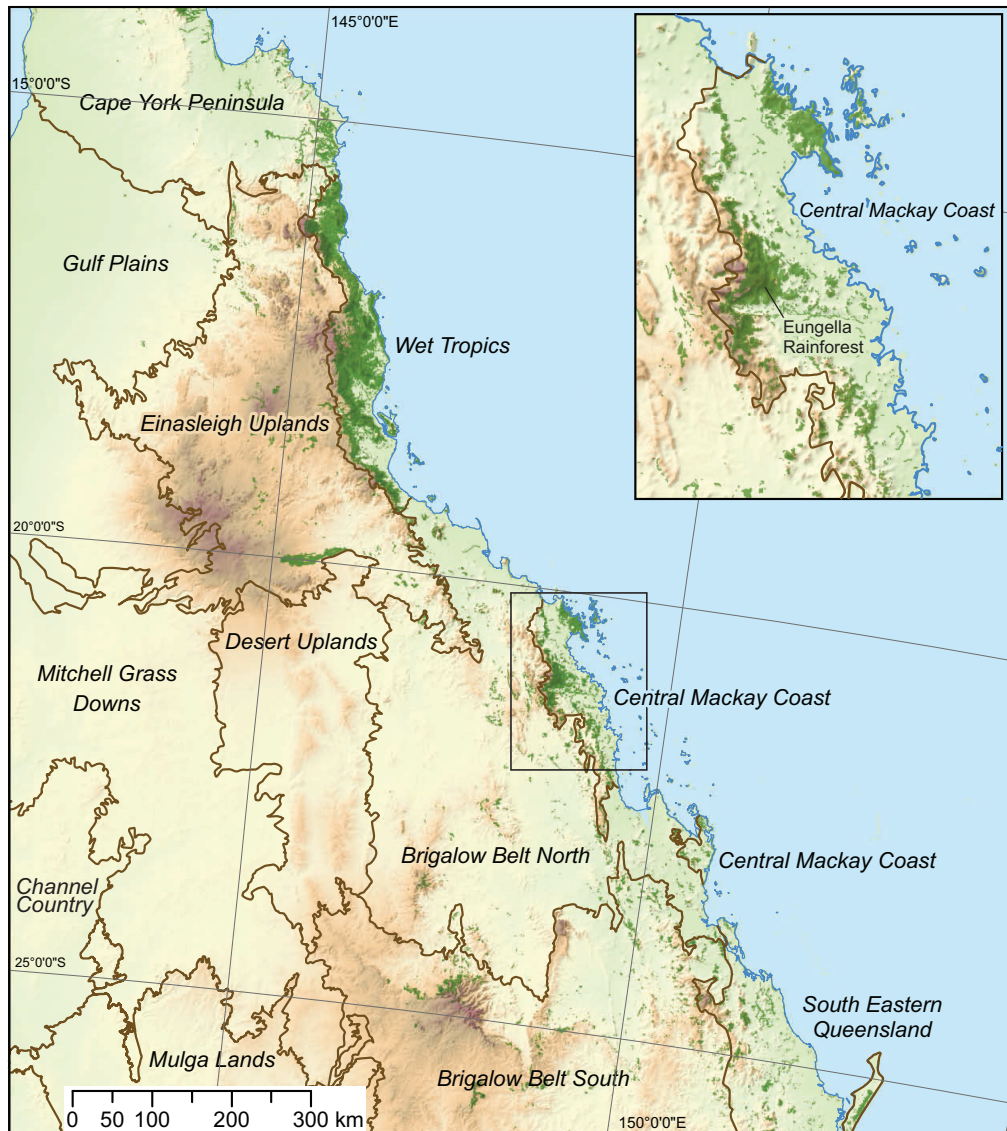
In contrast, the numerically large Australo-Papuan tree frog family, Pelodyadidae, is divided into three genera, *Litoria* (166 species), *Cyclorana* (13 species, restricted to Australia) and *Nyctimystes* (26 species, restricted to Papua New Guinea), although there is also considerable debate about generic level subdivision of *Litoria* (Duellman *et al.*, 2016). To simplify comparisons of geographic distribution in the analysis, here the intra-generic 'species groups' of *Litoria*, defined by Tyler & Davies (1978) and based on morphology and behaviour, are used.

All ALA records were scrutinised, and those records that failed two of the filters applied to indicate validity in the Atlas were removed as potentially

spurious. There are numerous sources of bias that occur in atlas records, and it is not possible to account for all of them. The approach taken was to accept that the majority of records provide a good overall picture of species distribution, and to scrutinise outliers based on expert knowledge of distribution and habitat preferences of the specific taxon. Undoubtedly, there are some spurious records that have been included in

the analysis since the correct species identification of some records, particularly those that are geographic outliers, can pose a significant problem if vouchers are not available in museum collections to support the observations. For the primary objective of this study, however, these records do not involve the significant anuran fauna that occur as endemic or disjunct populations in the closed forest at Eungella.

FIGURE 1. Mid-eastern Queensland with elevation (light colouring), rainforest vegetation communities (green) and the bioregions used in the comparisons of anuran distributions. Inset shows the distribution of rainforest and altitude at Eungella. The rainforest distribution is derived from the *Atlas of Living Australia* (NVIS 41. Major Vegetation Groups).



To enable a comparison of the anuran fauna among the refugia, records were divided into those found in closed forest vegetation communities (rainforest and wet sclerophyll forest) and those in open forest vegetation communities (dry sclerophyll forests, savannah woodlands, grasslands and heath communities). Species records were then scored by the bioregions in which they occurred, followed by their breeding habitat – predominantly lotic (stream), lentic (ponds, swamps and ephemeral pools), or direct development. For the majority of frog species, it is relatively straightforward to place them into the categories of closed or open forest dwellers. There are several species, however, for which this subdivision is difficult and possibly controversial, and these tend to be those species that are common and widespread generalists. I have applied a threshold of 80% of records (based on expert opinion) to categorise these species. *Litoria wilcoxii*, for example, is associated with the riparian zone of permanent watercourses. Streams that this frog occupies at higher altitude may be flowing through closed forest, while at lower altitude it may be predominantly open forests. Nevertheless, the riparian zone may include closed forest elements, and the frogs occupy a stream habitat that provides moisture through all seasons. My observations are that this frog will penetrate into closed forests (e.g. rainforest), but it is most abundant in streams in open forests (supported by observations by Meyer *et. al.*, this volume). In contrast, its close sibling species, *L. jungguy*, is most commonly found in stream habitats in closed forests in the WT bioregion.

Area of Occupancy (AAO) and Extent of Occupancy (EOO) are calculated for a small number of species following the IUCN Red List approach (IUCN 2006), and the AAO is based on a 0.02 degree grid and the EOO on a minimum convex polygon.

RESULTS

The Central Mackay Coast bioregion (CMC) has a relatively high diversity of frogs, with 24 species from three native families, 5 species of Limnodynastidae, 7 Myobatrachidae and 12 Pelodyadidae (Table 1).

Three anuran species are endemic to the CMC bioregion, and all are myobatrachids that are restricted to the closed forests of the Eungella escarpment and tablelands. One of these species, *Rheobatrachus vitellinus*, is presumed to be extinct, and *Taudactylus eungellensis* has suffered serious declines in distribution in the past 30 years (see Meyer *et. al.*, this volume). These species occur in close association with stream habitats, with the third endemic species, *T. liemi*,

often found in seepages and rock scree at the edge of streams and not directly in pools or riffles in the stream. Each of these species has a derived breeding biology: *Rheobatrachus* has direct development of the tadpoles and is a gastric brooder, and the *Taudactylus* species deposit a small number of large, yolky eggs beneath rocks or deep in crevices, and the tadpole stage is free living. *Rheobatrachus* showed, and *T. eungellensis* shows, strong morphological and behavioural adaptations to living in fast-flowing streams. There are no members of these genera in the habitats of the hot and drier open forest/savannah communities of the BBN bioregion to the north, south and west of the CMC bioregion, but they do have conspecifics in closed forest in the further removed WT bioregion to the north (*Taudactylus*) and SEQ bioregion to the south (*Rheobatrachus* and *Taudactylus*).

Not only are these species endemic to the CMC bioregion, but their distributions are tightly limited to the fast-flowing streams of the tableland and escarpment at Eungella, such that their area of occupancy (AOO) and Extent of Occupancy (EEO) are among the smallest of Australian frogs (Table 2). *Rheobatrachus vitellinus* occurred only at Eungella, and its congener *R. silus* (also presumed extinct), was restricted to closed forest habitats in the Conondale and Blackall Ranges in the SEQ bioregion, to the south of the St Lawrence Gap (Table 1). Both have very restricted ranges; the AOO are 108 and 48 sq. km, and EEO are 753 and 98 sq. km, respectively. There is no record of this genus in the WT bioregion to the north of the Burdekin Gap, despite this area supporting a much larger area of closed forest than that at Eungella.

Species of the genus *Taudactylus* are closely associated with recognised closed forest refugia in eastern Australia. Two extant species occur at Eungella (CMC bioregion), two in the WT bioregion (considered extinct), and two in the SEQ bioregion (Table 1). The two species in the SEQ bioregion occupied separate, isolated refugia: *Taudactylus pleione* at Kroombit Tops to the south-west of Eungella, which is extant but critically endangered, and *T. diurnus* further south in the Conondale, Blackall and D'Aguilar Ranges. In the Conondale and Blackall Ranges, *T. diurnus* co-occurred with *R. silus*, and both are presumed extinct. Of the two species of *Taudactylus* that occurred in the WT bioregion, one (*T. acutirostris*) is presumed extinct, and the other (*T. rheophilus*) is listed as critically endangered (Table 1) with no known extant populations. Summarising, two species of *Rheobatrachus* and three species of *Taudactylus* that occurred

in the refugia have disappeared, and two of the remaining three species of *Taudactylus* have been subject to declines in distribution and abundance within the small refuges where they occur (Table 1).

There are only two other species of myobatrachid and three species of pelodyradid that are classed as closed forest species in the CMC bioregion (Table 1). Among the myobatrachids, *Adelotus brevis* and *Mixophyes fasciolatus* have disjunct populations in the closed forests at Eungella, and the nearest populations occur to the south in the SEQ bioregion. Eungella represents the northernmost populations of these species, and neither occur in the WT bioregion to the north. Unlike *Rheobatrachus* and *Taudactylus*, populations of these species are widespread in closed forest habitats of the SEQ bioregion and further south in NSW. Both also occur as disjunct populations at Kroombit Tops, at the northern extent of the SEQ bioregion, to the south-east of Eungella.

Among the pelodyradids there is no species endemic to Eungella or the CMC bioregion (Table 1). Two species, *L. chloris* and *L. revelata*, classed as closed forest inhabitants, have disjunct populations at Eungella. I have classified both species as pond breeders ('lentic') although they are often encountered along streams, but where they do occur in the riparian zone they breed in slow-moving ponds or isolated rock pools (see Meyer *et al.*, this volume). *Litoria chloris* will also often breed in small ephemeral pools away from the riparian zone. There are no records of this frog in the BBN bioregion, and the species does not occur in the WT bioregion where a sister sibling, *L. xanthomera*, occurs (Davies *et al.*, 1986). At Eungella, *L. revelata* is known only from high altitude on the plateau and escarpment, where it is associated with riparian habitats and human-constructed ponds. *Litoria revelata* has a disjunct population in the WT bioregion and is more widespread in the SEQ bioregion, but it does not have a population at Kroombit Tops. It has an extensive southern latitudinal distribution in closed forest habitats in eastern NSW.

The other seven species of *Litoria* with records in the CMC bioregion also occur in suitable habitats in the surrounding BBN bioregion, and these species are classed as habitat generalists. Apart from *L. wilcoxii*, none are stream specialists and none have tadpoles showing morphological adaptations to fast-flowing water. *Litoria wilcoxii* is widely distributed in streams that flow east from the Great Dividing Range from the Sydney Basin bioregion in the south to the WT bioregion, and occurs in most streams that

have riparian vegetation. This frog occurs across the entire altitudinal range at Eungella, but is most common along slower-flowing open streams in the valley and on the tablelands, and is not common in the dense rainforest riparian zone or well adapted to the fast-flowing streams of the escarpment that are favoured by *Rheobatrachus* and *Taudactylus* (see Meyer *et al.*, this volume).

Six species of myobatrachid frog (*Limnodynastes peronii*, *Limnodynastes terrareginae*, *Platyplectrum ornatum*, *Pseudophryne raveni*, *Pseudophryne major* and *Uperoleia fusca*) that are not dependent on closed forest habitats, occur at Eungella, and all but one (*Limnodynastes terrareginae*) breed in pools and ephemeral habitats (Table 1). Four of these species (*L. peronii*, *P. ornatum*, *P. major* and *L. terrareginae*) also occur in the open woodland/savannah habitats of the BBN bioregion and have extensive distribution outside these bioregions. In the CMC bioregion, *Uperoleia fusca* occurs only in the far south in the moist forests of the Byfield area, with a disjunct population at higher altitude at Eungella. This frog is common south of the St Lawrence Gap and along the eastern seaboard to southern NSW, where it is not a specialist of closed forest habitats. *Pseudophryne major* is also at the northern limit of its distribution in the CMC bioregion, and has a more extensive distribution to the south. This species does not penetrate into rainforest communities and is usually found in sclerophyll forest, both open and closed. A sibling species (*P. covacevichae*) occurs in the WT bioregion and is also associated with sclerophyll forest communities, not rainforest.

Closed forest refugia to the north and south of Eungella, in the WT and SEQ bioregions, also have high levels of species diversity and endemic anuran taxa (Table 1). The WT bioregion has 14 species of Microhylidae, and no species of this family are found south of this bioregion. Similarly, there is one species of the family Ranidae found in the WT bioregion and further north on Cape York. Evidently, the Burdekin Gap is a considerable barrier to southern dispersal of these frogs. Species in these families are widely accepted to have entered Australia from the north when the Australia continental plate collided with the Asia plate.

There are five species of myobatrachid frogs that are endemic to the WT bioregion (3 species of *Mixophyes*, and 2 species of *Taudactylus*). One species of *Pseudophryne* (*P. covacevichae*) is found mostly in the bioregion but has some populations in the adjacent western Einsleigh Uplands bioregion. No genus of myobatrachid is endemic to the WT bioregion.

TABLE 1. Frogs of Eungella and the surrounding bioregions classified into closed forest and open forest habitats, and by breeding location. The uplands of Eungella are dominated by closed rainforest and wet sclerophyll vegetation communities due to the high annual rainfall, whereas the lowlands are dominated by open forest communities with lower annual rainfall. Species are arranged with those occurring in the Eungella Central Mackay Coast bioregion listed first, followed by the other bioregions. To emphasise the importance of the high rainfall habitats, they are presented in the first column. Conservation Status is based on the National *Environmental Protection and Biodiversity Conservation Act* (2000) listing of threatened species, and categories follow the IUCN (2004) classification: *E* Extinct, *CE* Critically Endangered, *END* Endangered.

Species	Closed Forest (rainforest and wet sclerophyll forest communities)	Open Forest communities	Wet Tropics bioregion	Brigalow Belt North bioregion	Eungella, Central Mackay Coast bioregion	South Eastern Queensland bioregion	Stream (lotic)	Pool (lentic)	Direct Development	Conservation status (EPBC Act)
<i>Rheobatrachus vitellinus</i>	X				X		X			E
<i>Taudactylus eungellensis</i>	X				X		X			END
<i>Taudactylus liemi</i>	X				X		X			
<i>Adelotus brevis</i>	X				X	X	X	X		
<i>Mixophyes fasciolatus</i>	X				X	X	X			
<i>Limnodynastes peronii</i>		X	X	X	X	X	X	X		
<i>Limnodynastes tasmaniensis</i>			X	X	X	X		X		
<i>Limnodynastes terraereginae</i>		X		X	X	X	X	X		
<i>Platyplectrum ornatum</i>		X	X	X	X	X		X		
<i>Pseudophryne raveni</i>		X		X	X	X		X		
<i>Pseudophryne major</i>		X		X	X	X		X		
<i>Uperoleia fusca</i>		X		X	X	X		X		
<i>Litoria chloris</i>	X				X	X		X		
<i>Litoria gracilenta</i>	X	X	X	X	X	X		X		
<i>Litoria revelata</i>	X		X		X	X		X		
<i>Litoria wilcoxii</i>		X	X	X	X	X	X			

Species	Closed Forest (rainforest and wet sclerophyll forest communities)	Open Forest communities	Wet Tropics bioregion	Brigalow Belt North bioregion	Eungella, Central Mackay Coast bioregion	South Eastern Queensland bioregion	Stream (lotic)	Pool (lentic)	Direct Development	Conservation status (EPBC Act)
<i>Litoria caerulea</i>		X	X	X	X	X		X		
<i>Litoria fallax</i>		X	X	X	X	X		X		
<i>Litoria latopalmata</i>		X	X	X	X	X		X		
<i>Litoria rothii</i>		X	X	X	X			X		
<i>Litoria rubella</i>		X	X	X	X			X		
<i>Mixophyes carbinensis</i>	X		X				X			
<i>Mixophyes coggeri</i>	X		X				X			
<i>Mixophyes schevilli</i>	X		X				X			
<i>Mixophyes fleayi</i>	X					X	X			
<i>Mixophyes iteratus</i>	X					X	X			
<i>Philoria</i> spp.	X					X			X	
<i>Rheobatrachus silus</i>	X					X	X		X	E
<i>Taudactylus acutirostris</i>	X		X				X			E
<i>Taudactylus rheophilus</i>	X		X				X			END
<i>Assa darlingtoni</i>	X					X			X	
<i>Taudactylus diurnus</i>	X					X	X			E
<i>Taudactylus pleione</i>	X					X	X			CE
<i>Limnodynastes convexiusculus</i>			X	X				X		
<i>Pseudophyrne covacevichae</i>			X							
<i>Uperoleia altissima</i>			X	X				X		
<i>Limnodynastes fletcheri</i>			X	X				X		

Species	Closed Forest (rainforest and wet sclerophyll forest communities)	Open Forest communities	Wet Tropics bioregion	Brigalow Belt North bioregion	Eungella, Central Mackay Coast bioregion	South Eastern Queensland bioregion	Stream (lotic)	Pool (lentic)	Direct Development	Conservation status (EPBC Act)
<i>Linnodynestes salmini</i>				X		X		X		
<i>Crinia desarticola</i>				X				X		
<i>Crinia parinsignifera</i>				X		X		X		
<i>Crinia remota</i>				X				X		
<i>Crinia signifera</i>				X		X		X		
<i>Crinia tinnula</i>						X		X		
<i>Uperoleia lithomoda</i>				X				X		
<i>Litoria dayi</i>	X		X				X			END
<i>Litoria eucnemis</i>	X		X				X			
<i>Litoria jungguy</i>	X		X				X			
<i>Litoria lorica</i>	X		X				X			CE
<i>Litoria myola</i>	X		X				X			END
<i>Litoria nannotis</i>	X		X				X			END
<i>Litoria nyakalensis</i>	X		X				X			CE
<i>Litoria rheocola</i>	X		X				X			END
<i>Litoria serrata</i>	X		X				X			
<i>Litoria xanthomera</i>	X		X					X		
<i>Litoria brevipalmata</i>	X					X		X		
<i>Litoria dentata</i>	X	X				X		X		
<i>Litoria kroombitensis</i>	X					X	X			
<i>Litoria pearsoniana</i>	X					X	X			

Species	Closed Forest (rainforest and wet sclerophyll forest communities)	Open Forest communities	Wet Tropics bioregion	Brigalow Belt North bioregion	Eungella, Central Mackay Coast bioregion	South Eastern Queensland bioregion	Stream (lotic)	Pool (lentic)	Direct Development	Conservation status (EPBC Act)
<i>Litoria bicolor</i>			X	X				X		
<i>Litoria inermis</i>			X	X			X			
<i>Litoria infrafrenata</i>			X	X				X		
<i>Litoria microbelos</i>			X					X		
<i>Litoria nigrofrenata</i>			X					X		
<i>Litoria pallida</i>			X					X		
<i>Litoria nasuta</i>			X	X		X		X		
<i>Litoria olongburensis</i>						X		X		
<i>Litoria cooloolensis</i>						X		X		
<i>Cyclorana alboguttata</i>				X				X		
<i>Cyclorana brevipes</i>				X				X		
<i>Cyclorana novaehollandiae</i>				X				X		
<i>Litoria aurea</i>						X	X	X		
<i>Litoria freycineti</i>						X		X		
<i>Litoria verreauxii</i>						X		X		
<i>Uperoleia laevisgata</i>						X		X		
<i>Lechriodus fletcheri</i>	X					X		X		
<i>Hylarana daemeli</i>	X		X				X			
<i>Austrochaperina</i> (4 spp.)	X		X						X	
<i>Cophixalus</i> (17 spp.)	X		X						X	

TABLE 2. Area of Occupancy (AOO) and Extent of Occupancy (EOO) for the three endemic anuran species found at Eungella, based on records in the *Atlas of Living Australia*. AOO is based on a 0.02 degree grid, and the EOO on the minimum convex polygon.

Species	Number of Records	Area of Occupancy (sq. km.)	Extent of Occupancy (sq. km.)
<i>Rheobatrachus vitellinus</i>	33	48	98
<i>Rheobatrachus silus</i>	127	108	753
<i>Taudactylus eungellensis</i>	579	28	405
<i>Taudactylus liemi</i>	144	16	115

Similarly, there are eight species of pelodyadid frogs in the WT, all of which belong to two species groups that show adaptations to stream dwelling. No members of these species groups occur south of the WT bioregion and, once again, the Burdekin Gap is regarded as a barrier that has prevented southward dispersal. Only one other closed forest pelodyadid occurs in the WT bioregion, *Litoria jungguy*, which is a close sibling of the southern stream frog *L. wilcoxii*.

Closed forest habitats in the SEQ bioregion have three myobatrachid genera (*Assa*, *Lechriodus* and *Philoria*) not found at Eungella, and which do not extend north across the St Lawrence Gap, and there are no populations of these at Kroombit Tops. Among the pelodyadid frogs, four closed forest species of *Litoria* (*L. brevipalmata*, *L. dentata*, *L. pearsoniana* and *L. kroombitensis*) do not cross the St Lawrence Gap. *Litoria pearsoniana* and *L. kroombitensis* are members of the '*L. phyllochroa* species group', which has five members in closed forest habitats of south and central eastern Australia. *Litoria kroombitensis* is the only endemic pelodyadid frog found in the isolated closed forest refugium at Kroombit Tops (northern SEQ bioregion), with the lower Mary-Burnett River basins separating it from *L. pearsoniana*. *Litoria dentata* does not occur north of the lower Mary-Burnett river basins in the SEQ bioregion, where it is most commonly found in wet sclerophyll forest. It is a member of the '*Litoria rubella* species group', and *L. rubella* is common in the open forests and woodlands of the CMC and BBN bioregions and extends farther to the north and west. It is a generalist, and its wide distribution in drier habitats indicates adaptations to these habitats in contrast to *L. dentata*. The remaining closed forest species, *Litoria brevipalmata*, is the only member of its species group, is distributed from mid-eastern NSW to SEQ, and breeds exclusively in ephemeral pools.

Last, there is a considerable diversity of species of myobatrachid and pelodyadid frogs that do not have

records in the CMC bioregion (Table 1), but do occur in the open forest/savannah communities in the surrounding bioregions. Most of these species breed in still waters (permanent or ephemeral ponds and swamps). Several of these frogs (*Limnodynastes salmini*, *Crinia parinsignifera* and *C. signifera*) reach their northern limits in the BBN bioregion, but have extensive distributions to the south and west. Among the tree frogs, there are several species of *Litoria* (*L. fallax*, *L. inermis*, *L. latopalmata*, *L. caerulea*, *L. nasuta* and *L. rothii*) that are common in drier habitats of the coastal lowlands that have extensive distributions in eastern Australia; most do not have records in the closed forest habitats at Eungella (Table 1).

Several species found in the SEQ bioregion (*Crinia tinnula*, *Litoria cooloolensis*, *L. freycineti* and *L. olongburensis*) that do not extend north into the St Lawrence Gap are habitat specialists. These species are found in coastal sandy habitats known as the Wallum (wet heaths on sandy soils) (Coaldrake, 1962), that occur south of the St Lawrence Gap.

Several species of the pelodyadid genera *Cyclorana* occur in the drier and hotter open forest, woodland and grassland communities of the CMC, BBN, EU and BS bioregions, and traverse the Burdekin and St Lawrence Gaps. These 'burrowing' tree frogs do not enter closed forest communities.

DISCUSSION

To understand and interpret the evolutionary history of Australian amphibians, with particular reference to eastern Australia, the isolated closed forest refugium of Eungella represents an area of great importance. Eungella, along with other isolated closed forest refugia that are associated with upland areas of the Great Dividing Range, provides evidence of a long evolutionary relationship and adaptive radiation of the old endemic amphibian fauna whose ancestors were present in Australia from the time it was part of the ancient supercontinent of Gondwana, at least 32 Mya

(Crisp *et al.*, 2001; Byrne *et al.*, 2008; Byrne *et al.*, 2011). At Eungella, three old lineages that are basal in the branching tree of the Australian ground frogs occur and their distributions are extremely narrow.

Three endemic frog species (*Rheobatrachus vitellinus*, *Taudactylus eungellensis* and *T. liemi*) occur at Eungella, and isolated populations of five other species (*Adelotus brevis*, *Myxophyes fasciolatus*, *Uperoleia fusca*, *Litoria chloris* and *L. revelata*) are present. A measure of endemism that tallies species that are restricted to a particular area does not effectively account for the evolutionary depths of those species or their lineages. Diversity or evolutionary history is distributed unequally among taxa as well as between areas (Rosauer *et al.*, 2009), and the concepts of phylogenetic diversity and phylogenetic endemism have been defined to capture these important values (Rosauer *et al.*, 2009; Moritz & Faith, 1998; Faith *et al.*, 2004). Rosauer *et al.* (2009) defined phylogenetic endemism as the combination of phylogenetic depth and range-weighted species endemism, and used it to identify areas where a substantial component of phylogenetic diversity is restricted to small distributions. When these values of phylogenetic depth and small distribution are considered, the evolutionary history represented among the anuran fauna at Eungella takes on an important perspective. Three of the genera occurring at Eungella (*Mixophyes*, *Rheobatrachus* and *Taudactylus*) represent ancient lineages (Frost *et al.*, 2006; Read *et al.*, 2001; Mahony *et al.*, 2006).

Phylogenetic studies have shown that *Rheobatrachus*, along with *Mixophyes*, forms the sister lineage to all other Australian myobatrachids (Frost *et al.*, 2006). Read *et al.* (2001) provided a phylogenetic study of the subfamily Myobatrachinae, without the inclusion of *Rheobatrachus* and *Mixophyes* as it was considered at the time, and they assumed monophyly of the group and used only *Limnodynastes* as a representative of the subfamily Limnodynastinae to root the tree. Their results provided strong evidence that *Taudactylus* was the sister lineage to all other members of the subfamily Myobatrachinae (=Myobatrachidae) as then considered (see Frost *et al.*, 2006 for a discussion). Although there remains uncertainty around the higher-level taxonomy and the most reliable phylogenetic reconstruction, there is no doubt of the ancient evolutionary history of the lineages of *Rheobatrachus*, *Taudactylus* and *Mixophyes*. On this basis, Eungella supports exceptionally high phylogenetic endemism, as represented by the long phylogenetic branches and extremely narrow distributions of *Rheobatrachus* and *Taudactylus*. Investigations

of several anuran lineages have found that species endemism in the east coast, closed forest refugia tends to reflect deeper evolutionary processes and underestimates recent phylogeographic dynamics (Roseaur *et al.*, 2015).

Also important in considering the evolutionary history and biogeography of the Australian ground frogs and the information that comes from Eungella is which closed forest taxa do not occur there. Several genera of Limnodynastidae (*Philoria* and *Lechriodus*) and Myobatrachidae (*Assa*) do not occur there, but are found in closed forest of the SEQ bioregion. These taxa do not extend northwards across the St Lawrence Gap to the south of Eungella. Similarly, there are several taxa (Microhylidae and Ranidae) found in the closed forest refugia of the WT bioregion to the north of Eungella, which have not dispersed across the Burdekin Gap that separates Eungella from the WT bioregion. However, there is no myobatrachid genus found in the WT bioregion that does not occur at Eungella.

In addition to the high level of phylogenetic endemism, Eungella also supports high species richness of anurans, with over 21 species of frog recorded in the CMC bioregion. Several genera of closed forest frogs (*Rheobatrachus* and *Adelotus*), and several species (*Mixophyes fasciolatus*, *Litoria chloris* and *Uperoleia fusca*), reach their northern distributional limit at Eungella. The high level of species richness results from a combination of the endemic elements: a diversity of species that occur in the lowlands and that have more extensive distributions in the coastal zone, plus a small number of species whose adaptations are to savannah and semi-arid environments.

Many studies have investigated the historical biogeography and evolution of the biota of the cool and wet upland closed forest habitats of the eastern seaboard of Australia, and there is a general consensus on the role of refugia and barriers among them (Joseph *et al.*, 1995; Stuart-Fox *et al.*, 2001; Mahony *et al.*, 2006; Rosauer *et al.*, 2009, 2015). The closed forests form an archipelago of refugia dominated by rainforest communities (temperate, sub-tropical and tropical rainforests) surrounded by lowlands of hot and drier open forest dominated by sclerophyll communities (Crisp *et al.*, 2001). Eungella (the Clarke Range) in particular is considered an area of long-term mesic forest persistence (Stuart-Fox *et al.*, 2001). Closed forest habitats are restricted to upland areas usually associated with the great escarpment, and eastern uplands of the Great Dividing Range, and there is compelling

evidence that these habitats are mostly due to an altitudinal (i.e. topographic) effect. However, the distance of the mountain ranges from the coast is also an important component since it is associated with rainfall patterns driven by maritime influences (Hampe & Jump, 2011). This latter orographic rainfall effect cannot be underestimated, and coastal fog commonly settles on the high peaks at Eungella in the late afternoon. Indeed, it is the origin of Eungella's Aboriginal name, 'mountains of the mist'. Understanding of the historical climate of eastern Australia, derived mostly from palynology and karst deposits, demonstrates a rapid and widespread change from extensive rainforest habitats to a much drier landscape dominated by woodland and savannah ecosystems since the late Pleistocene (Bryant & Krosch, 2016). Many of the refugia have apparently experienced relatively long climate stability, and they retain ancient lineages that do not occur in habitats outside the closed forests (Byrne *et al.*, 2011).

Eight major biogeographical disjunctions, termed barriers or gaps, for closed forest taxa were identified in eastern Australia by Bryant & Krosch (2016), based on evidence of common barriers that separated many wet forest adapted biota. Two of these barriers are significant with respect to Eungella, namely the Burdekin Gap to its north (Burdekin River Catchment, also referred to as the Bowen Basin) and the St Lawrence Gap (Fitzroy River Catchment) to its south, both of which are in the BBN bioregion that surrounds the MCC bioregion. Bryant & Krosch (2016) synthesised common phylogeographic patterns for a range of taxa, and provided inferred timing where studies had estimated age of separation using molecular genetic approaches. The outcome is that the Burdekin Gap has been a stronger barrier to movement of closed forest taxa than the St Lawrence Gap. The Burdekin Gap coincides with the northern extent of the 'Brigalow Belt North' bioregion, a large dry corridor that stretches from the southern boundary of both the Wet Tropics bioregion and what is considered the Australian Monsoonal Tropics, to the Bowen Basin in the south (Cattullo & Keogh, 2014). Studies show that there is currently very little closed forest habitat within the putative bounds of the Burdekin Gap, providing limited opportunities for taxa to disperse across the barrier using smaller patches of suitable habitat as stepping stones (Bryant & Krosch, 2016).

The cool upland closed forests form refugia for those taxa that are unable to disperse across the hotter and drier barriers. These refugia provide a window to the past when the climate was wetter

and cooler, and rainforest communities were more widespread (Byrne *et al.*, 2011). At that time, there must have been some interconnection among the current refugia, since the ancestors of the extant species must have been more widely distributed and able to disperse across what are now drier barriers. Isolation of populations in refugia is known to break gene flow among populations, potentially leading to speciation and, for some, taxa extinction (Moritz & Faith, 1998; Moritz *et al.*, 2005; Hampe & Jump, 2011). Amphibians that are adapted to closed forest habitats are one group for which drying and possibly warming of climate leads to population isolation in closed forest refugia, since their complex life history and physiology (Hillman, 2008) mean that most are reliant on a constant source of water. However, not all anurans have responded to these changes in the same way, which most likely reflects differences in physiological tolerances and ecology. At Eungella, there are several anurans that are endemic, other species with isolated populations but which are not endemic, and still others that have continuous distributions with the surrounding drier habitats. Typically, the species that occur in the drier forest habitats are adapted to breed in permanent and ephemeral wetlands, whereas those in the closed forest are reliant on stream habitats (Table 1). One stream-breeding frog, *Litoria wilcoxii*, traverses the St Lawrence and Burdekin Gaps. This frog occurs in most eastern-flowing catchments and in the upper reaches of western-flowing streams of the Great Dividing Range from the Sydney Basin bioregion to the WT bioregion (see Meyer *et al.*, this volume). It occurs in streams across the altitude range at Eungella, and is most abundant in the wet forests that fringe the dense rainforest. Interestingly, in the WT a sister taxon, *Litoria jungguy*, is found almost exclusively in the closed forest, and *L. wilcoxii* occurs in the adjacent drier and open forests. Biogeographic studies have demonstrated a similar pattern for many taxa, with refugia harbouring species of varying dispersal abilities and ecologies, and with varying capacity to move across zones of otherwise unsuitable habitat (Byrne *et al.*, 2011).

Estimates of the age of the divergence among amphibian taxa that occur in the refugia are of considerable importance to understanding the evolutionary history of these ecosystems. However, there is limited information available on the age of separation of two important taxa, *Rheobatrachus* and *Taudactylus*. Divergences calculated from intra-generic comparisons reveal an inferred age from the late Miocene to the

late Pleistocene (12–7 Mya) for species of *Mixophyes* (Mahony *et al.*, 2006), and mid-Miocene to Oligocene (23–10 Mya) among species of *Uperoleia* (Catullo & Keogh, 2014). These intra-generic speciation events logically post-date the differentiation of the generic lineages, and differentiation of the older lineages, such as *Rheobatrachus* and *Taudactylus*, must predate these time estimates. Apart from *R. vitellinus* at Eungella, the only other species of *Rheobatrachus* (*R. silus*) occurred in the closed forests of the Conondale and Blackall Ranges (SEQ bioregion), and both species have very similar derived reproductive biology and morphological adaptations to stream habitats (Liem, 1973). The distribution of *Taudactylus* is more widespread among the refugia, with one species found in the Dawes Range (Kroombit Tops) to the south-east of Eungella, another further south in the Conondale, Blackall and D’Aguilar Ranges (all in the SEQ bioregion), and two species to the north in the rainforests of the WT bioregion. Kroombit Tops is isolated from Eungella by the St Lawrence Gap and represents an important closed forest refugium between those at Eungella and those to the south. Kroombit Tops is isolated from the other closed forests of the SEQ bioregion by the lower Mary-Burnett River basins. This barrier is not considered by Bryant & Krosch (2016) as being significant for birds or flora, but it appears to have been significant for anurans.

Further evidence of the antiquity of *Rheobatrachus* and *Taudactylus* come from their life history and adaptations. *Rheobatrachus* is Australia’s only truly aquatic frog, apparently spending its whole life in water and not venturing for any extended period onto land during the adult stage (Mahony *et al.*, 1984; Liem, 1973). Evidence can be seen in the convergence of external morphology with other unrelated aquatic anurans such as xenopipids (flattening of the body, protuberant eyes, well-developed muscular hind limbs with extensively webbed toes, the occurrence of lateral line organs and production of copious epidermal mucous secretions). All *Taudactylus* species have a derived reproductive biology in which a relatively small number (average 30) of large unpigmented eggs are laid beneath rock or debris in streams or rocky crevices associated with stream habitats.

In contrast to the ground frogs (Myobatrachidae and Limnodynastidae) which have endemic species and isolated populations from ancient lineages at Eungella, there is no endemic species of tree frog (Pelodryadidae) at Eungella. Two species (*Litoria chloris* and *L. revelata*) have disjunct populations

at Eungella and, in each case, they are examples of species that are more widely distributed to the south of the St Lawrence Gap. A sister species of *L. chloris*, *L. xanthomera*, and an isolated population of *L. revelata* occur in the closed forests of the WT bioregion. In these cases, the Burdekin Gap has provided some level of isolation but apparently has not prevented the dispersal of *L. revelata* across the Gap. It is assumed that the dispersal is northward on the basis that this species is more widely distributed in southern bioregions, but this has not been tested by a robust phylogenetic analysis. Perhaps more telling of the strength of the Burdekin Gap as a barrier is the absence of any species of the WT stream-adapted clade of tree frogs (*‘Litoria nannotis species group’*) at Eungella. In this case, it is assumed that the Burdekin Gap is a barrier to southward dispersal of this group which has several sibling species in closed forest of the WT bioregion.

Evidence of closer historical connections between the closed forest refugium of Eungella and those to the south (in the SEQ bioregion), rather than those to the north in the WT bioregion, is indicated by taxa that have isolated populations at Eungella and that occur in the southern but not the northern bioregion. This indicates that for anurans, the Burdekin Gap has been important in both limiting southward-colonising and northward-colonising mesic forest species, and promoting divergence among populations of species that span the barrier (Bryant & Krosch, 2016). *Adeleotus brevis*, *M. fasciolatus*, *Uperoleia fusca* and *L. chloris* have disjunct populations at Eungella that are conspecific with populations to the south but not to the north of Eungella (Table 1). All of these frogs, with the exception of *Uperoleia fusca*, are considered to be associated with closed forest communities. *Uperoleia fusca* is widely distributed in open and closed forest habitats to the south of Eungella, but apparently not in the St Lawrence Gap. In contrast, there is a stronger differentiation with northern closed forest species of the WT bioregion. Five species of *Litoria* tree frogs, three species of *Mixophyes* and two species of *Taudactylus* do not extend south of the WT bioregion. In addition, there are no members of the family Microhylidae (14 species in the WT bioregion), or Ranidae (*Hylarana daemeli*) that occur south of the WT bioregion. Biogeographic and phylogenetic studies are in strong agreement that the Australian members of these two families have dispersed into Australia from the north and that they are not of Gondwanan origin (Tyler, 1979).

FIGURE 2. Three of the endemic closed forest anurans of Eungella, a) *Rheobatrachus vitellinus*, b) *Taudactylus liemi*, and c) *Taudactylus eungellensis*; and species that have disjunct populations at Eungella, d) *Adelotus brevis*, e) *Mixophyes fasciolatus*, f) *Litoria chloris*, and g) *Litoria revelata*.



Rosauer *et al.* (2015) found that regions of high species endemism that identify hotspots of highly restricted, isolated and independently evolving populations are central to identifying taxa and areas of conservation priority. The closed forest habitats of Eungella within the CMC bioregion support a disproportionate amount of restricted evolutionary diversity and provide a prime example of this priority.

The occurrence of three endemic species from two basal lineages, isolated populations of more widespread taxa, and high species richness demonstrates its significance as a conservation hotspot. Further research is required to understand more fully the ages of divergence and antiquity of the endemic anuran fauna of Eungella and the other closed forest refugia of eastern Australia.

ACKNOWLEDGEMENTS

Special thanks to Olivier Rey-Lescure who produced the map that is Figure 1, and to Stephen Mahony for the photographs of *T. liemi* and *T. eungellensis*. Harry Hines gave important advice on the distribution of several species of frogs in the bioregions surrounding Eungella.

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