A phylogeographic and taxonomic assessment of the squirrel – mahogany glider complex

Thesis submitted by

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Declarations

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Statement on the Contribution of Others

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Data Acquisition

The highly endangered mahogany glider is notoriously difficult to trap, requiring large investments of both time and money to gather sufficient samples for robust morphological and genetic datasets. As such, field work for this research was conducted in conjunction with Queensland Parks and Wildlife Services (QPWS), namely Mark Parsons (QPWS Wet Tropics) and Tina Ball (QPWS Mackay), who provided morphological information and tissue samples from 78 mahogany gliders. Additional morphological and genetic data for the mahogany glider was sourced from Queensland Museum (20 individuals) and the personal collection of Dr Steve Jackson (33 individuals). QPWS also collected morphological and molecular data from 89 squirrel gliders. Further squirrel glider data was sourced from a number of eastern Australian research institutions, specifically Queensland Museum (35 individuals), Australia Museum (104 individuals) and Museum Victoria (24 individuals). Jane DeGabriel also provided tissue samples and morphological measurements from 16 adult squirrel gliders.

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Abstract

Quaternary climate fluctuations, such as the contraction-expansion cycles of eastern Australia's widespread forested biome, are widely cited as driving factors in speciation and extinction. Incorporating morphological and molecular data, I examined two representatives of an eastern Australian open forest species complex with contrasting distributional patterns, the geographically restricted mahogany glider (*Petaurus gracilis*) and its widespread congener, the squirrel glider (*P. norfolcensis*), with the aim of assessing existing taxonomic boundaries and establishing an accurate biogeographic narrative.

Current taxonomy of the squirrel – mahogany glider complex, as defined by existing distributional, behavioural and ecological data, support species status for each glider. However, molecular and morphological data presented in this study intimate a more nuanced evolutionary scenario. Mitochondrial (mtDNA) sequences assorted independent of taxonomy yet identified two partially overlapping, geographically oriented lineages, one restricted to north-eastern Australia and the other more widespread across eastern Australia. MtDNA substructure was also observed among south-eastern Australian squirrel glider populations. Although less clearly defined, geographic orientation among nuclear (nDNA) sequences was also detected. In contrast, morphological variation within the complex clearly differentiated the mahogany glider from the squirrel glider, with the former significantly larger. Minor morphological variation was also detected in squirrel glider populations in south-eastern Australia, mirroring mtDNA substructure.

Phylogeographic structure of the squirrel – mahogany glider complex was then compared to that of two co-distributed open forest congeners, namely the sugar (*P. breviceps*) and yellow-bellied (*P. australis*) gliders. MtDNA diversity was similarly structured across all species, with each represented by two divergent mtDNA lineages, although the depth of divergence differed. Biogeographic subdivisions in the squirrel – mahogany glider complex were more similar to those of the patchily distributed yellow-bellied glider than the widespread sugar glider. In the squirrel – mahogany glider complex, north-eastern Australian populations were clearly isolated from eastern and south-eastern populations by the Burdekin Gap, an expanse of dry, open woodland habitat well documented as a biogeographic barrier to open forest fauna. South-north introgression across the Burdekin Gap, not detected in other *Petaurus* gliders, was interpreted as evidence of intermittent open forest habitat connectivity in line with Quaternary contraction-expansion cycles. MtDNA substructure in south-eastern Australia was associated with the Hunter River Valley and Great Dividing Range, both biogeographic barriers to the sugar glider. MtDNA and morphological substructure also supports the recent recognition of the south-eastern Australian populations of the squirrel glider as a distinct evolutionary significant entity for conservation and management purposes.

In conclusion, results presented here do not reflect the clearly defined taxonomy of the squirrel – mahogany glider complex as currently recognised. When considering the taxonomic status of the mahogany glider, the available data permits two largely complementary interpretations. Firstly, the mahogany glider as a geographic variant of the widespread squirrel glider. The absence of reciprocal monophyly therefore represents evidence of ongoing gene flow between the two gliders, specifically between neighbouring populations, while the observed ecological and morphological differentiations are a consequence of the distinct environmental profile of the mahogany gliders' coastal lowland habitat. Secondly, the data available does not preclude a scenario whereby the clear morphological divergence observed between the two gliders reflects character displacement driven by strong divergent selection across a steep moisture gradient. In this scenario, minor partitioning of phylogenetic diversity between the mahogany and squirrel gliders reflects incipient speciation of two allopatric species that are only recently isolated. It is arguably premature, however, to suggest changes to *Petaurus* systematics without data from more rapidly evolving loci and greater representation of north-eastern Australian populations of the squirrel – mahogany glider complex.

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Photo: P. Ferraro

1. Introduction

1.1 Historical biogeography of eastern Australia's mesic biome

Composed primarily of a mosaic of relictual rainforest remnants distributed among widespread sclerophyllous woodland and forest (Byrne *et al*., 2008, 2011; Bowman *et al*., 2010), Australia's eastern seaboard is recognised as a critical component in understanding the evolution of the continent's biodiversity (Blakers *et al*., 1984; Van Dyck and Strahan, 2008; Cogger, 2000; Slayter *et al*., 2007). At the broad biogeographic scale, and relative to the arid and semi-arid environments that dominate the greater part of the Australian continent, this largely continuous forest biome spans tropical to temperate latitudes (Nix, 1982) and parallels the western edge of the region's dominant topological feature, the Great Dividing Range (Frakes, *et al*., 1987; Taylor, 1994). Nevertheless, climate and topography are highly variable across this region and interact to generate a rich mosaic of varying ecological conditions and barriers to dispersal (Keast, 1981; Bowler, 1982; Kershaw *et al*., 1994; Schodde, 2006, Byrne *et al*., 2008; Mackey et al., 2008; Williams *et al*., 2009).

Historical biogeography recognises several prominent biogeographic barriers throughout the forested biomes of eastern Australia, each associated with a unique set of topographic and bioclimatic features (Kershaw, 1981; Nix, 1982; Ford, 1987a, 1987b; Cracraft, 1991; Crisp *et al*., 1995; Lambeck and Chappell, 2001; Dickinson *et al*., 2002). Perhaps the most prominent and well documented of these breaks is the Burdekin Gap, a dry lowland corridor separating the Wet Tropics of north-eastern Queensland from the sclerophyll forests of mid-eastern Queensland (Figure 1). Across this barrier strong taxonomic and deep phylogeographic turnover is well documented for a wide spectrum of taxa endemic to both wet and dry forest biomes (e.g. Joseph and Moritz, 1994; James and Moritz, 2000; Schäuble and Moritz, 2001; Brown *et al*., 2006; Dolman and Moritz, 2006; Chapple *et al*., 2011a; Edwards and Melville, 2010). Although not as pronounced, the relatively dry corridors of the St Lawrence Gap, Hunter River Valley and the Gippsland and Murray basins have also contributed prominently to biogeographic subdivision of the eastern Australian biota (e.g. McGuigan *et al*., 1998; Donnellan *et al*., 1999; Keogh *et al*., 2003, 2005; Chapple *et al*., 2005; Moussalli *et al*., 2005; Symula *et al*., 2008; Dubey and Shine, 2010).

The influence of such biogeographic barriers is most evident in the closed forest communities, with considerable concordance in geographic orientation in phylogenetic diversity (both inter- and intraspecifically) having been documented across a broad spectrum of rainforest restricted taxa (see review in Moritz *et al.*, 2005). There is increasing appreciation, however, that dispersal barriers typically associated with closed forest fauna have also influenced biogeographic subdivisions among open forest fauna (e.g. James and Moritz, 2000; Schäuble and Moritz, 2001; Edwards and Melville *et al*., 2010), though concordance across taxa tends to be more idiosyncratic. High altitude wet forest barriers such as the McPherson Range and the temperate uplands of the southern reaches of the Great Dividing Range have contributed to phylogenetic subdivisions among open forest taxa (McGuigan *et al*., 1998; Donnellan *et al*., 1999; Keogh *et al*., 2003; Symula *et al*., 2008; Chapple *et al*., 2011b). For instance, phylogeographic analysis of a non-rainforest anuran identified the McPherson Range, an east-west aligned montane block of wet forest on the Queensland / New South Wales border, as a dispersal barrier to *Litoria fallax* (James and Moritz, 2000). A subsequent study, however, found no comparable phylogeographic structure across two closely related and broadly sympatric frogs (*Limnodynastes tasmaniensis* and *L. peronii*; Schäuble and Moritz, 2001) but identified an alternative phylogenetic break in the south-eastern region of the frogs' range not present in *L. fallax*.

Such advances in the field of historical biogeography stem from the recent advent of comparative phylogeography (Zink, 1996; Bermingham and Moritz, 1998; Bernatchez and Wilson, 1998; Moritz and Faith, 1998; Schneider *et al*., 1998; Avise, 2000; Riddle *et al*., 2000; Sullivan *et al*., 2000; Arbogast and Kenagy, 2001). Comparative phylogeography provides comparisons of geographically oriented phylogenetic diversity across co-distributed species, thereby identifying common spatial patterns of evolutionary subdivision. This 'quantitative and integrative approach' (Arbogast and Kenagy, 2001) to the elucidation of cross-species biogeographic processes has been utilised to great effect in north-eastern Australia's Wet Tropics (e.g. Schneider *et al*., 1998; Moritz *et al*., 2000; Hugall *et al*., 2002; Bell *et al*., 2004; Hoskin et al., 2005; Moussalli et al., 2005; Dolman and Moritz, 2006; Bell *et al*., 2007; Krosch *et al*., 2009) in addition to the sclerophyll forests of eastern Australia (e.g. Donnellan *et al*., 1999; Fowler *et al*., 2000; Keogh *et al*., 2003; Symula *et al*., 2008; Sumner *et al*., 2010).

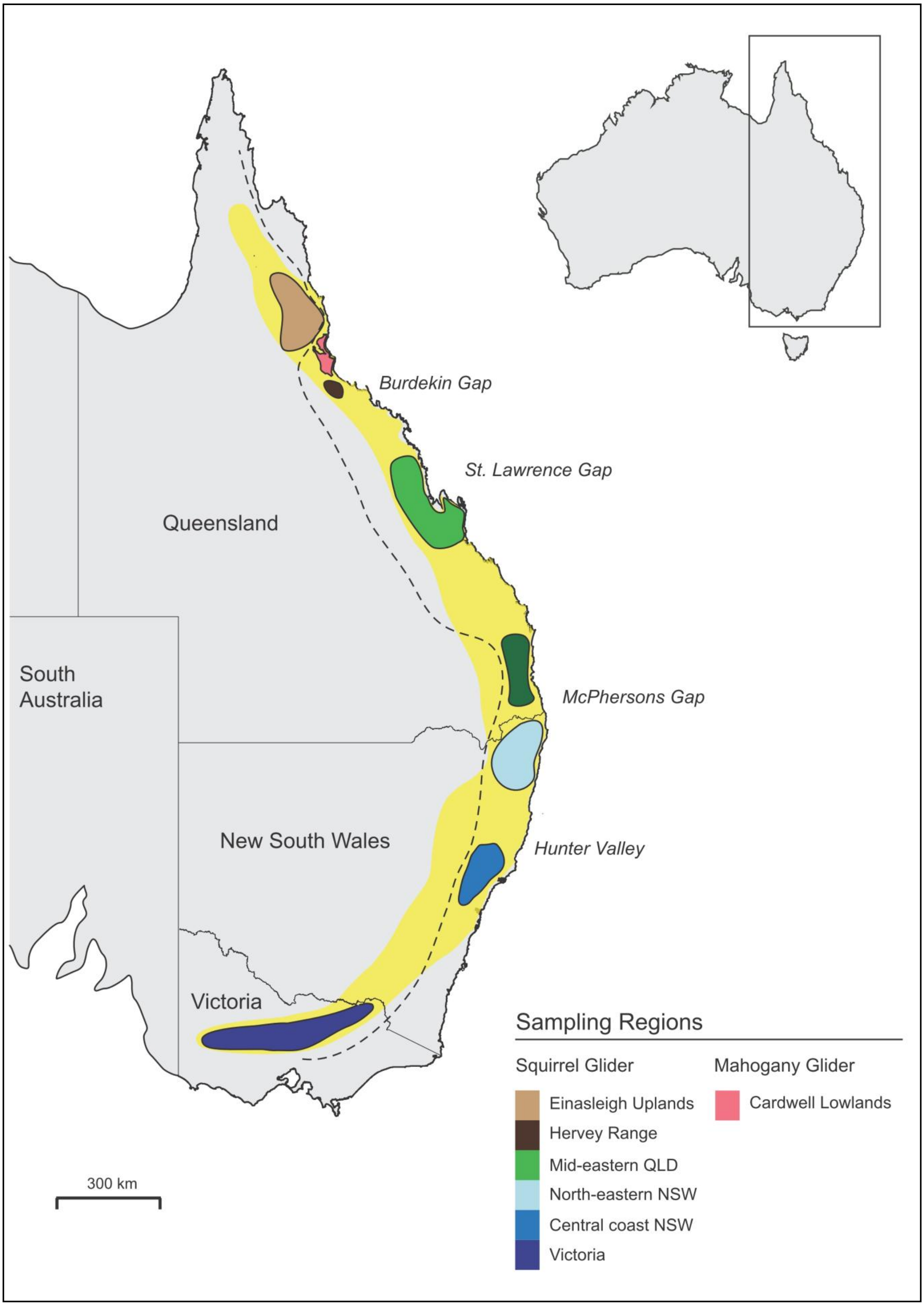


Figure 1: Distribution of the squirrel glider (yellow) and mahogany glider (pink) with the approximate position of five major biogeographic breaks in eastern Australia (italicised text) and the Great Dividing Range (broken line). Sampling regions represented by coloured areas (see legend for details). A map of Australia is inset (top right).

Due largely to the paucity of species with distributions that span eastern Australia's forests there remains few phylogeographic studies encompassing the greater part of that biome (see Chapple *et al*., 2011a). In one such example, Joseph and Moritz (1994) identified comparable phylogeographic structure across the Burdekin Gap in two closed forest *Sericornis* scrubwrens. Results were not consistent across all species, however, with a third scrubwren exhibiting markedly lower levels of phylogenentic divergence across the Burdekin Gap. This variation was attributed to the broader habitat preferences of the third species, specifically its capacity to exploit both the wet and dry components of eastern Australia's forest biome. Outside of this example, however, the majority of related studies limit their focus to a single component; where the weight of research is skewed toward the remnant wet forests (e.g. Nicholls and Austin, 2005; Joseph and Omland, 2009; Eldridge *et al*., 2011; Krosch, 2011) over the widespread dry forests (James and Moritz, 2000; Schäuble and Moritz, 2001; Taylor and Foulkes, 2004; Chapple *et al*., 2011a). Fewer again focus on the region's widely distributed mammals (e.g. Houlden *et al*., 1999; Spencer *et al*., 2001; Potter *et al*., 2012) with the marsupial gliders of the genus *Petaurus* one of the few taxonomic groupings well represented in the phylogeographic literature (Brown *et al*., 2006; Malekian *et al*., 2010a; Pavlova *et al*., 2010).

1.2 The petaurid gliders of eastern Australia

Considered as keystone taxa in Australia's forest biome (Goldingay and Jackson, 2004), the arboreal petaurid gliders (genus *Petaurus*) represent ideal taxa for phylogeographic studies of open forest fauna at the broad biogeographic scale. Of the seven recognised petaurid species, four are strongly associated with eastern

Australia's sclerophyll habitats (*P. australis, P. breviceps, P. norfolcensis* and *P. gracilis*; Goldingay and Jackson, 2004), where they utilise mature *Eucalyptus* stands for breeding, migration, diet and shelter (e.g. Quin *et al*., 1996a; Jackson, 2001; Goldingay and Quin, 2004; Eyre, 2007; Ball *et al*., 2009, 2011). Although these species are co-distributed to varying degrees at the broad scale, there exist divergent habitat preferences at the ecological scale, particularly when in sympatry (Jackson, 2000a; Lindenmayer, 2002; Rowston and Catterall, 2004). The geographically widespread sugar glider (*P. breviceps*), for example, also exploits *Acacia* species across much of its distribution (Goldingay and Jackson, 2004) and exhibits a preference for a more enclosed canopy and mid-storey rainforest flora than its larger congeners when in sympatry (Jackson, 2000a). In a study of petaurid habitat preferences, Davey (1984) observed niche partitioning whereby the sugar glider foraged in the lower stratum, while the much larger squirrel glider (*P. norfolcensis*) spent its time predominantly in the upper stratum, a partition also observed between the sugar and mahogany glider, *P. gracilis* (Jackson, 2000b).

Within *Petaurus*, the squirrel glider and mahogany glider are of particular interest given that they collectively cross the wet-dry open forest continuum of eastern Australia (see Figure 1). Like the sugar glider, the squirrel glider is widely distributed across eastern Australia's open sclerophyllous communities (van der Ree and Suckling, 2008), including transitional wet sclerophyll forests bordering the rainforest remnants of Queensland's Wet Tropics (Suckling, 1983a). Conversely the mahogany glider (Plate 2) has a highly limited distribution, endemic to northern Queensland and restricted to coastal open forests characterised by very high seasonal rainfall and high floral diversity (e.g. Plate 1); both conditions traditionally associated with rainforest communities (Van Dyck, 1993).

Morphological variation among the lesser gliding possums is generally low, with body size, pelage colouration, tail length and the length of tail fur considered as the key diagnostic characters separating the squirrel, sugar and mahogany gliders (Van Dyck, 1993; Quin et al., 1996b; Lindenmayer, 2002). With such subtle morphological variation (see Plate 3, Plate 4), there remained an element of uncertainty in the taxonomic validity of the mahogany glider during the preceding century. The species was first described in 1883 (De Vis, 1883), although the subsequent loss of the type specimens and the brevity of De Vis' description saw the mahogany glider considered a geographic variant of the squirrel glider by Thomas (1888), a view later reinforced by Iredale and Troughton (1934) and more recently Van Dyck (1990). The rediscovery of the De Vis' missing type specimens and subsequent identification of live specimens engendered a comprehensive review of the taxonomy of the mahogany glider, leading to its resurrection to specific status (Van Dyck, 1993).

Arising from Van Dyck's (1993) revision was a greater appreciation of the extent to which habitat loss and fragmentation had caused a substantial decline in the geographic range and abundance of the mahogany glider from pre-European levels (Van Dyck, 1993; Jackson *et al*., 2011), leading to its IUCN red listing as an endangered species in 1996 (see Burnett *et al*., 2008). The mahogany glider was subsequently listed as Endangered under both state and federal law (via the *Nature Conservation Act 1992* and *Environment Protection and Biodiversity Conservation Act 1999*, respectively), thereby providing an impetus for a series of comprehensive ecological studies (Jackson and Claridge, 1999; Jackson, 2000a, 2000b, 2000c, 2001; Jackson and Johnson, 2002). Securing existing mahogany glider populations and expanding currently protected habitat remains a state and federal priority (see Parsons and Latch, 2006).

Despite its widespread distribution the squirrel glider has also been affected by the expansion of agricultural and residential development (Gibbons and Lindenmayer, 2002; Rowston *et al*., 2002); and is now limited to non-continuous habitat along eastern Australia's forest biome (van der Ree, 2002; van der Ree and Bennett, 2003; Claridge and van der Ree, 2004). Consequently, it is listed as vulnerable in New South Wales (*Threatened Species Conservation Act 1995*) and threatened in Victoria (*Flora And Fauna Guarantee Act 1988*), while presumed extinct in South Australia (Malekian *et al*., 2010b). The scarce data for Queensland populations indicates that implications of ongoing habitat loss and fragmentation remain a serious concern (Eyre, 2004; Winter *et al*., 2004).

1.3 Molecular systematic of the petaurid gliders

Recent molecular work supports the monophyly of *Petaurus* within Petauridae (Osborne and Christidis, 2001; Osborne *et al*., 2002; Malekian *et al*., 2010b), with the yellow bellied glider (*P. australis*) basal to all remaining petaurids. However, the evolutionary relationships among the three closely allied species – the sugar, squirrel and mahogany gliders – remain unresolved; a situation further complicated by the fact that the squirrel and sugar gliders are known to interbreed (Fleay, 1947; Suckling, 1983b). Further, a recent phylogeny of the genus *Petaurus* (Malekian *et* *al*., 2010b) identified potential nDNA and mtDNA introgression between the two, suggesting hybridisation in eastern Australia's open forest gliders may be more widespread than currently recognised. Indeed, contrary to Colgan and Flannery's (1992) allozyme work which showed three fixed differences across 21 loci between the squirrel and mahogany gliders, recent mitochondrial (ND2 and ND4 genes) and nuclear (omega-globin gene) data exhibit levels of genetic differentiation between the mahogany and squirrel glider (Malekian *et al*., 2010b) that, in contrast with the large difference in body mass, is comparable to intraspecific divergence in the yellow-bellied glider (Brown *et al*., 2006).

Further, recent assessments of intraspecific taxonomy of the polytypic yellow-bellied glider (Brown *et al*., 2006) and sugar glider (Malekian *et al*., 2010a) found little concordance between phylogeographic structure and current subspecific delineation, recommending instead the recognition of two highly divergent, geographically oriented lineages as Evolutionary Significant Units (ESUs). While no subspecific units are recognised in the squirrel glider, Pavlova *et al.* (2010) similarly identified strong phylogeographic structure among southern populations of the squirrel glider, also arguing for the recognition of two ESUs. In each instance, the revised intraspecific distributional limits coincided with documented eastern Australia open forest barriers, namely the Burdekin Gap (yellow-bellied glider) and the Great Dividing Range (sugar and squirrel gliders).

1.4 Thesis aims

In this study I present a phylogeographic investigation of the squirrel – mahogany glider complex, with representation spanning its entire distribution, based on the complete mitochondrial ND2 gene and the partial sequence of the nuclear ApoB1 gene. Phylogeographic patterns in the complex are also compared and contrasted with those of other broadly co-distributed petaurid gliders, with particular interest in whether a correlation exists between habitat specialisation and phylogeographic structure across the petaurids. The objective of the study is not only to further our understanding of the historical biogeography of eastern Australia's forest biome but to also provide a more detailed investigation of the taxonomic placement of the mahogany glider within *Petaurus*. To this end, I also collate and revise the morphometrics underpinning the squirrel – mahogany glider complex, with a particular emphasis on assessing interpopulation variance across its entire distribution. It is only with such measures of regional variance that the apparent morphological divergence of the mahogany glider can be effectively assessed. It is hoped this work will contribute to the conservation effort of both the mahogany and squirrel gliders and guide future research into the evolution and conservation of Australia's more iconic species.

Plate 2: Mounted mahogany glider (Museum Victoria)

Photo: P. Ferraro

2. Methodological Approach

2.1 Study region

Tissue samples were obtained from 67 squirrel gliders and 92 mahogany gliders from a range of sources (full sampling information is presented in Appendix I). The large number of samples enabled an investigation of phylogeographic structure of the squirrel – mahogany glider complex at two geographic scales: a distribution-wide broadscale analysis encompassing eastern Australia; plus a finescale analysis focused exclusively on north-eastern Australia – a zone of potential contact between the two taxa. Squirrel glider sampling incorporated the majority of the species' widespread yet patchy (Lindenmayer *et al*., 2003) open forest distribution (Figure 1). To aid comparison to existing studies squirrel glider samples were assigned to the seven pre-defined eastern Australian bioregions detailed in James and Moritz (2000) and Moussalli *et al*. (2005): Einasleigh Uplands (EU), Hervey Range (HR), mid-eastern Queensland (MEQ), south-eastern Queensland (SEQ), north-eastern New South Wales (NEN), central coast New South Wales (CCN) and Victoria (VIC). Mahogany glider representation encompassed its limited distribution in the Cardwell Lowlands (CL) of north-eastern Australia (Figure 1), with samples originating from one of four areas: Tully (Tu), Two Creeks (Tc), Rangeview (Ra) and Bambaroo (Ba).

2.2 Lab procedures

Total genomic DNA was extracted from all samples following the phenol-chloroform protocol outlined in Gemmell and Akiyama (1996). Sequences from the complete mitochondrial ND2 gene (1,040bp) were amplified using a combination of the following primers: mrND2F, ACCCCGAAAATGTTGGTTTA; pND2R, TGATTTGCGTTCGAATGATG; pND2iF, AATTGCCCCAACAGCATTAC; pND2iR, CATGTGGGCAATTGATGAGT. With the exception of mrND2F (Osborne and Christidis, 2001), primers were designed using the programs Primer3 v0.4.0 (Rozen and Skaletsky, 2000) and Amplify v3.1.4 (Engels, 2005). A 720 base pair fragment of the nuclear ApoB1 marker was amplified using primers F90 and R820 (AATTCCTGAAATGACTCTGCC and TYGTCCCATCTAACTTATACTG, respectively) (Amrine-Masden *et al*., 2003). ND2 was preferred over other mtDNA markers due to its previous application to *Petaurus* (Osborne and Christidis, 2001; Osborne *et al*., 2002), while ApoB1 was selected for its ability to generate species-level distinctions within Diprotodontia (Wilson-Wilde, 2010). All primers incorporated M13 tails to optimise amplification efficacy. Polymerase chain reaction (PCR) protocol was as follows: 10.3ul of DNA template (1/100 dilution) was combined with 13ul GoTaq Green Master Mix (Promega) plus 0.35ul (10uM) of each primer and the targeted fragment amplified using an initial denaturing step for two minutes at 95^{o}C, 40 cycles of 95^{o}C denaturing for 20 seconds / 50^{o}C annealing for 20 seconds / 72^{o}C extension for 90 seconds, and a final extension for three minutes at 72^{o}C. PCR products were then purified with the GFX PCR DNA and gel band purification kits (Amersham Biosciences). Sequence reaction and capillary separation was undertaken by either Macrogen Inc. (Seoul, Korea) or the Australian Genome Research Facility (AGRF). Sequences were aligned and translated using SEQUENCHER 4.2 (Gene Codes Corporation, USA). PHASE v2.1 (Stephens *et al*., 2001) was used to resolve haplotypes from heterozygous individuals at the ApoB1 locus.

2.3 Phylogeographic analyses

The program NETWORK v4.6 (www.fluxus-engineering.com) was used to construct median joining networks for each dataset. The default median joining (MJ) algorithm (Bandelt *et al*., 1999) was employed for mtDNA sequences and the reduced median (RM) algorithm (Bandelt *et al*., 1995) for nDNA sequences. The maximum parsimony (MP) algorithm (Polzin and Daneschmand, 2003) was applied to each dataset before finalising each network to purge superfluous links and median vectors. Haplotype connection ambiguities were resolved according to the criteria defined by Crandall and Templeton (1993). During this analysis a single MEQ squirrel glider mtDNA sequence grouped unexpectedly. This outlier was excluded from further analyses due to concerns over the validity of the sample's origin and identity.

The program BEAST v1.5.4 (Drummond and Rambaut, 2007) was used to assess the phylogenetic depth underlying the mtDNA diversity within the squirrel – mahogany glider complex dataset. The Hasegawa, Kishino and Yano model of sequence evolution (HKY; Hasegawa *et al*., 1985) was selected as the most parsimonious based on AIC criteria using the program jMODELTEST v0.1.1 (Posada, 2008; incorporating PHYML (Guindon and Gascuel, 2003)). To exclude uninformative parameters, thereby maximising the MCMC search efficiency, preliminary BEAST runs (not shown) indicated that the dataset conformed to a constant population size and a strict molecular clock rate. The standard mtDNA substitution rate of 1% per lineage per million years (Brown *et al*., 1979) was preferred over more recent alternatives (e.g. 0.7% per lineage per million years, Bininda-Emonds, 2007) due to its application in marsupial studies (e.g. Krajewski *et al*., 2000; Malekian *et al*., 2010a, 2010b). Three randomly seeded runs of 10 million generations were logged every 1,000 generations and convergence and mixing was checked in TRACER v1.5 (Drummond and Rambaut, 2007). The resultant raw files were combined within LOGCOMBINER v 1.5.4 and summarised with TREEANNOTATOR v1.5.4 (excluding a 10% burn-in). The final tree was visualised within FIGTREE v1.3.1 (Rambaut, 2006).

Standard diversity indices, incorporating the number of haplotypes (H) (Tajima, 1983) and haplotype (h) and nucleotide (π_x) diversities plus standard deviations (Nei, 1987) were calculated within ARLEQUIN v3.5.1.2 (Excoffier and Lischer, 2010), as were pairwise genetic distances (Φ_{ST}) and Nei's net sequence divergence (D_A). As the HKY model of sequence evolution is not offered by the current version of ARLEQUIN the Tamura-Nei (TrN) model (Tamura and Nei, 1993) was used as a surrogate. Statistical significance was tested after 10,000 permutations with Bonferroni correction (Rice, 1989).

Spatial structuring of mtDNA diversity was estimated using SAMOVA v1.0 (Dupanloup *et al*., 2002). For a given number of groupings (K) this method uses a simulated annealing procedure to maximise the F_{CT} index (the proportion of total genetic variance due to the difference between groups of populations). More importantly, geographical locations are explicitly taken into account within the simulated annealing procedure. An indirect outcome of this analysis therefore is the identification of potential biogeographic barriers, reflecting relatively high genetic differentiation over a short geographic distance. SAMOVA was preferred over alternative approaches for the following reasons: a) it relies solely upon genetic data to determine population groupings, thereby removing the requirement for pre-defined biogeographic assumptions, as it the case in the classic AMOVA approach; and b) it does not utilise interpolation-driven methodology; an approach that can generate biologically inaccurate results when sampling points are not regularly spaced (Dupanloup *et al*., 2002), as is the case in this study. Six groupings were assessed (i.e. K=2 through to K=7), with the lowest grouping to exhibit significant F_{CT} index in conjunction with non-significant F_{SC} (i.e. proportion of variance among populations within groups) assumed to reflect the most probable set of geographic subdivisions.

To assess whether the SAMOVA-derived scenario provided the most parsimonious partitioning of molecular variance, it was compared to the following *a priori* biogeographic scenarios, generated via analysis of molecular variation (AMOVA) in ARELQUIN. Firstly, a simple unstructured analysis of the seven regions was conducted, labelled *Unstructured*. Next, regions were clustered to assess the influence of three major east Australian biogeographic barriers upon the squirrel – mahogany glider complex; the Wet Tropics, Burdekin Gap and Hunter River Valley. These scenarios were: *Biogeography A*, the Burdekin Gap only*; Biogeography B*, the Burdekin Gap and Hunter River Valley; *Biogeography C*, the Wet Tropics and the Burdekin Gap; *Biogeography D*, the Wet Tropics, Burdekin Gap and Hunter River Valley. A final AMOVA was run along taxonomic lines, labelled *Taxa*.

To complement the SAMOVA analysis I also calculated Hudson's nearest neighbour statistic (*Snn*; Hudson, 2000) using the program DNASP v5.10.01 (Librado and Rozas, 2009). This statistic is shown to be more robust in cases of low sample sizes and high haplotype diversity. High values of *Snn* (i.e. approaching one) reflect a high degree of population structure, while low values (i.e. half to one-third) indicate panmixia. The significance of *Snn* was evaluated via 10,000 permutations where significance was defined as the proportion of permuted values to be equal to or larger than the observed value.

2.4 Comparative phylogeography

To provide a wider comparative context for the observed phylogeographic structure between the squirrel glider and mahogany glider, mtDNA sequences from two recent petaurid phylogeographies were examined (yellow-bellied glider, Brown *et al*., 2006; and sugar glider, Malekian *et al*., 2010a). To complement the northern focus of this study, mtDNA (CytB) sequences from a recent study of the evolutionary distinctiveness of southern squirrel populations (Pavlova *et al*., 2010) were also included. Unless otherwise noted, ARLEQUIN was employed to generate all statistics using the methodologies described above. For ease of interpreting interspecific phylogeographic patterns, sequences were grouped into one of three biogeographic subdivisions - north-eastern Australia (NEA; regions north of the Burdekin Gap), eastern Australia (EA; regions between the Burdekin Gap and the Hunter River Valley) or south-eastern Australia (SEA; regions south of the Hunter River Valley). The Burdekin Gap and Hunter River Valley were selected because of their recognition as important dry habitat barriers in a diverse range of eastern Australian taxa (see Chapple *et al*., 2011a).

2.5 Morphometrics

Body measurements of six external characters were made available from 252 adult squirrel gliders and 107 adult mahogany gliders from a range of sources (see Appendix II for full morphological information). These measurements were: snout-vent length (SVL), the distance in centimetres from the tip of the nose to the base of the tail; vent-tail length (VTL), the distance in centimetres from the base of the tail to the tip of the tail; snout-tail length (STL), the distance in centimetres from the tip of the nose to the tip of the tail; head length (HL), the distance in centimetres from the tip of the nose to the base of the head; body weight (WT), the total weight in grams; and body to tail ratio (BTR), calculated by dividing SVL by VTL. This final measure represents an additional proxy for body mass, where lower measures of BTR correspond with higher body mass and vice versa (Jackson, 1999).

The software package SYSTAT 12.02 (Systat Software Inc., 2007) was used for all morphological analyses. Outliers were identified (studentized residuals, SYSTAT) and removed to minimise type II errors associated with interobserver measurement variances in both small mammals (Blackwell *et al*., 2006) and multi-source morphological data (Palmeirim, 1998). For both species, all external characters except BTR were regressed with SVL to control for the effects of body size. The normal distribution of each variable was confirmed via Shapiro-Wilk test (Shapiro and Wilk, 1965). Either residuals (STL, VTL, HL and WT) or raw data (SVL and BTR) were then used in a two-factor analysis of variation (ANOVA) to assess the differences between sex and regions (i.e. pre-defined eastern Australian bioregions; Figure 1). Tukey's post hoc Honestly-Significant-Difference (HSD) pairwise comparisons were then conducted for all significant effects.

Plate 3: As assortment of mahogany glider and squirrel glider specimens (Museum Victoria)

Photo: P. Ferraro

3. Results

3.1 Phylogeography

3.1.1 Sequence characteristics

A total of 159 mitochondrial (mtDNA, ND2) and 59 nuclear (nDNA, ApoB1) sequences were generated from the available tissue samples. All sequences were free of ambiguous nucleotides, indels or internal stop codons, while it was considered unlikely that PHASE generated underestimates of π_x in the nDNA dataset as all genotypes were fully resolved (see Garrick *et al*., 2010). At the broadscale, 44 mtDNA haplotypes and 76 polymorphic sites (41 of which were parsimony informative) were identified across 62 ND2 sequences, with 13 nDNA haplotypes and eight polymorphic sites (seven parsimony informative) detected across 59 ApoB1 sequences. Three samples in the ApoB1 dataset failed to produce complete ApoB1sequences (EU03, VIC05, VIC06). The seven regions comprising the finescale mtDNA dataset contained 137 ND2 sequences, with 37 haplotypes and 64 polymorphic sites documented. Due to the markedly lower phylogenetic signal in the ApoB1 dataset, it was determined that nDNA phylogeographic analyses be conducted exclusively at the broadscale level. Full sequence information from all datasets can be found in Appendix I.

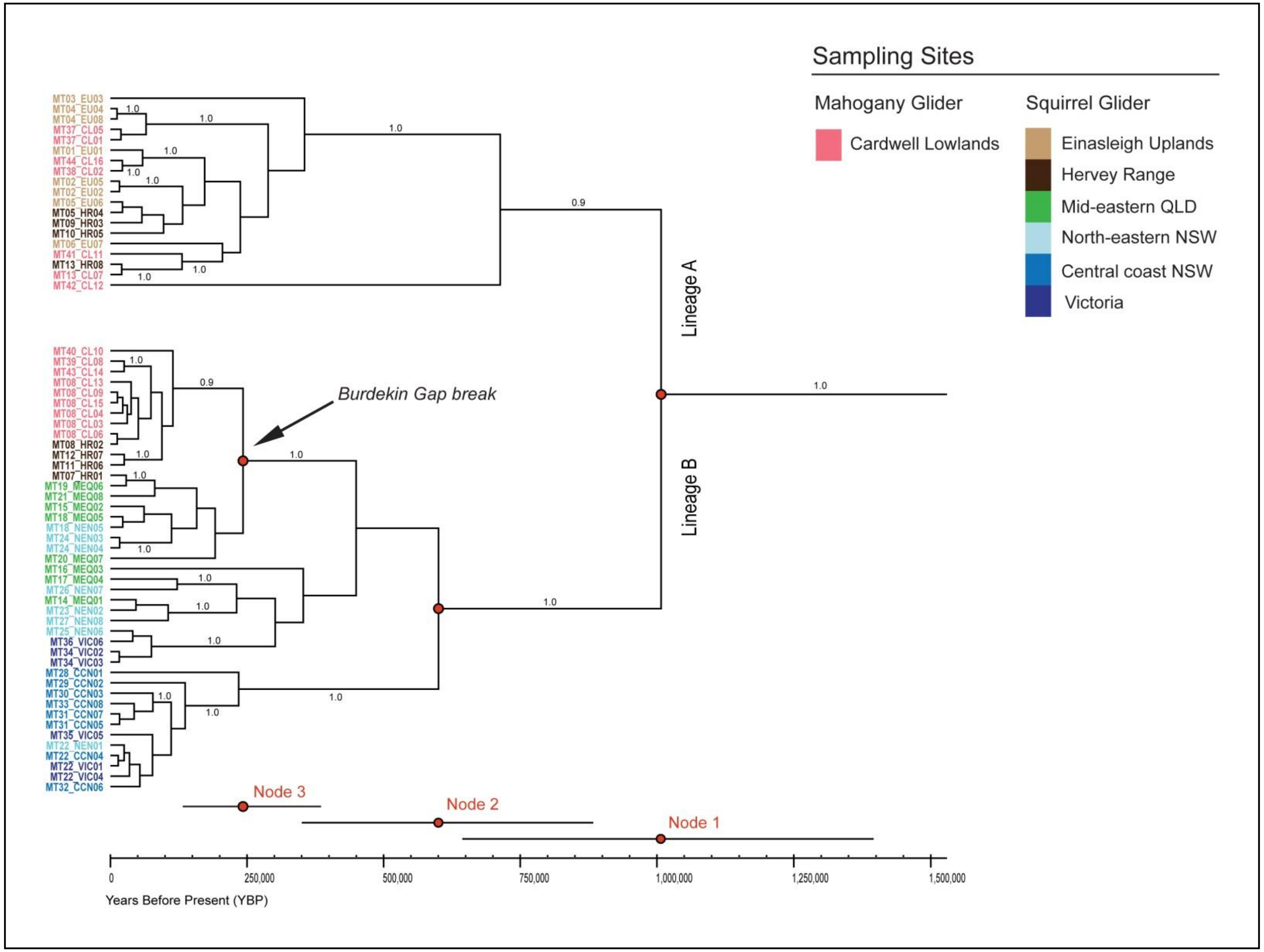


Figure 2: ND2 phylogeny of the squirrel – mahogany glider complex, including posterior probability (>0.9), obtained with Bayesian analysis. Divergence estimates of three noteworthy nodes presented below the tree. Samples coloured according to origin. See text for details.

3.1.2 Analysis of phylogenetic diversity and phylogeographic structure

Sequences assorted into two taxonomically independent lineages across eastern Australia, thereby providing no support for a reciprocally monophyletic clade representing the mahogany glider. This pattern was most evident in the mtDNA phylogeny, with divergence between the two lineages estimated as early Pleistocene (0.65 - 1.39 million years before present; see Node 1 in Figure 2). Within the mtDNA network (Figure 3a) there exists a broad geographic orientation of haplotypes. The first lineage (Lineage A) was predominantly restricted to north-eastern Australia (NEA), while the second, more widespread lineage (Lineage B) was detected across the squirrel glider's sampled distribution except the Einasleigh Uplands (EU). A narrow zone of admixture of the two mtDNA lineages was observed, encapsulating the distributional limits of the mahogany glider in the Cardwell Lowlands (CL) and the neighbouring squirrel glider region in the Hervey Ranges (HR). The Queensland subset (Figure 3b) reiterated this pattern, while also presenting variable levels of mtDNA admixture across the five geographically intermediate regions (Figure 4). Regional measures of the percentage of haplotypes per region by lineage (%H) present a broad geographic trend, with the proportion of Lineage B haplotypes increasing with latitude. A trend in the percentage of individuals per lineage (%N) across the region was less clear, with the proportion of Lineage A haplotypes roughly equivalent at either end of the admixture zone. Phylogeographic substructure was also observed in the southern lineage, with sequences from the central coast of New South Wales (CCN) clustering with a selection from north-eastern NSW (NEN) and Victoria (VIC), as highlighted in Figure 2 and Figure 3a.

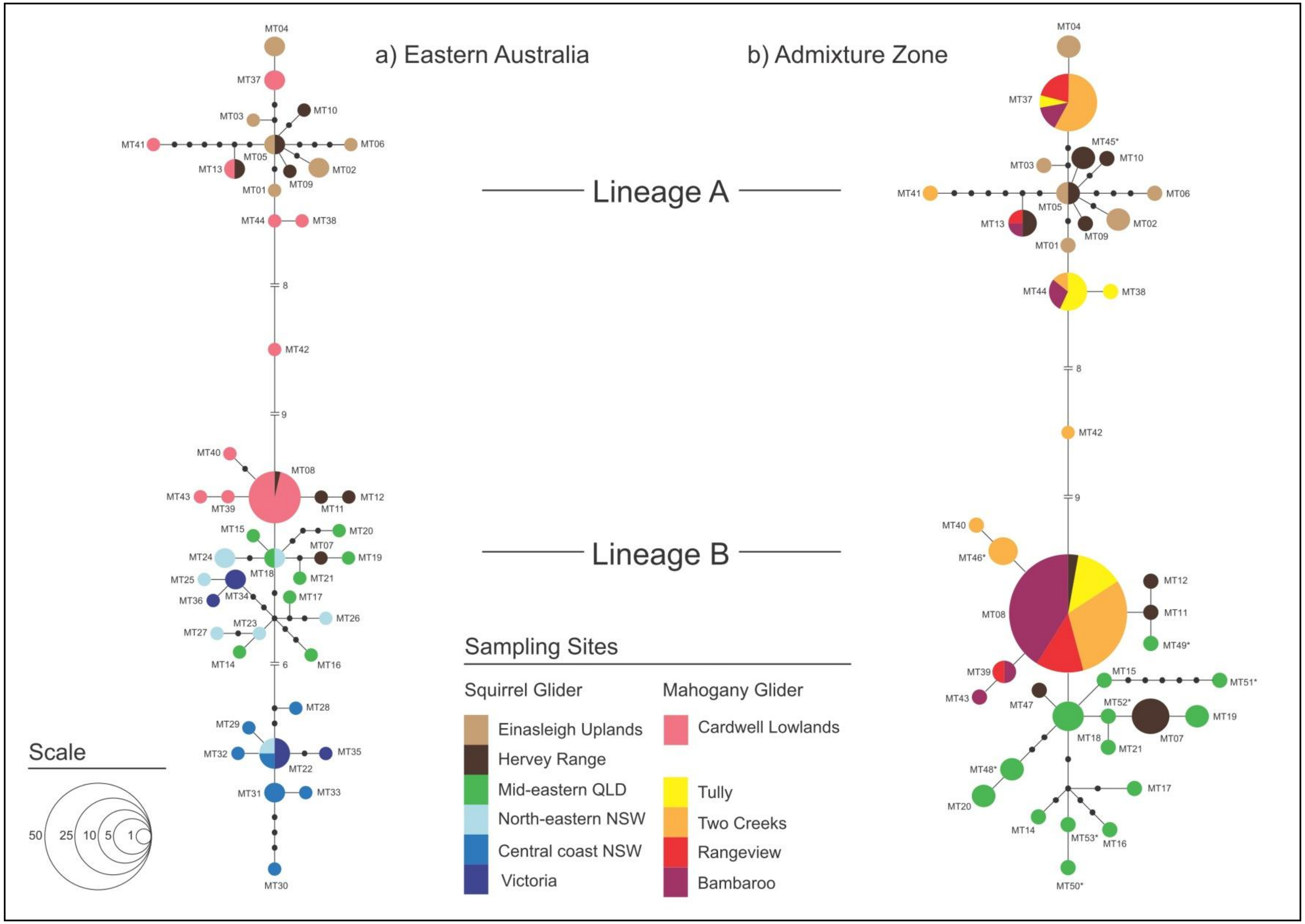


Figure 3: Median joining haplotype networks (mtDNA ND2) for the squirrel - mahogany glider complex; a) full eastern distribution of both gliders, and b) limited to the admixture zone between the two gliders in north-eastern Australia. Haplotypes are coloured according to sample origin, scaled according to frequency and connected by solid lines representing a single base pair substitution. Black solid circles represent unsampled haplotypes and double dashed lines and their accompanying numbers represent the number of unsampled haplotypes.

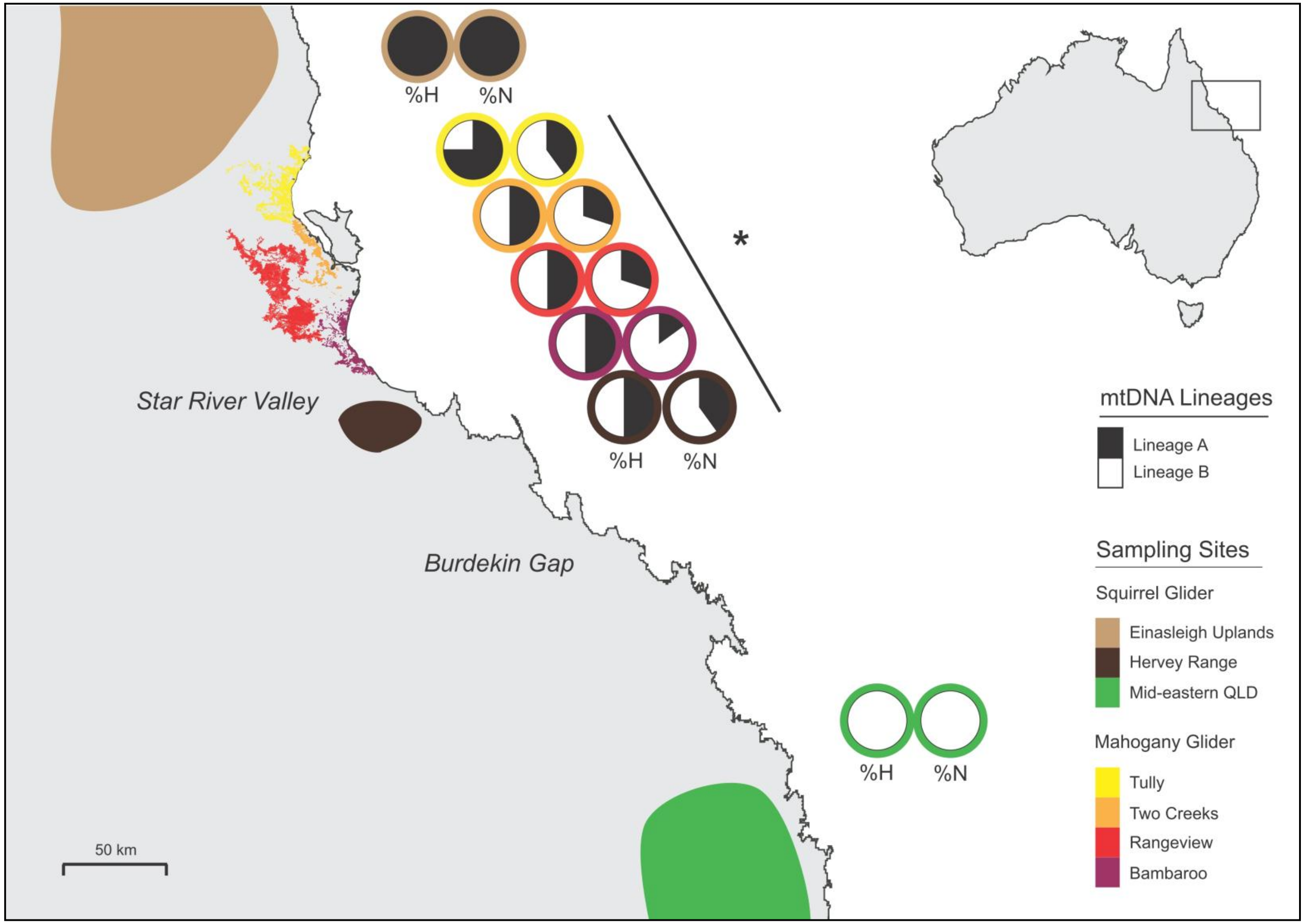


Figure 4: Location and composition of mtDNA admixture in north-eastern Australia. Coloured rings surrounding pie charts correspond to sample origin. Pie chart fill colour indicates presence of either Lineage A (black) or Lineage B (white). %H, proportion of haplotypes by lineage; %N, proportion of individuals by lineage. Admixture zone identified with an asterisk (*).

The primary characteristics of the mtDNA dataset were also apparent in the nDNA – haplotypes assorted independent of taxonomy yet with a broad geographic orientation of phylogenetic diversity (Figure 5). Specifically, the four most common nDNA haplotypes (N01 – N04, comprising over 80% of all ApoB1 sequences) had strong geographic associations, with N01 and N04 common north of the Burdekin Gap but less so to the south, while haplotypes N02 and N03 showed the reverse pattern.

Measures of both haplotypic and nucleotide diversity were higher in the squirrel glider than the mahogany glider for ND2 and ApoB1 (Table 1a). Notably, mtDNA nucleotide diversity (Table 1a) was markedly higher in CL and HR, the previously described zone of admixture, than the remaining regions. Haplotypic diversity was broadly consistent across all regions, marginally lower in CL and Victoria (VIC). No clear patterns, however, were observed in either nucleotide or haplotypic diversities of the nDNA dataset (Table 1b).

Based on pairwise distances (Figure 6a) both EU and CCN were the most divergent regions, with each significantly differentiated from the remaining regions (except HR and VIC, respectively). Conversely, HR was the least distinct, exhibiting significant differentiation from only the two most geographically removed regions (CCN and VIC). Although appreciably lower than their mtDNA counterparts, results of nDNA pairwise comparisons (Figure 6b) support the geographically oriented phylogenetic diversity presented in the nDNA haplotype network. Specifically, statistical significance was limited to comparisons made across the Burdekin Gap.

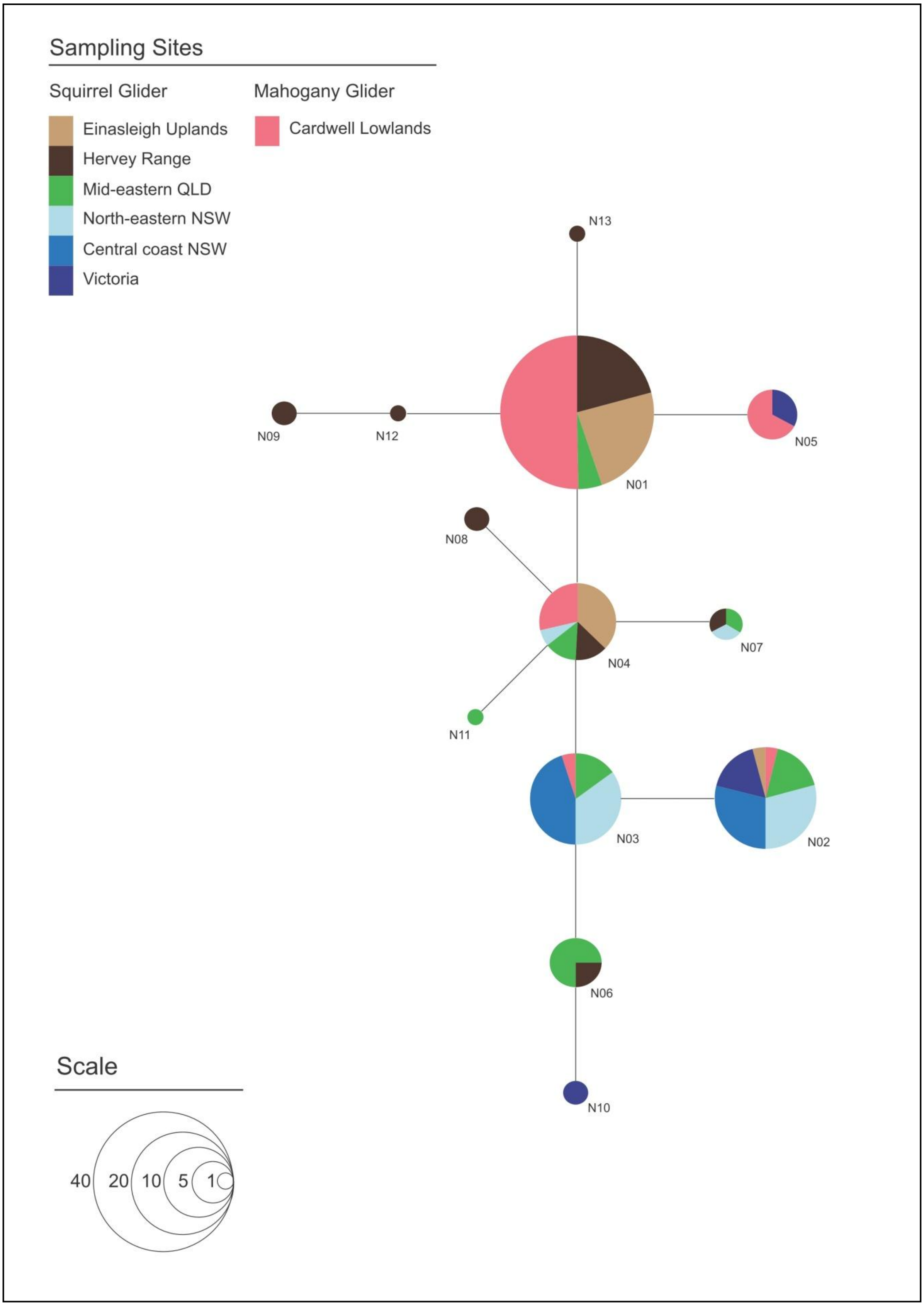


Figure 5: Median joining haplotype network (nDNA ApoB1) for the eastern Australian distribution of the squirrel - mahogany glider complex. Haplotypes are coloured according to sample origin, scaled according to frequency and connected by solid lines representing a single base pair substitution.

*Table 1: Genetic diversity data for the squirrel - mahogany glider complex for: a) eastern Australian mtDNA dataset, b) north-eastern Australian mtDNA dataset and c) eastern Australian nDNA dataset. n, number of sequences; H, number of haplotypes; P, number of private haplotypes; Hd, haplotype diversity; π_x, nucleotide diversity; K, population grouping; ns, non-significant ($p > 0.05$); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; [1], most parsimonious SAMOVA scenario. Underlined text indicates mahogany glider regions.*

	Diversity Measures			
a) ND2	n	H (P)	Hd	π_x
squirrel glider	*46*	*36 (34)*	*0.987*	*0.011*
mahogany glider	*16*	*10 (8)*	*0.867*	*0.010*
Regions				
Einasleigh Uplands	8	6 (5)	0.929	0.004
<u>Coastal Lowlands</u>	16	10 (8)	0.867	0.010
Hervey Range	8	8 (5)	1.000	0.010
Mid-eastern QLD	8	8 (7)	1.000	0.005
North-eastern NSW	8	7 (5)	0.964	0.006
Central coast NSW	8	7 (6)	0.964	0.003
Victoria	6	4 (3)	0.867	0.007
b) ApoB1	n	H (P)	Hd	π_x
squirrel glider	*43*	*11 (8)*	*0.822*	*0.0023*
mahogany glider	*16*	*7 (0)*	*0.629*	*0.0014*
Regions				
Einasleigh Uplands	7	3 (0)	0.582	0.0011
<u>Coastal Lowlands</u>	16	7 (0)	0.629	0.0014
Hervey Range	8	6 (4)	0.683	0.0017
Mid-eastern QLD	8	7 (1)	0.883	0.0023
North-eastern NSW	8	4 (0)	0.650	0.0011
Central coast NSW	8	2 (0)	0.525	0.0007
Victoria	4	3 (1)	0.714	0.0038

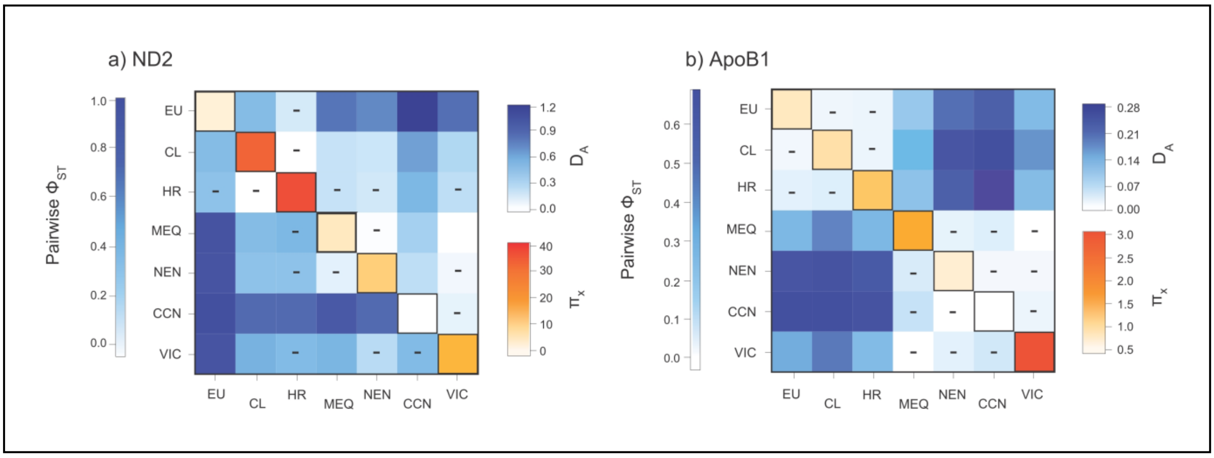
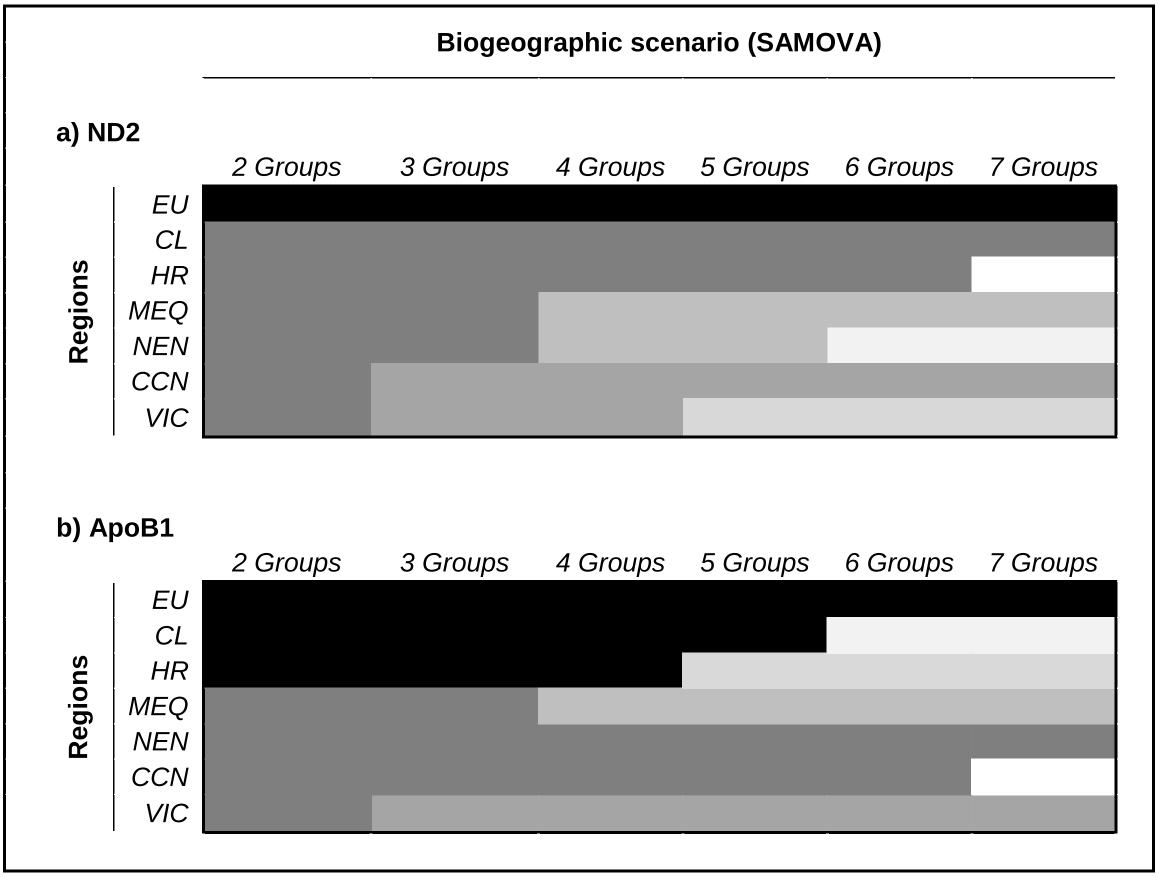


Figure 6: Pairwise comparisons of nDNA and mtDNA variation in the squirrel - mahogany glider complex a) ND2 and b) ApoB1. Φ_{ST} below diagonal, D_A above diagonal and π_x on diagonal. Dashes represent statistically non-significant ($p > 0.05$) pairwise comparisons.

Two consistent patterns were noted across the six mtDNA scenarios generated by SAMOVA (i.e. K=2 through to K=7): 1) the Einasleigh Uplands (EU) remained isolated from all other regions, and 2) Hervey Range (HR) and Cardwell Lowlands (CL) were always partitioned within the same group (Table 2).For the mtDNA data, a series of four groupings (i.e. K=4) was identified by SAMOVA as the most appropriate biogeographic scenario. When compared to the *a priori* scenarios, the SAMOVA scenario provides the most parsimonious partitioning of genetic variation (Table 3a). Within this scenario, Hudson's nearest neighbour statistic (*Snn*) identified moderate differentiation between the central coast of NSW (CCN) and Victoria (VIC) (*Snn* = 0.69, p = 0.05), plus between HR and CL (*Snn* = 0.73, p = 0.02). Minimal differentiation, however, was detected between regions comprising eastern Australia (EA), MEQ and NEN (*Snn* = 0.45, p = 0.54).

Table 2: SAMOVA derived biogeographic scenarios, based upon a) mtDNA and b) nDNA datasets. Shaded blocks indicate regional groupings by scenario.



For ApoB1, K=2 was the preferred biogeographic scenario, with each group comprised exclusively of regions from either side of the Burdekin Gap. As with the mtDNA dataset, the SAMOVA scenario provided a better explanation of phylogeographic structure than the *a priori* scenarios (Table 3b) while assorting the sampling regions into taxonomic groupings again provided the least parsimonious scenario.

Table 3a: mtDNA structure data across the squirrel - mahogany glider complex according to a number of biogeographic scenarios. Regions are either connected by a '-' (dash) or separated by a '/' (backspace). NEA = EU, HR and CL; EA = MEQ and NEN; SEA = CCN and VIC. See text for a description of biogeographic scenarios and explanation of abbreviations.

a) ND2

Biogeographic Scenario	No. of groups	Variance component	% variation	P-value
SAMOVA	4	Among groups	44%	**
EU / CL-HR / EA-SEA		Among regions	3%	ns
		Within regions	53%	***
Unstructured	1	Among regions	43%	***
EU-CL-HR-MEQ-NEN-CCN-VIC		Within regions	57%	-
Biogeography B	3	Among groups	37%	**
NEA-EA-SEA		Among regions	12%	**
		Within regions	51%	***
Biogeography D	4	Among groups	34%	*
EU-HR / CL-EA-SEA		Among regions	11%	**
		Within regions	55%	***
Biogeography A	2	Among groups	30%	*
NEA / EA-SEA		Among regions	20%	***
		Within regions	50%	***
Biogeography C	3	Among groups	22%	ns
EU-HR / CL / EA-SEA		Among regions	24%	***
		Within regions	54%	***
Taxa	2	Among groups	-22%	ns
CL / EU-HR-MEQ-NEN-CCN-VIC		Among regions	59%	***
		Within regions	64%	***

Table 3b: nDNA structure data across the squirrel - mahogany glider complex according to a number of biogeographic scenarios. Regions are either connected by a '-' (dash) or separated by a '/' (backspace). NEA = EU, HR and CL; EA = MEQ and NEN; SEA = CCN and VIC. See text for a description of biogeographic scenarios and explanation of abbreviations.

b) ApoB1

Biogeographic Scenario	No. of groups	Variance component	% variation	P-value
SAMOVA (Biogeography D)	2	Among groups	47%	*
NEA / EA-SEA		Among regions	3%	ns
		Within regions	50%	***
Biogeography B	3	Among groups	42%	*
NEA-EA-SEA		Among regions	3%	*
		Within regions	55%	***
Biogeography C	3	Among groups	40%	*
EU-HR / CL / EA-SEA		Among regions	4%	*
		Within regions	56%	***
Biogeography A	4	Among groups	34%	ns
EU-HR / CL-EA-SEA		Among regions	6%	*
		Within regions	60%	***
Unstructured	1	Among regions	38%	***
EU-CL-HR-MEQ-NEN-CCN-VIC		Within regions	62%	-
Taxa	2	Among groups	11%	ns
CL / EU-HR-MEQ-NEN-CCN-VIC		Among regions	31%	***
		Within regions	58%	***

3.2 Comparative phylogeography

Phylogeographic structure was broadly consistent across the four eastern Australian petaurid datasets examined here (Figure 7). Each network was composed of two divergent lineages that, with the exception of the sugar glider, were of comparable depth. The biogeographic subdivisions recognised in the squirrel glider - mahogany glider complex (NEA, EA and SEA; Figure 7a) provided an appropriate explanation of phylogeographic structure in each glider, accounting for between one-third (squirrel glider and mahogany glider) to two-thirds (sugar glider and yellow-bellied glider) of the observed mtDNA variation (Table 4). The single NEA squirrel glider from Pavlova *et al*. (2010) was clearly distinct from the remaining EA and SEA samples (Figure 7b). This differentiation mirrors that of the single NEA squirrel glider region used in this study (EU, n = 8), which was composed exclusively of NEA haplotypes. In fact, phylogeographic structure was broadly comparable for the squirrel glider – mahogany glider complex and yellow-bellied glider, with NEA gliders clearly distinct from those in EA and SEA. In contrast, the most distinct subdivision in the sugar glider network was EA, with populations exhibiting approximately 8% net sequence divergence from NEA and SEA populations (Figure 7b).

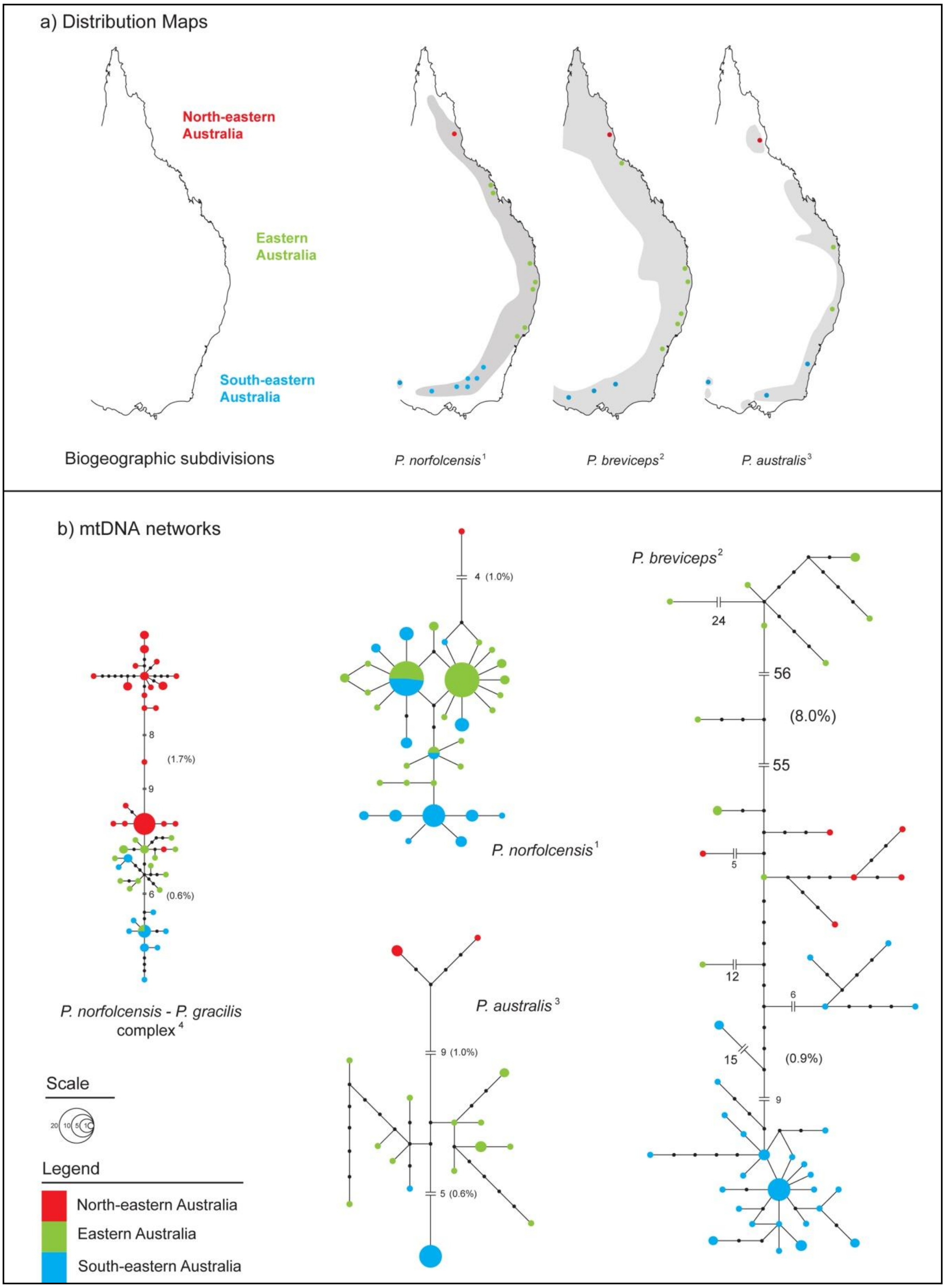


Figure 7: a) Biogeographic subdivisions (coloured text), species distributions (grey shading), sample origins (coloured circles) and b) median joining haplotype networks for Australia's Petaurus *gliders. Haplotype colouring corresponds with biogeographic subdivision with unsampled haplotypes coloured black. Haplotypes are scaled according to frequency and are separated by single (solid lines) or multiple (line broken by double dash) base pair substitution. Numbers accompanying double dashed lines refer to the number of substitutions while percentages represent notable percentage sequence divergences. Networks adapted from: [1], Pavlova et al, (2010); [2], Malekian et al. (2010a); [3], Brown et al. (2006), and [4], this study.*

Table 4: Comparative a) source and b) phylogeographic data for four petaurid gliders. n, number of sequences; r, number of sampled regions. Biogeographic subdivisions: NEA, north-eastern Australia; EA, eastern Australia; SEA, south-eastern Australia. Underlined text represents mtDNA diversity and structure measures for the Einasleigh Uplands (EU) region. Superscript text corresponds with source of mtDNA data.

a) Comparative dataset information

Source	Gene	Fragment size	Model of sequence evolution
[a] This study	ND2	1,040bp	Tamura & Nei
[b] Pavlova *et al*., 2010	CytB	397bp	Tamura & Nei
[c] Malekian *et al*., 2010a	ND2/4	1,392bp	Tamura & Nei
[d] Brown *et al*., 2006	ND4	873bp	Tamura & Nei

b) *Petaurus* diversity and structure

	% nucleotide diversity (π_x) within subdivision (n / p)						% sequence divergence (D_A) between subdivisions			% variance among subdivisions	
Taxon	NEA		EA		SEA		NEA-EA	NEA-SEA	EA-SEA	Variation	P-value
P. n - P. g complex [a]	1.0	(32/3)	0.5	(16/2)	0.6	(14/2)	1.2	1.6	1.0	44%	***
	0.4	(8/1)	-	-	-	-	- 1.7	1.9	-		
P. norfolcensis [b]	0.0	(1/1)	0.6	(66/7)	1.0	(53/7)	1.8	2.4	1.1	32%	***
P. breviceps [c]	0.6	(6/1)	4.9	(12/6)	0.6	(44/3)	5.8	1.7	6.3	66%	***
P. australis [d]	0.3	(4/1)	0.7	(15/2)	0.1	(13/3)	1.8	1.9	1.0	67%	***

Genetic diversity was generally comparable within biogeographic subdivisions across the four *Petaurus* datasets, with a few exceptions (Table 4). Firstly, comparable levels of diversity were recorded in the NEA subdivisions across all taxa except for the squirrel glider – mahogany glider complex. This distinction is explained by the presence of both highly divergent lineages within two of the three regions that comprise the NEA subdivision of the squirrel glider – mahogany glider complex. An additional estimate of π_x was generated for the single region from the squirrel glider – mahogany glider complex comprised exclusively of Lineage A sequences, EU. Results highlighted the relatively depauperate nature of EU (π_x = 0.4%) and brought the level of NEA divergence in line with those of the other three datasets. Secondly, genetic diversity in the SEA subdivision of the yellow-glider was markedly lower than all other gliders, due primarily to the ubiquity of a single haplotype across the subdivision. Thirdly, nucleotide diversity in the EA subdivision of the sugar glider was five-fold higher than the remaining gliders. This large differentiation explains the notably higher value for D_A between EA and the other subdivisions in the sugar glider. All other measures of D_A are broadly consistent across the subdivisions and species.

3.3 Morphometrics

Body measurements of the six external characters (Table 5) are consistent with those published elsewhere for both the squirrel glider (Quin, 1995; Quin *et al*., 1996b; Traill, 1998; Millis and Bradley, 2001) and mahogany glider (Van Dyck, 1993; Jackson, 2000a). Despite the large geographic range, no clear clinal variation in morphology was detected for the squirrel glider - mahogany glider complex. This contrasts with previous examinations of eco-geographic variation in squirrel and sugar gliders (Quin *et al*., 1996b) and yellow-bellied glider (Brown *et al*., 2006).

Preliminary two-factor ANOVA of the four mahogany glider subregions (i.e. Tu, Tc, Ra and Ba) generated no significant geographic or sex differences in any of the six morphological characters analysed (results not shown). Morphological data from the four subregions was therefore grouped in line with molecular analyses (i.e. Cardwell Lowlands, CL). Due to low sample sizes, morphological data from CCN and VIC were merged into a broader south-eastern Australian (SEA) region that conformed to the biogeographic zones of James and Moritz (2000) and Moussalli *et al*. (2005). Although available data for EU and HR were also limited, both were maintained as separate regions due to their geographic proximity to, and phylogeographic relationship with, the mahogany glider. As such, caution was taken in interpreting these data with results from these regions considered preliminary in nature.

Table 5: Raw measurements for six external morphological characters of the squirrel - mahogany glider complex. N, number of samples; min, minimum value; Mean, mean value; max, maximum value; SE, one standard error of Mean. Bracketed text accompanying morphological variables represent the unit of measurement for that variable (cm, centimetres; gm, grams). Regional abbreviations described in-text.

	Snout-tail length (cm)					**Snout-vent length (cm)**					**Vent-tail length (cm)**				
	N	min	Mean	max	SE	N	min	Mean	max	SE	N	min	Mean	max	SE
Mahogany glider	**104**	**480**	**615.4**	**715**	**4.2**	**99**	**200**	**260.5**	**320**	**2.1**	**106**	**240**	**356.1**	**430**	**3.1**
Sex															
male	53	548	621.9	715	4.9	53	215	261.6	320	2.5	55	280	360.6	430	4.0
female	51	480	608.6	700	6.9	46	200	259.2	320	3.5	51	240	351.2	405	4.7
Region															
Tu	25	510	596.2	700	9.9	23	200	250.9	310	4.7	26	270	346.9	430	7.3
Tc	35	480	627.3	715	6.9	33	215	259.5	320	3.7	35	305	367.7	405	3.5
Ra	10	595	627.5	695	8.7	10	240	270.0	320	7.1	10	325	357.5	375	4.8
Ba	34	530	613.7	677	6.8	33	230	265.1	300	2.7	35	240	350.9	414	6.3
Squirrel glider	**188**	**212**	**447.4**	**660**	**4.0**	**184**	**170**	**203.7**	**260**	**1.5**	**188**	**150**	**247.7**	**330**	**1.8**
Sex															
male	77	212	456.0	660	6.6	73	170	208.3	260	2.7	77	199	248.6	330	2.7
female	111	220	441.5	540	5.0	111	170	200.7	255	1.7	111	150	247.0	320	2.5
Region															
EU	4	450	503.8	560	23.0	4	170	210.0	260	18.7	4	240	293.8	320	18.4
HR	2	425	542.5	660	117.5	2	195	212.5	230	17.5	2	230	280.0	330	50.0
MEQ	74	399	437.0	495	3.6	70	170	206.2	260	3.0	74	210	252.0	295	2.1
SEQ	23	380	437.0	495	5.9	23	175	201.0	227	2.9	23	195	236.1	285	4.5
NEN	64	212	417.0	502	8.4	65	173	197.7	244	1.9	64	150	237.4	290	2.7
SEA	21	419	482.1	540	7.7	20	179	215.3	245	3.3	21	220	264.3	320	6.2

Table 5 [cont]: Base measurements for six external morphological characters of the squirrel - mahogany glider complex. N, number of samples; min, minimum value; Mean, mean value; max, maximum value; SE, one standard error of Mean. Bracketed text accompanying morphological variables represent the unit of measurement for that variable (cm, centimetres; gm, grams). Regional abbreviations described in-text.

	Weight (gm)					**Body-tail ratio**					**Head length (cm)**				
	N	min	Mean	max	SE	N	min	Mean	max	SE	N	min	Mean	max	SE
Mahogany glider	**102**	**195**	**333.5**	**450**	**5.8**	**98**	**0.57**	**0.73**	**1.00**	**0.01**	**85**	**41.0**	**55.4**	**68.3**	**0.6**
Sex															
male	52	200	341.0	450	8.8	52	0.61	0.73	0.98	0.01	47	47.7	55.6	68.3	0.8
female	50	195	325.7	410	7.3	46	0.57	0.74	1.00	0.01	38	41.0	55.2	67.0	0.8
Region															
Tu	22	195	318.6	410	12.0	23	0.57	0.74	1.00	0.02	6	48.8	56.6	63.5	2.3
Tc	34	200	358.6	450	10.4	33	0.61	0.71	0.86	0.01	34	41.0	55.7	68.0	0.9
Ra	10	215	335.2	380	17.5	10	0.65	0.76	0.85	0.02	9	48.9	57.1	68.3	2.0
Ba	36	220	318.5	420	8.6	32	0.64	0.75	0.98	0.02	36	46.0	54.5	67.0	0.8
Squirrel glider	**157**	**111**	**205.5**	**325**	**3.2**	**179**	**0.53**	**0.83**	**1.11**	**0.01**	**76**	**41.4**	**47.9**	**57.5**	**0.4**
Sex															
male	66	128	214.6	320	4.8	71	0.61	0.84	1.04	0.01	40	42.0	48.7	57.5	0.5
female	91	111	198.9	325	4.2	108	0.53	0.82	1.11	0.01	36	41.4	47.0	52.2	0.4
Region															
EU	4	320	322.5	325	1.4	4	0.53	0.73	0.88	0.09	4	45.3	46.2	48.5	0.8
HR	2	200	204.0	208	4.0	2	0.70	0.78	0.85	0.08	1	51.6	51.6	51.6	.
MEQ	72	128	217.7	279	3.5	70	0.61	0.82	1.11	0.01	71	41.4	47.9	57.5	0.4
SEQ	19	111	178.5	301	9.9	23	0.73	0.86	1.10	0.02	0	.	.	.	.
NEN	55	121	190.4	294	4.2	60	0.66	0.83	1.03	0.01	0	.	.	.	.
SEA	5	130	205.2	270	25.3	20	0.63	0.83	1.02	0.02	0	.	.	.	.

No interaction between region and sex was observed across any character (Table 6). Significant regional differences were found for all characters assessed, while only one, namely SVL, significantly differed between the sexes. Post hoc pairwise comparison of regional variation identified significant geographic differences in only two characters, SVL and BTR, with the primary pattern being the differentiation of the Cardwell Lowlands (CL) from the remaining regions. Specifically, mahogany gliders were clearly and significantly longer than the squirrel glider (Figure 8a). Among the squirrel glider regions, little morphological differentiation was noted, with minor variation restricted to the southern portion of its distribution (NEN and SEA). Regional patterns of BTR – a proxy for body mass - exhibited a similar trend, with gliders from CL significantly heavier (i.e. lower BTR) than those from the remaining regions (Figure 8b). Although EU and HR exhibited non-significant variation from both the mahogany glider and four squirrel glider regions south of the Burdekin Gap in both SVL and BTR, this was considered an artefact of under-representation of the squirrel glider north of the Burdekin Gap in this dataset.

Table 6: Two-factor ANOVA of six external morphological characters of the squirrel - mahogany glider complex, depicting variation of a) sampling regions, b) sexual dimorphism and c) their interaction. Red bold p-values indicate statistical significance (at $p < 0.05$). n/a, insufficient samples. Morphological character abbreviations: weight (WT), snout-tail length (STL), snout-vent length (SVL), vent-tail length (VTL), body-tail ratio (BTR), head length (HL).

	region		**sex**		**interaction**	
Morphological Variable	F	p	F	p	F	p
SVL	59.05	**0.000**	8.68	**0.003**	0.94	0.469
BTR	9.67	**0.000**	0.55	0.471	0.92	0.483
WT	8.93	**0.000**	0.82	0.366	1.06	0390
STL	13.54	**0.000**	0.19	0.665	1.55	0.163
VTL	19.06	**0.000**	0.38	0.539	1.10	0.362
HL	4.20	**0.000**	2.39	0.124	*na*	*na*

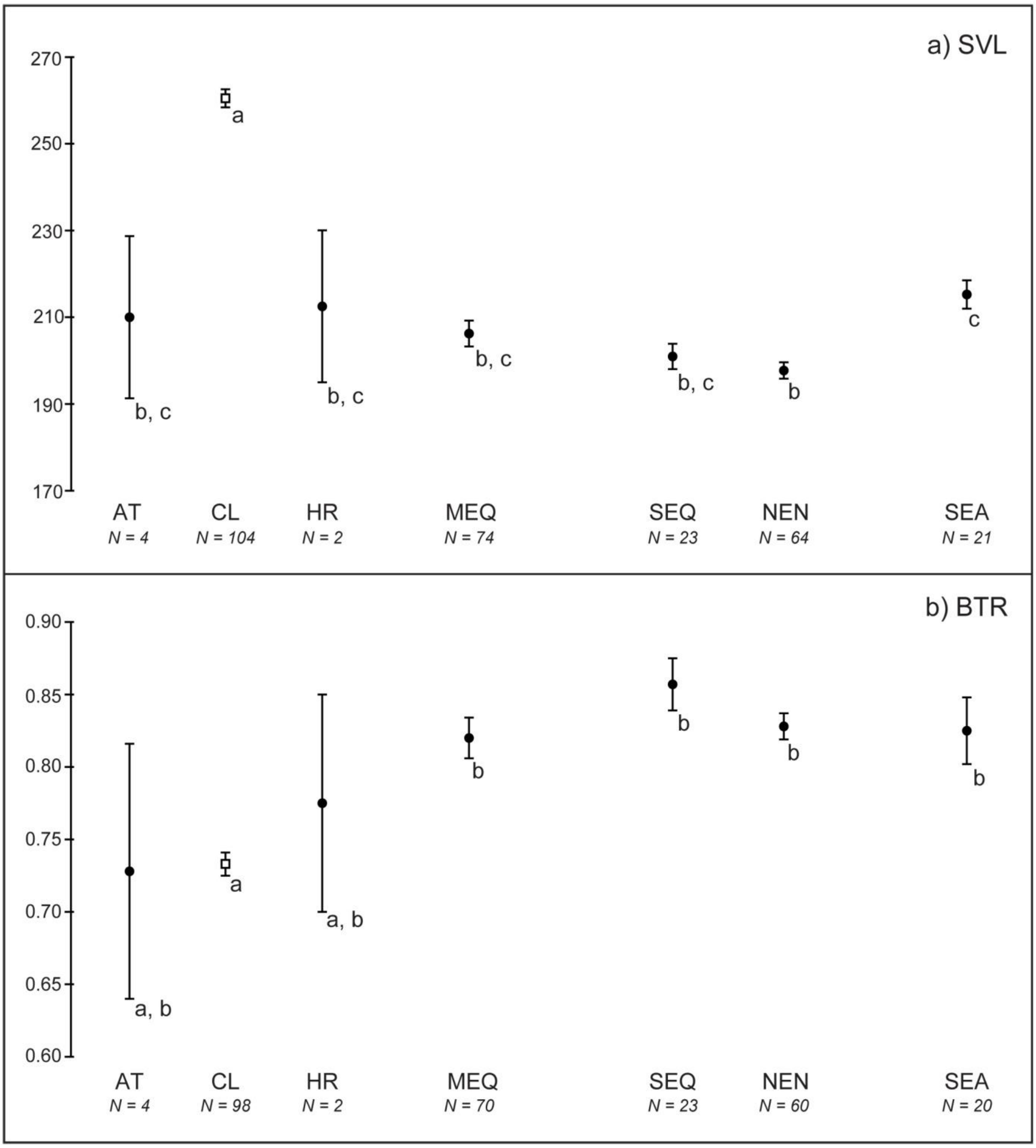


Figure 8: Mean values plus standard error of morphological variation in the squirrel - mahogany glider complex for the two characters to exhibit significant post-hoc pairwise differences: a) snout-vent length (SVL), and b) body-tail ratio (BTR). Subscript letters represent region groupings, as defined by Tukey's post-hoc HSD pairwise comparisons. N, sample size; open square, mahogany glider; closed circles, squirrel glider. Regions are ranked by increasing latitude while the gap width between regions provides a rough measure of geographic distance. Regional abbreviations explained in-text.

Plate 4: Skins of the squirrel glider (left and centre) and the mahogany glider (right) (Museum Victoria)

Photo: P. Ferraro

4. Discussion

The mahogany glider (*Petaurus gracilis*) and squirrel glider (*P. norfolcensis*) share a more complex evolutionary history than currently understood. Results from mtDNA analyses identified two well differentiated, reciprocally monophyletic lineages that exhibit a strong geographic orientation, but are not congruent with current taxonomy. One lineage is restricted to north-eastern Australia (NEA) while the second is distributed across all sampling regions except Einasleigh Uplands (EU), the northern limit of the dataset. Thus, a narrow zone of admixture exists, restricted to the mahogany glider in the Cardwell Lowlands (CL) and the squirrel glider population in the adjacent Hervey Range (HR). Although exhibiting a much slower mutation rate with perhaps minimal lineage sorting, the nuclear data also suggests a north-eastern Australia – eastern, south-eastern Australia split. Divergence estimates date the split between lineages to approximately the early Pleistocene. Converse to the molecular data, however, morphology does support current taxonomy, with the mahogany glider significantly larger (i.e. SVL and BTR) than the squirrel glider. In the following sections I first provide a detailed discussion of the molecular findings, followed by the implications of these results for the taxonomic status of the mahogany glider.

4.1 Phylogeography of the squirrel glider – mahogany glider complex

The primary phylogeographic split within the squirrel – mahogany glider complex coincides with north-eastern Queensland’s Burdekin Gap; an expanse of dry, sparse woodland and savannah separating the Wet Tropics from higher latitude subtropical rainforests and open Eucalyptus forests (Keast, 1961; Ford, 1986; Cracraft, 1991). Consistent with previous studies that have focussed on eastern Australia’s forest communities, it is clear that the Burdekin Gap represents a persistent, long-term dispersal barrier. These results join a growing list of studies that attribute coincidental phylogeographic structure in open forest communities to the Burdekin Gap. Among petaurids for instance, the dry and open woodlands of the Burdekin Gap are recognised as the primary barrier to dispersal in the patchily distributed yellow-bellied glider (Brown *et al*., 2006). More broadly, the Burdekin Gap is invoked as the geographic feature responsible for notable phylogeographic structure in a wide range of vertebrate taxa, including amphibians (James and Moritz, 2000), reptiles (Edwards and Melville, 2010), birds (Joseph and Moritz, 1994) and mammals (Taylor and Foulkes, 2004).

The Pleistocene origin of mtDNA divergence detailed in this study also compares with those of both mammalian and non-mammalian open forest taxa, the majority of which fall within the Pliocene – Pleistocene epochs. This correlates with the established scenario of historical biogeography of eastern Australia, where genetic divergence in closed forest taxa is earlier (typically Miocene – Pliocene c.f. Pliocene – Pleistocene) and more highly geographically structured than amongst their open forest counterparts (e.g. Schneider *et al*., 1998; Moritz *et al*., 2000; Moussalli *et al*., 2005; Bell *et al*., 2007, 2010). As petaurid gliders have a strong association with mature *Eucalyptus* stands for a range of ecological requirements, including diet, breeding, shelter and movement (Dettmann *et al*., 1995; Quin *et al*., 1996b; Jackson, 2000c, 2001; Goldingay and Jackson, 2004; Eyre, 2007) and despite the major climatic fluctuation associated with the Quaternary, results indicate that even open tall forest communities rarely establish across the Burdekin Gap. Nevertheless, admixture of the two major lineages of the squirrel – mahogany glider complex north of the Burdekin Gap clearly suggest periods of intermittent connectivity of such communities. Considering the estimated divergence between mtDNA clades within only the southern lineage that span the Burdekin Gap (see Node 3 in Figure 2), such connectivity may have been as recent as the current glacial or the penultimate interglacial (Kershaw, 1976; Kershaw, 1983; Moss and Kershaw, 2000).

In contrast, the relatively deeper divergence observed among major lineages within the sugar glider is hypothesised to have an alternative origin, namely the geographic uplift of the Great Dividing Range (Malekian *et al*., 2010a). Although eastern Australia's petaurid gliders are largely analogous in ecological preferences the sugar glider is considered relatively more vagile and more of a generalist in terms of habitat and dietary preferences (Lindenmayer, 2002). Malekian *et al*. (2010b) proposed that these characteristics may be responsible for the lack of phylogenetic divergence across the Burdekin Gap in the sugar glider. The narrower habitat preferences of the less widespread yellow-bellied glider, conversely, correspond with a greater degree of phylogenetic partitioning across the Burdekin Gap (Brown *et al*., 2006). These interspecific phylogeographic patterns mirror those among *Sericornis* scrubwrens (Joseph and Moritz, 1994), which were determined to be a consequence of interspecific ecological differentiation. Joseph and Moritz (1994) observed that the most ecologically diverse and widely distributed species, *S. frontalis*, exhibited less phylogeographic structure than its congeners, especially across the Burdekin Gap.

Contrary to previous published work on open forest taxa, no phylogenetic break was associated with either the open woodlands of St. Lawrence Gap or the montane wet forests of the McPherson Range. The St. Lawrence Gap, a lowland dry corridor considered analogous to that of the Burdekin Gap (Chapple *et al*., 2011a), has previously been cited as a long-term dispersal barrier to open forest taxa (McGuigan *et al*., 1998; James and Moritz, 2000; Keogh *et al*., 2003), although to a lesser extent. One possible explanation for the lack of divergence across the St. Lawrence Gap in the squirrel – mahogany glider complex is the relatively higher dispersal capacity of the petaurids among open forest vertebrate taxa (van der Ree *et al*., 2003) paired with their ability to traverse habitat breaks (van der Ree and Bennett, 2003). In regards to the McPherson Range, a bioregion noted for its high phylogentic endemicity among wet forest taxa (e.g. James and Moritz, 2000; Nicholls and Austin, 2005; although see Edwards and Melville, 2010), few cases of associated phylogeographic structure exist among open forest taxa, as highlighted by Chapple *et al*. (2011a).

North of the Burdekin Gap, mtDNA substructure suggests isolation of the Einasleigh Uplands from its neighbouring populations, Hervey Range and Cardwell Lowlands. The cause of such isolation is likely multi-faceted, with the region’s complex mosaic of vegetation types (i.e. Figure 1, Edwards and Melville, 2010) providing numerous potential barriers to dispersal. For instance, the strong phylogenetic differentiation between the Einasleigh Uplands and Cardwell Lowlands populations is likely strongly influenced by the Wet Tropics; the largely continuous high altitude rainforest that lies to the northern and western extremes of the Cardwell Lowlands. Petaurid gliding techniques are unsuited to movement through the closed canopy and dense understorey characteristic of the Wet Tropics (Jackson, 1999), rendering this habitat impassable (see Brown *et al*., 2006).

Resembling an ecological cul-de-sac, the comparatively wetter and more floristically diverse Cardwell Lowlands appear to meld with the wider open forests of north-eastern Australia only toward its southern reaches – as illustrated by the phylogenetically homogeneous nature of the neighbouring Cardwell Lowlands and Hervey Range populations. The cause of reduced gene flow between the Einasleigh Uplands and the Hervey Range populations is less apparent, however, as each inhabit the open sclerophyll forests that replace the closed rainforests on the western slopes of the of the Wet Tropics. The forests are themselves replaced by woodland savannahs at lower altitudes, producing patches of unfavourable petaurid habitat. One such dry open woodland habitat is the Star River Valley (Williams *et al*., 1993), a minor subcatchment of the Upper Burdekin River Basin located to the north-east of the predominant biogeographic barrier of north-eastern Australia, the Burdekin Gap. This potential vicariant barrier lies directly between the Hervey Range and Einasleigh Uplands populations and is comprised largely of grazing natural pastureland, habitat highly unsuited to petaurid gliders.

Relative to the deep divergence associated with the Burdekin Gap, phylogeographic structure and phylogenetic depth among southern squirrel glider populations is less clearly defined and due to much more recent biogeographic events. Phylogeographic structure broadly follows that of Pavlova *et al*., (2010), who described the central coast NSW as an Evolutionary Significant Unit (ESU) from an appreciably larger dataset, albeit derived primarily from populations south of the Burdekin Gap. This south-eastern Australian substructure appears concordant also with that observed in the sugar glider (Malekian *et al*., 2010a) and, to a lesser degree, the yellow-bellied glider (Brown *et al*., 2006). Both Pavlova *et al*. (2010) and Malekian *et al*. (2010b) proposed that the observed substructure was a consequence of recent glaciations along the Great Dividing Range, specifically confined to the Snowy Mountains (Barrows *et al*., 2001). Such an evolutionary scenario has previously been posited for open forest endemics, including frogs (Donnellan *et al*., 1999), skinks (Chapple *et al*., 2011b) and lizards (Dubey and Shine, 2010).

Further to the Great Dividing Range, an additional southern New South Wales biogeographic barrier, the Hunter River Valley, may also be involved in the isolation of central coast NSW populations of the squirrel glider. This dry and open lowland river valley (Keast, 1961; Ford 1987a; Cracraft, 1991) bisects traditional open forest habitat between the north-eastern and central coast of New South Wales. Although not previously considered a significant dispersal barrier to petaurids (Malekian *et al*., 2010a; Pavlova *et al*., 2010), it has previously been cited in other vertebrate taxa (e.g. Schäuble and Moritz, 2001; Chapple *et al*., 2005).

4.2 Taxonomic implications for the squirrel glider – mahogany glider complex

Synthesis of the molecular, ecological and morphological data suggests a complex relationship between the mahogany glider and squirrel glider. While there exists no molecular support for reciprocal monophyly of the mahogany and squirrel glider, morphological differentiation appears well established. Results presented here, specifically in terms of body length and mass, clearly show a degree of divergence in body size between the mahogany and squirrel glider that is considerably greater than interpopulation variation across the squirrel glider's distribution. Hence, the molecular data must be considered alongside Van Dyck's (1993) taxonomic revision.

Such discordance between the partitioning of genetic variation and taxonomy based on animal morphometrics is not uncommon (e.g. Omland *et al*., 2006; Spellman *et al*., 2007; Joseph and Omland, 2009; Edwards *et al*., 2011; Roberts *et al*., 2011; Rogers *et al*., 2011; Silva-Segundo *et al*., 2011). To this end, three primary factors, which act either independently or in tandem, have been described to explain such conflict (hereafter referred to as species-level paraphyly; Funk and Omland, 2003). Imperfect taxonomy, the failure of taxonomic nomenclature to pair with gene flow patterns, is considered to comprise the plurality of observed cases of species-level paraphyly (e.g. Omland *et al*., 1999; Appleton *et al*., 2004; Fouquet *et al*., 2007). Two further factors, incomplete lineage sorting and the associated retention of ancestral polymorphisms (e.g. Omland *et al*., 2006; Fujita *et al*., 2010; Lack *et al*., 2010; Nakamura *et al*., 2012) plus mitochondrial introgression following hybridisation (e.g. Degnan, 1993; Pidancier *et al*., 2006; Spinks *et al*., 2012), account for most other cases. Both can be notoriously difficult to differentiate via traditional phylogeographic methods (Holder *et al*., 2001; Nielsen and Wakeley, 2001; Funk and Omland, 2003).

Two scenarios are thereby offered which go to explain the species-level paraphyly discovered by the current study. The first is that ecological and morphological differentiation reflects adaptation to local environmental conditions, and that the mahogany glider is simply a geographic variant of the squirrel glider (i.e. imperfect taxonomy). This scenario assumes that the diagnostic characters traditionally cited to differentiate the two gliders do not share concomitant evolutionary divergence. It may also explain in part the asymmetrical dispersal suggested by the molecular data, namely the unidirectional gene flow from the southern lineage across the Burdekin Gap.

To this end, size differences between the two gliders may be an effect of the correlation of the mahogany glider's restricted distribution with distinct temperature, moisture, precipitation and floristic diversity profiles (Jackson and Claridge, 1999). On account of this habitat differentiation, Van Dyck (1993) argued that the larger size of the mahogany glider reflects higher habitat resource availability when compared to the typically drier and more open forests of the squirrel glider. In support of this hypothesis, Jackson and Johnson (2002) later found that, contrary to a positive correlation between foraging and body mass in exudivorous possums, the larger mahogany glider maintained its size advantage for relatively less foraging effort than the squirrel glider.

It is also possible that the distinct buff coloured ventral surface from which the mahogany glider derives its common name reflects habitat associated polymorphisms. This hypothesis was recently put forward to explain morphological variation between rainforest and sclerophyll forest populations of the north-eastern Australian brushtail possum (*Trichosurus vulpecula johnstonii*) (S. Kerr, pers. comm.). While exhibiting clear size and colour association with habitat (broadly analogous to that documented between the mahogany glider and squirrel glider), brushtail possums from each habitat were nevertheless genetically indistinguishable at both mtDNA and microsatellite loci. It was suggested that strong habitat fidelity and maternal diet played a role in the maintaining habitat-specific morphological characters in the face of high levels of gene flow.

A comparable case of imperfect taxonomy example exists among petaurids. Brown *et al*. (2006) found no concordance between molecular data and the recognised subspecific delineation of the yellow-bellied glider, one based primarily on pelage colouration (Thomas, 1923). These findings supported earlier doubts surrounding the veracity of yellow-bellied glider taxonomy (Goldingay and Kavanah, 1990; Goldingay *et al*., 2001), which hypothesised that pelage polymorphisms were an artefact of age rather than biogeography. Rather, Brown et al., (2006) argued that the disjunct Wet Tropics population – restricted to a narrow band of atypical transitional wet forest between dry open forest and rainforest – was sufficiently genetically differentiated (1.4% net sequence divergence) to warrant separate consideration and management. A national recovery plan for the yellow-bellied glider (Wet Tropics) has since been produced, with the objectives of protecting and recovering this population throughout its limited range (Department of Environment and Resource Management, 2011).

The underlying rationale for imperfect taxonomy, particularly species oversplitting, is that phenotypic divergence occurs despite gene flow and is subsequently either environmentally induced or maintained by the counter-balancing effect of strong selection (Funk and Omland, 2003). This may arguably explain the high degree of genetic similarity between the mahogany glider and the nearest sampled squirrel glider population, Hervey Range. Available ecological evidence, namely a lack of sympatry, suggests that the squirrel – mahogany glider complex does not comply with this pre-requisite of imperfect taxonomy. As both gliders inhabit similar ecological niches (Jackson, 2000a) and replace one another outside their distribution

(Quin, 1995), existing taxonomy is underpinned by an understanding of allopatry (e.g. Van Dyck, 1993; Jackson, 2011). This is highlighted by bioclimatic models of Jackson and Claridge (1999), which clearly indicate a significant and restrictive association for the mahogany glider with environmental characteristics traditionally associated with rainforest communities.

While the data generally support the mahogany glider as a geographic variant of a larger polytypic squirrel glider complex, results do not explicitly exclude a more nuanced interpretation. Namely, variations in size and pelage are indicative of two genetically and morphologically divergent species, with the lack of reciprocal monophyly a signature of intermittent northward migration of squirrel gliders across the Burdekin Gap. This hypothesis is underpinned by the assumption that the association of the mahogany glider with the zone of molecular admixture is non-coincidental. Although insufficient evidence is available in this study, it is feasible that character displacement between the mahogany glider and neighbouring populations of the squirrel glider has arisen via strong divergent selection across a steep moisture gradient within the region. With rainforest barriers to the west and north, such character displacement would ensure minimal gene flow between the mahogany glider and the squirrel glider populations in and around the Hervey Range, approximately 50km to the south. If so, then while there does exist a high degree of apparent morphological conservatism within this species complex (even when incorporating the sugar glider, see Quin *et al*., 1996b), the significant divergence in size alone between the mahogany glider and squirrel glider suggests taxonomic relevance and, when considering the recent timeframe in which this divergence arose, may be indicative of incipient speciation.

Although the effects of mtDNA introgression can be difficult to discern from those of incomplete lineage sorting (Funk and Omland, 2003), the presence of the southern lineage (i.e. Lineage B) in north-eastern Australian populations of the squirrel – mahogany glider complex can be interpreted as a genetic signature of dispersal of southern squirrel glider across the Burdekin Gap throughout the Quaternary. Such instances of introgression may have been facilitated by periodic shifts in habitat composition across the Burdekin Gap, namely the replacement of dry and open woodland with open forests throughout the Quaternary. This scenario is supported by BEAST analyses, which date the most recent instance of this purported introgression to approximately 0.12 – 0.39 million YBP, a time when Eucalyptus forests replaced open woodland along the Burdekin Gap (Keast, 1961). This would therefore have had the effect of re-establishing contact both between northern and southern populations of squirrel glider and between the mahogany glider and southern populations of the squirrel glider.

Signatures of both introgression and incipient speciation may arguably be observed in the expanded Queensland dataset. While the introgressed southern lineage is similarly distributed across the majority of the admixture zone (excluding Tully), the abundance of individuals carrying the southern haplotypes is markedly different between populations of the two taxa. The greater abundance of southern haplotypes in Hervey Range may be evidence of low levels of gene flow from the Einasleigh Uplands squirrel glider population. That this contact appears not to extend into the southern reaches of the mahogany glider's distribution may potentially reflect the aforementioned character displacement. Further, equal representation of both the northern lineage and introgressed southern lineage across the majority of the admixture zone may be indicative of hybridisation, suggesting that character displacement may only be in effect between individuals of the squirrel – mahogany glider complex from populations north of the Burdekin Gap.

4.3 Conclusions and future actions

In the current study the taxonomic validity of the mahogany glider within *Petaurus* remains unresolved, necessitating further investigation. Whether this concludes with the retention of *P. gracilis*, recognition of subspecific status for the mahogany glider (*P. norfolcensis gracilis*), creation of a broader north-eastern Australian subspecies comprising both taxa (*P. n. norfolcensis*) or the subsumption of the mahogany glider within *P. norfolcensis* relies upon additional well-constructed research. It is recommended that future research address two important issues, namely clarifying the dimensions of the admixture zone between the mahogany and squirrel glider and defining the extent, composition and direction of gene flow among squirrel glider populations across the Burdekin Gap.

Most critical is the generation of a definitive description of the dimensions, composition and location of the zone of admixture between the mahogany glider and neighbouring squirrel glider populations. Considering gene flow between the two gliders appears restricted by the Wet Tropics to the north and west, sampling should focus upon the 50km transect of open forest between the Cardwell Lowlands and Hervey Range populations (see Figure 4). Intense sampling along such an ecologically defined transect would allow for the identification of genotypic and phenotypic intermediates via supplementary analysis of highly polymorphic microsatellite markers and morphometric characters.

Secondly, the identification of uni-directional gene flow between two divergent mtDNA lineages across the Burdekin Gap requires further investigation, namely mapping the extent of northward introgression from populations south of the Burdekin Gap and investigating the apparent absence of concomitant north-south introgression. This is especially important given that the under-representation of squirrel gliders from north of the Wet Tropics may mask further evidence of genetic admixture. Unlike the two other eastern Australian petaurid gliders with a widespread distribution, the sugar and yellow-bellied gliders, no intraspecific subdivisions are currently recognised within the squirrel glider. As Pavlova *et al*. (2010) argued for the evolutionary distinctness of southern populations of the squirrel glider using mtDNA and microsatellite data, this study suggests a similar status for the species' poorly understood – yet genetically distinct – northern range. Any future research should therefore prioritise the increased of both the molecular and morphological representation across north-eastern Australia to allow for a more accurate interpretation of taxonomy within the polytypic squirrel glider. This is especially critical when considering the incomplete distributional information of the squirrel glider in northern Australia, particularly the Cape York Peninsula and inland of the Great Dividing Range (Winter *et al*., 2004) and the purported smaller size of squirrel gliders within this region (Menkhorst and Knight, 2001).

Such strategies are known to have succeeded in the past. Barrowclough *et al*. (2005) detected a pattern of limited mtDNA introgression across a narrow hybrid zone between two phenotypically defined subspecies of the spotted owl (*Strix occidentalis*), one of which was ESA-listed (*S. o. caurina*). Not only was this demographic pattern later confirmed by complementary microsatellite analyses (Funk *et al*., 2008), but previously undetected congeneric introgression into the endangered subspecies was detected. In another instance, Joseph *et al*. (2009) employed complementary microsatellite data to confirm incomplete lineage sorting as the cause of mtDNA paraphyly between two Australian species of *Anas* teals, as identified by Kennedy and Spencer (2000). The synthesis of mtDNA and microsatellite data (King *et al*., 2006) also revealed the evolutionary distinctiveness of an endangered jumping mouse (*Zapus hudsonius preblei*) from its conspecifics, thereby contradicting an existing recommendation for its synonymisation within *Z. hudsonius* (Ramey *et al*., 2005); an action that would have resulted in its delisting from the US Endangered Species Act. As these studies indicate, finescale molecular and morphological analyses can be critical tools in defining taxonomic boundaries for the management of taxa with high conservation values, such as those within the squirrel – mahogany glider complex.

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Appendices

*Appendix I: Raw genetic data. Samples marked with * comprised the broadscale dataset, while those marked with ^ comprised the finescale dataset. B^S refers to samples associated with the Lineage B mtDNA substructure. Source abbreviations as follows: QPWS(WT), Queensland Parks and Wildlife Services (Wet Tropics); Department of Environment and Resource Management; SJ, Steve Jackson (unpublished data); ANWC, Australian National Wildlife Collection; QM, Queensland Museum; JCU, James Cook University; AM, Australia Museum; MV, Museum Victoria*.

Sample		Locality		ND2		ApoB1		
ID	Source	Lat	Long	Haplotype	Lineage	State	Genotype	
Mahogany Glider (92)								
Tully (14); -18.22, 146.01								
TU01^	QDERM	-18.18	145.98	MT08	B	--	--	--
TU02^	QDERM	-18.18	145.99	MT08	B	--	--	--
TU03^	QDERM	-18.07	145.59	MT44	A	--	--	--
TU04^	QDERM	-18.23	146.00	MT44	A	--	--	--
TU05^	QDERM	-18.24	146.00	MT08	B	--	--	--
TU06^	QDERM	-18.23	146.00	MT44	A	--	--	--
TU07^	QDERM	-18.24	145.94	MT08	B	--	--	--
TU08/CL02*^	QDERM	-18.24	145.98	MT38	A	Het	1	13
TU09^	QDERM	-18.25	145.98	MT08	B	--	--	--
TU10/CL03*^	QDERM	-18.24	145.98	MT08	B	Hom	1	1
TU11^	QDERM	-18.12	145.90	MT44	A	--	--	--
TU12/CL01*^	QDERM	-18.12	145.90	MT37	A	Hom	5	5
TU13/CL04*^	QDERM	-18.09	145.85	MT08	B	Hom	1	1
TU14^	QDERM	-18.05	145.91	MT08	B	--	--	--
Two Creeks (33); -18.44, 146.12								
TC01^	QDERM	-18.44	146.12	MT46	B	--	--	--
TC02^	QDERM	-18.44	146.12	MT44	A	--	--	--
TC03^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC04^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC05^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC06^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC07^	QDERM	-18.44	146.12	MT08	B	--	--	--

TC08^	QDERM	-18.44	146.12	MT46	B	--	--	--
TC09^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC10^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC11^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC12^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC13^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC14^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC15^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC16^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC17/CL09*^	QDERM	-18.43	146.13	MT08	B	Het	3	2
TC18/CL10*^	QDERM	-18.42	146.13	MT40	B	Hom	1	1
TC19^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC20^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC21^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC22^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC23^	QDERM	-18.44	146.12	MT46	B	--	--	--
TC24^	QDERM	-18.44	146.12	MT37	A	--	--	--
TC25^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC26^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC27^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC28^	QDERM	-18.44	146.12	MT08	B	--	--	--
TC29/CL11*^	QDERM	-18.44	146.12	MT41	A	Hom	4	4
TC30/CL12*^	QDERM	-18.44	146.12	MT42	A	Hom	1	1
TC31^	QDERM	-18.45	146.13	MT08	B	--	--	--
TC32^	QDERM	-18.45	146.13	MT08	B	--	--	--
TC33^	QDERM	-18.45	146.13	MT08	B	--	--	--
Rangeview (13); -18.75, 145.93								
RA01^	QDERM	-18.52	145.93	MT08	B	--	--	--
RA02/CL08*^	QDERM	-18.50	145.92	MT39	B	Hom	1	1
RA03^	QDERM	-18.75	145.93	MT08	B	--	--	--
RA04^	QDERM	-18.75	145.93	MT08	B	--	--	--
RA05^	QDERM	-18.75	145.92	MT08	B	--	--	--
RA06^	QDERM	-18.75	145.92	MT08	B	--	--	--
RA07/CL05*^	QDERM	-18.42	145.78	MT37	A	Hom	8	8

RA08^	QDERM	-18.65	146.03	MT08	B	--	--	--
RA09/CL06*^	QDERM	-18.65	146.02	MT08	B	Hom	1	1
RA10^	QDERM	-18.65	146.01	MT37	A	--	--	--
RA11^	QDERM	-18.65	146.01	MT37	A	--	--	--
RA12CL07*^	QDERM	-18.65	146.02	MT13	A	Hom	4	4
RA13^	QDERM	-18.65	146.02	MT08	B	--	--	--
Bambaroo (32); -18.89, 146.23								
BA01^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA02^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA03^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA04/CL14*^	QDERM	-18.88	146.22	MT43	B	Hom	5	5
BA05^	QDERM	-18.88	146.22	MT13	A	--	--	--
BA06^	QDERM	-18.87	146.19	MT37	A	--	--	--
BA07^	QDERM	-18.87	146.19	MT08	B	--	--	--
BA08^	QDERM	-18.86	146.17	MT08	B	--	--	--
BA09^	QDERM	-18.87	146.19	MT08	B	--	--	--
BA10^	QDERM	-18.87	146.19	MT08	B	--	--	--
BA11^	QDERM	-18.87	146.19	MT08	B	--	--	--
BA12/CL16*^	QDERM	-18.87	146.19	MT44	B	Hom	1	1
BA13^	QDERM	-18.87	146.19	MT37	A	--	--	--
BA14^	QDERM	-18.92	146.27	MT08	B	--	--	--
BA15^	QDERM	-18.93	146.27	MT08	B	--	--	--
BA16^	QDERM	-18.93	146.27	MT08	B	--	--	--
BA17^	QDERM	-18.99	146.33	MT08	B	--	--	--
BA18^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA19^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA20^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA21^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA22/CL13*^	QDERM	-18.88	146.22	MT08	B	Hom	1	1
BA23^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA24^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA25^	QDERM	-18.88	146.22	MT08	B	--	--	--
BA26^	QDERM	-18.89	146.23	MT39	B	--	--	--
BA27^	QDERM	-18.85	146.12	MT08	B	--	--	--

BA28^	QDERM	-18.86	146.12	MT08	B	--	--	--
BA29^	QDERM	-18.86	146.12	MT08	B	--	--	--
BA30^	QDERM	-18.86	146.13	MT44	A	--	--	--
BA31^	QDERM	-18.85	146.13	MT08	B	--	--	--
BA32/CL15*^	QDERM	-18.86	146.13	MT08	A	Hom	1	1

Squirrel Glider (67)

Einasleigh Uplands (8); -17.26, 144.56								
EU01*^	QM	-16.53	143.68	MT01	A	Hom	1	1
EU02*^	ANWC	-17.56	145.45	MT02	A	Hom	1	1
EU03*^	QDERM	-17.62	145.51	MT03	A	--	--	--
EU04*^	QDERM	-18.19	145.26	MT04	A	Hom	1	1
EU05*^	QDERM	-18.19	145.26	MT02	A	Hom	1	1
EU06*^	QDERM	-18.19	145.26	MT05	A	Hom	4	4
EU07*^	QDERM	-18.19	145.26	MT06	A	Het	4	2
EU08*^	QDERM	-18.19	145.26	MT04	A	Hom	4	4
Hervey Range (17); -19.21, 146.20								
HR01*^	JCU	-19.36	146.33	MT07	B	Hom	1	1
HR02*^	JCU	-19.36	146.33	MT08	B	Hom	1	1
HR03*^	JCU	-19.36	146.33	MT09	A	Het	4	6
HR04*^	JCU	-19.36	146.33	MT05	A	Hom	1	1
HR05*^	JCU	-19.36	146.33	MT10	A	Het	1	9
HR06*^	JCU	-19.36	146.33	MT11	B	Het	1	9
HR07*^	JCU	-19.36	146.33	MT12	B	Het	4	7
HR08*^	JCU	-19.36	146.33	MT13	A	Het	1	12
HR09^	JCU	-19.36	146.33	MT45	A	--	--	--
HR10^	JCU	-19.36	146.33	MT07	B	--	--	--
HR11^	JCU	-19.36	146.33	MT07	B	--	--	--
HR12^	JCU	-19.36	146.33	MT07	B	--	--	--
HR13^	JCU	-19.36	146.33	MT07	B	--	--	--
HR14^	JCU	-19.36	146.33	MT13	A	--	--	--
HR15^	JCU	-19.36	146.33	MT47	B	--	--	--
HR16^	JCU	-19.36	146.33	MT08	B	--	--	--

HR17^	QDERM	-19.26	146.67	MT45	A	--	--	--
Mid-eastern Queensland (20); -21.46, 149.10								
MEQ01*^	QDERM	-21.08	149.04	MT14	B	Hom	1	1
MEQ02*^	QDERM	-21.03	149.01	MT15	B	Het	4	3
MEQ03*^	QDERM	-21.13	148.54	MT16	B	Het	4	6
MEQ04*^	QDERM	-21.34	149.18	MT17	B	Hom	2	2
MEQ05*^	QDERM	-21.08	149.11	MT18	B	Het	3	6
MEQ06*^	QDERM	-21.03	149.13	MT19	B	Het	11	7
MEQ07*^	QDERM	-21.13	148.54	MT20	B	Het	3	2
MEQ08*^	QDERM	-21.34	149.18	MT21	B	Het	6	2
MEQ09^	QDERM	-21.34	149.18	MT20	B	--	--	--
MEQ10^	QDERM	-22.15	148.57	MT48	B	--	--	--
MEQ11^	QDERM	-22.15	148.57	MT48	B	--	--	--
MEQ12^	QM	-23.22	150.30	MT49	B	--	--	--
MEQ13^	ANWC	-23.38	150.51	MT50	B	--	--	--
MEQ14^	ANWC	-23.38	150.51	MT18	B	--	--	--
MEQ15^	QDERM	-21.08	149.11	MT19	B	--	--	--
MEQ16^	QDERM	-22.15	148.57	MT18	B	--	--	--
MEQ17^	QDERM	-21.08	149.11	MT18	B	--	--	--
MEQ18^	QDERM	-21.43	149.19	MT51	B	--	--	--
MEQ19^	QDERM	-20.57	148.44	MT52	B	--	--	--
MEQ20^	QDERM	-23.22	150.30	MT53	B	--	--	--
North-eastern New South Wales (8)								
NEN01	AM	-29.35	152.46	MT22	B[1]	Hom	2	2
NEN02	AM	-29.35	152.46	MT23	B	Het	3	2
NEN03	AM	-29.00	153.27	MT24	B	Hom	3	3
NEN04	AM	-29.02	153.14	MT24	B	Het	3	2
NEN05	AM	-29.53	152.53	MT18	B	Hom	3	3
NEN06	AM	-28.50	153.03	MT25	B	Het	3	2
NEN07	AM	-29.21	153.17	MT26	B	Het	4	7
NEN08	AM	-28.56	153.28	MT27	B	Hom	2	2
Central Coast New South Wales (8)								
CCN01	AM	-32.11	152.31	MT28	B[1]	Hom	2	2
CCN02	AM	-32.56	151.46	MT29	B[1]	Het	3	2

CCN03	AM	-33.16	151.27	MT30	B[1]	Het	3	2
CCN04	AM	-33.17	151.25	MT22	B[1]	Het	3	2
CCN05	AM	-32.12	152.31	MT31	B[1]	Het	3	2
CCN06	AM	-33.10	151.35	MT32	B[1]	Hom	3	3
CCN07	AM	-32.23	151.45	MT31	B[1]	Het	3	2
CCN08	AM	-32.57	151.41	MT33	B[1]	Hom	3	3
Victoria (6)								
VIC01	MV	-36.22	145.24	MT22	B[1]	Hom	2	2
VIC02	MV	-37.06	142.78	MT34	B	Hom	5	5
VIC03	MV	-36.31	146.29	MT34	B	Hom	10	10
VIC04	MV	-36.45	145.34	MT22	B[1]	Hom	2	2
VIC05	MV	-36.45	145.34	MT35	B[1]	--	--	--
VIC06	MV	-36.45	145.34	MT36	B	--	--	--

Appendix II: Raw morphological data. Source abbreviations as follows: QPWS(WT), Queensland Parks and Wildlife Services (Wet Tropics); SJ, Steve Jackson (unpublished data); ANWC, Australian National Wildlife Collection; QM, Queensland Museum; JCU, James Cook University; AM, Australia Museum; MV, Museum Victoria.

Sample			External character					
ID	Source	Sex	WT	STL	SVL	VTL	BTR	HL
			(298)	(312)	(314)	(316)	(312)	(189)
Mahogany Glider (107)								
Tully (26)								
TU01	QPWS(WT)	F	335	700	340	360	0.94	54.5
TU02	QPWS(WT)	F	317	650	270	380	0.71	48.8
TU04	QPWS(WT)	M	300	640	260	380	0.68	.
TU07	QPWS(WT)	F	333	650	245	405	0.60	.
TU09	QPWS(WT)	F	350	620	310	310	1.00	63.5
TU11	QPWS(WT)	F	319	610	250	360	0.69	.
TU12	QPWS(WT)	F	350	630	280	350	0.80	57.0
TU14	QPWS(WT)	M	.	.	.	430	.	.
TU15	QPWS(WT)	F	385	575	260	315	0.83	62.7
TU16	QPWS(WT)	F	210	596	235	334	0.70	53.3
TU17	QM	M	350	603	249	354	0.70	.
TU18	QM	F	350	510	240	270	0.89	.
TU19	QM	M	.	625	260	365	0.71	.
TU20	QM	M	.	595	255	340	0.75	.
TU21	QM	F	.	607	252	355	0.71	.
TU22	QM	F	352	591	261	330	0.79	.
TU23	QM	M	410	600	265	335	0.79	.
TU24	QM	F	345	520	220	300	0.73	.
TU25	QM	F	195	520	200	320	0.63	.
TU26	QM	F	215	510	180	330	0.55	.
TU27	QM	F	255	640	250	390	0.64	.
TU28	QM	M	330	627	247	380	0.65	.
TU29	QM	F	325	595	215	380	0.57	.
TU30	QPWS(WT)		340	580	260	320	0.81	.

TU31	QM	F	370	602	256	346	0.74	.
TU32	QPWS(WT)		274	510	230	280	0.82	.
Two Creeks (35)								
TC01	SJ	M	335	655	250	405	0.62	62.0
TC02	SJ	M	355	605	245	360	0.68	58.0
TC03	SJ	M	440	635	250	385	0.65	62.0
TC04	SJ	M	435	635	265	370	0.72	61.0
TC05	SJ	F	297	480	175	305	0.57	52.0
TC09	SJ	M	368	595	245	350	0.70	56.0
TC10	SJ	M	400	630	270	360	0.75	55.0
TC11	SJ	M	415	650	260	390	0.67	53.0
TC12	SJ	M	268	610	240	370	0.65	68.0
TC13	SJ	F	335	630	240	390	0.62	57.0
TC14	SJ	F	410	635	250	385	0.65	62.0
TC15	SJ	F	340	620	240	380	0.63	54.0
TC16	SJ	F	390	652	280	372	0.75	57.6
TC17	SJ	M	395	656	275	381	0.72	55.1
TC18	SJ	F	395	661	305	356	0.86	58.2
TC19	SJ	M	353	635	285	350	0.81	61.1
TC20	SJ	M	380	610	280	330	0.85	58.9
TC21	SJ	M	391	610	250	360	0.69	56.0
TC22	SJ	M	350	650	260	390	0.67	57.5
TC23	SJ	F	306	580	240	340	0.71	51.6
TC24	SJ	F	385	620	250	370	0.68	53.6
TC25	SJ	M	.	666	280	386	0.73	53.6
TC26	SJ	M	200	570	215	355	0.61	48.0
TC27	SJ	M	213	560	220	340	0.65	49.0
TC28	SJ	M	365	610	245	365	0.67	52.0
TC29	SJ	M	450	640	275	365	0.75	57.0
TC30	SJ	M	372	630	265	365	0.73	55.0
TC31	SJ	M	353	640	265	375	0.71	59.0
TC32	SJ	F	400	660	270	390	0.69	55.0
TC33	SJ	M	402	660	265	395	0.67	54.0
TC34	SJ	M	265	640	255	385	0.66	51.1

TC35	QM	F	407	624	264	360	0.73	.
TC36	SJ	M	389	715	340	375	0.91	59.3
TC37	SJ	F	360	690	320	370	0.86	50.8
TC38	SJ	F	272	595	250	345	0.72	41.0
Rangeview (10)								
RA01	QPWS(WT)	M	370	695	320	375	0.85	48.9
RA02	QPWS(WT)	M	272	610	240	370	0.65	64.4
RA03	QPWS(WT)	M	375	630	260	370	0.70	58.0
RA04	QPWS(WT)	F	380	615	275	340	0.81	54.2
RA05	QPWS(WT)	F	355	625	275	350	0.79	55.3
RA06	QPWS(WT)	M	370	640	280	360	0.78	68.3
RA08	QPWS(WT)	M	215	640	280	360	0.78	80.0
RA12	QPWS(WT)	M	378	610	245	365	0.67	53.2
RA13	QPWS(WT)	F	328	595	270	325	0.83	53.1
RA14	QPWS(WT)	F	309	615	255	360	0.71	58.5
Bambaroo (36)								
BA01	QPWS(WT)	M	330	630	255	375	0.68	53.0
BA02	QPWS(WT)	F	330	656	256	400	0.64	52.6
BA06	QPWS(WT)	F	300	600	250	350	0.71	54.3
BA07	QPWS(WT)	M	285	614	280	334	0.84	54.1
BA09	QPWS(WT)	M	220	570	260	310	0.84	50.8
BA10	QPWS(WT)	F	315	530	290	240	1.21	52.7
BA11	QPWS(WT)	M	415	550	230	320	0.72	50.8
BA12	QPWS(WT)	M	350	595	270	325	0.83	53.0
BA13	QPWS(WT)	F	230	540	190	350	0.54	46.0
BA14	QPWS(WT)	F	348	635	300	335	0.90	55.4
BA15	QPWS(WT)	M	305	550	275	280	0.98	54.4
BA16	QPWS(WT)	F	302	640	255	385	0.66	53.7
BA17	QPWS(WT)	M	277	675	265	410	0.65	58.2
BA18	QPWS(WT)	F	242	635	255	380	0.67	53.3
BA20	QPWS(WT)	F	350	615	260	355	0.73	52.2
BA21	QPWS(WT)	F	350	635	270	365	0.74	55.6
BA22	QPWS(WT)	M	390	650	265	385	0.69	53.1
BA23	QPWS(WT)	M	345	605	255	350	0.73	50.1

BA24	QPWS(WT)	F	350	605	245	360	0.68	53.3
BA25	QPWS(WT)	M	340	620	265	355	0.75	55.3
BA27	QPWS(WT)	F	333	625	280	345	0.81	67.0
BA28	QPWS(WT)	M	300	625	250	375	0.67	54.2
BA29	QPWS(WT)	M	220	595	260	335	0.78	47.7
BA30	QPWS(WT)	F	335	565	235	330	0.71	51.3
BA31	QPWS(WT)	M	360	.	.	340	.	53.6
BA32	QPWS(WT)	M	225	580	270	310	0.87	52.0
BA33	QPWS(WT)	M	330	.	300	.	.	51.0
BA34	QPWS(WT)	M	305	548	265	283	0.94	48.6
BA35	QPWS(WT)	M	378	643	290	353	0.82	50.9
BA36	QPWS(WT)	F	332	645	265	380	0.70	54.6
BA37	QPWS(WT)	F	356	652	262	390	0.67	56.9
BA38	QPWS(WT)	F	310	613	268	345	0.78	60.4
BA39	QPWS(WT)	M	335	634	265	369	0.72	62.5
BA40	QPWS(WT)	M	420	677	263	414	0.64	66.9
BA41	QPWS(WT)	F	320	655	280	375	0.75	65.3
BA42	QPWS(WT)	F	233	660	285	375	0.76	58.6
Squirrel Glider (252)								
Einasleigh Uplands (4)								
EU04	QPWS(WT)	F	325	450	210	240	0.88	45.3
EU05	QPWS(WT)	M	320	560	260	300	0.87	45.6
EU06	QPWS(WT)	F	325	490	170	320	0.53	48.5
EU08	QPWS(WT)	F	320	515	200	315	0.63	45.3
Hervey Range (17)								
HR01	JCU	F	200	425	195	230	0.85	.
HR02	JCU	M	270	.	.	.	.	51.0
HR03	JCU	M	300	.	.	.	.	46.0
HR04	JCU	M	275	.	.	.	.	50.0
HR05	JCU	M	255	.	.	.	.	44.0
HR06	JCU	M	205	.	.	.	.	50.0
HR07	JCU	M	235	.	.	.	.	46.0
HR08	JCU	M	215	.	.	.	.	48.0

HR09	JCU	M	275	.	.	.	.	46.0
HR10	JCU	F	210	.	.	.	.	44.0
HR11	JCU	F	250	.	.	.	.	44.0
HR12	JCU	F	240	.	.	.	.	45.0
HR13	JCU	F	280	.	.	.	.	49.0
HR14	JCU	M	225	.	.	.	.	46.0
HR15	JCU	F	205	.	.	.	.	50.0
HR17	QPWS(WT)		208	660	230	330	0.70	51.6
HR18	JCU	F	275	.	.	.	.	46.0
Mid-eastern Queensland (84)								
MEQ02	QPWS(WT)	F	200	399	184	215	0.86	49.0
MEQ03	QPWS(WT)	F	232	450	190	260	0.73	46.9
MEQ04	QPWS(WT)	F	192	410	165	245	0.67	50.4
MEQ05	QPWS(WT)	F	234	391	161	230	0.70	49.0
MEQ06	QPWS(WT)	M	224	435	175	260	0.67	53.8
MEQ07	QPWS(WT)	M	250	445	180	265	0.68	48.1
MEQ08	QPWS(WT)	M	250	450	170	280	0.61	43.7
MEQ09	QPWS(WT)	F	240	300	150	150	1.00	48.3
MEQ10	QPWS(WT)	F	235	460	180	280	0.64	41.7
MEQ11	QPWS(WT)	F	242	455	220	235	0.94	46.9
MEQ15	QPWS(WT)	M	196	450	185	265	0.70	47.7
MEQ16	QPWS(WT)	M	228	445	205	240	0.85	47.5
MEQ17	QPWS(WT)	M	230	465	205	260	0.79	48.5
MEQ19	QPWS(WT)	M	218	500	235	265	0.89	55.0
MEQ21	QPWS(WT)	F	221	455	175	280	0.63	45.0
MEQ22	QPWS(WT)	F	169	450	185	265	0.70	47.4
MEQ23	QPWS(WT)	F	216	450	200	250	0.80	49.1
MEQ24	QPWS(WT)	F	199	445	185	260	0.71	52.2
MEQ25	QPWS(WT)	F	201	475	195	280	0.70	49.6
MEQ26	QPWS(WT)	F	240	440	175	265	0.66	49.6
MEQ27	QPWS(WT)	F	252	411	170	241	0.71	50.7
MEQ28	QPWS(WT)	F	218	445	225	220	1.02	44.3
MEQ29	QPWS(WT)	F	193	425	165	260	0.63	54.0
MEQ30	QPWS(WT)	F	210	410	190	220	0.86	46.0

MEQ31	QPWS(WT)	F	210	415	165	250	0.66	53.0
MEQ32	QPWS(WT)	F	176	415	160	255	0.63	44.2
MEQ33	QPWS(WT)	F	228	454	180	274	0.66	47.8
MEQ34	QPWS(WT)	F	180	450	195	255	0.76	45.0
MEQ35	QPWS(WT)	F	230	525	255	270	0.94	47.0
MEQ36	QPWS(WT)	F	172	480	210	270	0.78	46.6
MEQ37	QPWS(WT)	F	279	540	270	270	1.00	50.8
MEQ38	QPWS(WT)	F	241	500	235	265	0.89	49.6
MEQ39	QPWS(WT)	F	230	460	200	260	0.77	23.1
MEQ40	QPWS(WT)	F	181	445	170	275	0.62	47.3
MEQ41	QPWS(WT)	F	239	470	220	250	0.88	44.0
MEQ42	QPWS(WT)	F	199	445	200	245	0.82	49.1
MEQ43	QPWS(WT)	F	171	440	190	250	0.76	43.7
MEQ44	QPWS(WT)	F	209	492	222	270	0.82	51.5
MEQ45	QPWS(WT)	F	200	450	200	250	0.80	47.7
MEQ46	QPWS(WT)	F	240	475	235	240	0.98	47.2
MEQ47	QPWS(WT)	F	232	450	205	245	0.84	41.4
MEQ48	QPWS(WT)	F	170	435	225	210	1.07	46.1
MEQ49	QPWS(WT)	F	169	470	215	255	0.84	48.0
MEQ50	QPWS(WT)	F	122	390	165	225	0.73	45.8
MEQ51	QPWS(WT)	F	236	485	225	260	0.87	47.3
MEQ52	QPWS(WT)	F	224	465	245	220	1.11	42.1
MEQ53	QPWS(WT)	F	221	485	225	260	0.87	48.7
MEQ54	QPWS(WT)	F	99	385	145	240	0.60	41.0
MEQ55	AM	F	.	460	195	265	0.74	.
MEQ56	AM	F	.	422	172	250	0.69	.
MEQ57	QPWS(WT)	M	199	490	230	260	0.88	49.0
MEQ58	QPWS(WT)	M	233	430	180	250	0.72	45.4
MEQ59	QPWS(WT)	M	203	430	200	230	0.87	50.9
MEQ60	QPWS(WT)	M	202	460	190	270	0.70	52.9
MEQ61	QPWS(WT)	M	241	460	180	280	0.64	55.0
MEQ62	QPWS(WT)	M	230	410	185	225	0.82	52.1
MEQ63	QPWS(WT)	M	224	445	165	280	0.59	51.4
MEQ64	QPWS(WT)	M	228	410	170	240	0.71	46.4

MEQ65	QPWS(WT)	M	166	500	240	260	0.92	45.9
MEQ66	QPWS(WT)	M	243	470	260	210	1.24	49.1
MEQ67	QPWS(WT)	M	230	442	192	250	0.77	51.7
MEQ68	QPWS(WT)	M	178	495	230	265	0.87	48.4
MEQ69	QPWS(WT)	M	273	550	255	295	0.86	47.5
MEQ70	QPWS(WT)	M	249	460	220	240	0.92	48.7
MEQ71	QPWS(WT)	M	259	530	280	250	1.12	57.5
MEQ72	QPWS(WT)	M	221	485	230	255	0.90	50.4
MEQ73	QPWS(WT)	M	211	445	215	230	0.93	47.6
MEQ74	QPWS(WT)	M	202	461	250	211	1.19	46.9
MEQ75	QPWS(WT)	M	169	465	220	245	0.90	48.1
MEQ76	QPWS(WT)	M	262	465	195	270	0.72	46.6
MEQ77	QPWS(WT)	M	232	455	215	240	0.90	44.0
MEQ78	QPWS(WT)	M	244	480	245	235	1.04	51.0
MEQ79	QPWS(WT)	M	244	490	235	255	0.92	47.4
MEQ80	QPWS(WT)	M	146	430	185	245	0.76	47.6
MEQ81	QPWS(WT)	M	230	520	260	260	1.00	44.2
MEQ82	QPWS(WT)	M	242	470	220	250	0.88	46.7
MEQ83	QPWS(WT)	M	204	470	225	245	0.92	51.6
MEQ84	QPWS(WT)	M	230	475	230	245	0.94	45.5
MEQ85	QPWS(WT)	M	128	405	180	225	0.80	42.0
MEQ86	QPWS(WT)	F	202	480	240	240	1.00	44.0
MEQ87	QPWS(WT)	M	228	460	200	260	0.77	52.0
MEQ88	QPWS(WT)	M	241	495	250	245	1.02	45.8
MEQ89	QPWS(WT)	M	221	427	172	255	0.67	48.2
MEQ90	QPWS(WT)	M	90	268	135	133	1.02	41.7
South-eastern Queensland (30)								
SEQ01	QM	F	132	424	183	241	0.76	.
SEQ02	QM	F	111	390	165	225	0.73	.
SEQ03	QM	M	174	457	227	230	0.99	.
SEQ04	QM	F	148	420	190	230	0.83	.
SEQ05	QM	F	111	.	.	.	.	.
SEQ06	QM	M	.	480	210	270	0.78	.
SEQ07	QM	F	160	390	190	200	0.95	.

SEQ08	QM	F	111	380	185	195	0.95	.
SEQ09	QM	F	.	415	175	240	0.73	.
SEQ10	QM	F	.	495	210	285	0.74	.
SEQ11	QM	F	211	430	225	205	1.10	.
SEQ12	QM	F	177	422	199	223	0.89	.
SEQ13	QM	M	150	415	185	230	0.80	.
SEQ14	QM	M	.	420	200	220	0.91	.
SEQ15	QM	F	160	.	.	.	.	.
SEQ16	QM	M	160	430	190	240	0.79	.
SEQ17	QM	F	220	450	220	230	0.96	.
SEQ18	QM	F	147	.	.	.	.	.
SEQ19	QM	F	180	440	200	240	0.83	.
SEQ20	QM	M	301	455	212	243	0.87	.
SEQ21	QM	M	242	452	212	240	0.88	.
SEQ22	QM	F	138	430	195	235	0.83	.
SEQ23	QM	F	160	410	190	220	0.86	.
SEQ24	QM	F	168	450	200	250	0.80	.
SEQ25	QM	M	180	.	.	.	.	.
SEQ26	QM	F	162	.	.	.	.	.
SEQ27	QM	F	144	.	.	.	.	.
SEQ28	QM	M	203	489	217	272	0.80	.
SEQ29	QM	F	175	451	202	249	0.81	.
SEQ30	QM	F	182	447	205	242	0.85	.
North-eastern New South Wales (73)								
NEN01	QM	F	140	416	182	234	0.78	.
NEN02	AM	F	173	422	214	208	1.03	.
NEN03	AM	F	228	447	200	247	0.81	.
NEN04	AM	M	294	499	244	255	0.96	.
NEN05	AM	F	220	455	207	248	0.83	.
NEN06	AM	F	188	420	193	227	0.85	.
NEN07	AM	F	230	460	205	255	0.80	.
NEN08	AM	F	200	440	195	245	0.80	.
NEN09	AM	F	246	450	200	250	0.80	.
NEN10	AM	F	.	440	185	255	0.73	.

NEN11	AM	F	131	351	160	191	0.84	.
NEN12	AM	M	215	450	205	245	0.84	.
NEN13	AM	M	215	436	205	231	0.89	.
NEN14	AM	F	200	424	186	238	0.78	.
NEN15	AM	F	174	425	195	230	0.85	.
NEN16	AM	M	172	432	177	255	0.69	.
NEN17	AM	F	173	434	190	244	0.78	.
NEN18	AM	F	228	495	220	275	0.80	.
NEN19	AM	M	.	480	190	290	0.66	.
NEN20	AM	F	.	455	200	255	0.78	.
NEN21	AM	F	116	407	168	239	0.70	.
NEN22	AM	F	209	420	190	230	0.83	.
NEN23	AM	F	184	357	177	181	0.98	.
NEN24	AM	F	179	399	173	226	0.76	.
NEN25	AM	F	194	418	185	233	0.79	.
NEN26	AM	F	.	442	205	238	0.86	.
NEN27	AM	F	200	417	187	230	0.82	.
NEN28	AM	M	155	364	166	197	0.84	.
NEN29	AM	F	191	.	.	228	.	.
NEN30	AM	M	225	373	174	199	0.87	.
NEN31	AM	F	175	428	185	243	0.76	.
NEN32	AM	F	188	444	205	239	0.86	.
NEN33	AM	F	126	357	145	212	0.68	.
NEN34	AM	F	164	230	180	230	0.78	.
NEN35	AM	M	183	215	200	215	0.93	.
NEN36	AM	F	.	438	208	230	0.90	.
NEN37	AM	M	202	455	215	240	0.90	.
NEN38	AM	M	193	440	200	240	0.83	.
NEN39	AM	M	206	435	207	228	0.91	.
NEN40	AM	F	167	.	.	.	.	.
NEN41	AM	F	185	266	215	266	0.81	.
NEN42	AM	M	189	435	210	225	0.93	.
NEN43	AM	M	142	212	201	212	0.95	.
NEN44	AM	F	159	.	188	.	.	.

NEN45	AM	F	121	400	180	220	0.82	.
NEN46	AM	F	.	443	200	243	0.82	.
NEN47	AM	F	177	450	210	240	0.88	.
NEN48	AM	F	149	220	175	220	0.80	.
NEN49	AM	F	172	240	194	240	0.81	.
NEN50	AM	M	140	417	177	240	0.74	.
NEN51	AM	F	161	425	190	235	0.81	.
NEN52	AM	M	199	431	212	219	0.97	.
NEN53	AM	F	197	480	220	260	0.85	.
NEN54	AM	F	182	436	204	232	0.88	.
NEN55	AM	M	191	473	208	265	0.78	.
NEN56	AM	F	148	405	185	220	0.84	.
NEN57	AM	M	222	439	198	241	0.82	.
NEN58	AM	F	206	460	195	265	0.74	.
NEN59	AM	F	229	502	220	282	0.78	.
NEN60	AM	M	226	455	220	235	0.94	.
NEN61	AM	M	168	367	162	205	0.79	.
NEN62	AM	F	163	403	180	223	0.81	.
NEN63	AM	M	228	425	205	220	0.93	.
NEN64	AM	M	177	405	175	230	0.76	.
NEN65	AM	F	139	395	175	220	0.80	.
NEN66	AM	F	185	420	190	230	0.83	.
NEN67	AM	F	.	448	180	268	0.67	.
NEN68	AM	F	.	456	199	257	0.77	.
NEN69	AM	M	.	450	210	240	0.88	.
NEN70	AM	F	.	462	212	250	0.85	.
NEN71	AM	F	181	487	230	257	0.89	.
NEN72	AM	F	.	325	136	189	0.72	.
NEN73	AM	F	204	360	210	150	1.40	.
South-eastern Australia (26)								
SEA01	AM	M	130	419	179	240	0.75	.
SEA02	AM	F	.	500	220	280	0.79	.
SEA03	MV	F	.	420	200	220	0.91	.
SEA04	MV	F	.	350	147	203	0.72	.

SEA05	MV	F	.	350	147	203	0.72	.
SEA06	MV	F	.	350	148	202	0.73	.
SEA07	MV	F	.	460	210	250	0.84	.
SEA08	MV	F	.	485	228	257	0.89	.
SEA09	MV	F	.	.	.	275	.	.
SEA10	MV	F	.	467	202	265	0.76	.
SEA11	MV	F	177	522	232	290	0.80	.
SEA12	MV	M	.	448	226	222	1.02	.
SEA13	MV	M	.	460	218	242	0.90	.
SEA14	MV	M	270	460	213	247	0.86	.
SEA15	MV	M	.	540	270	270	1.00	.
SEA16	MV	M	.	522	245	277	0.88	.
SEA17	MV	F	.	504	206	298	0.69	.
SEA18	MV	M	.	520	200	320	0.63	.
SEA19	MV	F	.	500	220	280	0.79	.
SEA20	MV	M	.	.	.	.	.	.
SEA21	MV	F	.	490	220	270	0.81	.
SEA22	MV	M	.	470	215	255	0.84	.
SEA23	MV	F	.	435	212	223	0.95	.
SEA24	MV	F	251	525	225	300	0.75	.
SEA25	MV	M	.	470	230	240	0.96	48.0
SEA26	MV	F	198	508	204	304	0.67	.