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Historical biogeography, diversity and conservation of Australia's tropical rainforest herpetofauna

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INTRODUCTION

Faced with a combination of increasing degradation of habitats and sparse knowledge of species and their distributions, biologists are struggling to find ways of predicting spatial patterns of diversity and then to devise effective strategies for conservation. Area-based conservation planning typically applies complementarity algorithms to identify one or more combinations of areas that effectively represent the known pattern of species diversity (Margules & Pressey 2000). Usually, high-quality distribution data are available for only a limited number of taxonomic groups (e.g. trees, birds, butterflies), so geographic patterns of diversity in these groups must act as a 'surrogate' for those of other taxa. Even this level of knowledge may be lacking for some areas, or at finer spatial scales, leading to the use of environmental (e.g. climate, soil, etc.) data in addition to, or in place of, species' occurrence information (Ferrier 2002; see also Faith *et al.* 2001). The efficiency of such surrogates appears to vary, especially at the finer spatial scales relevant to most conservation planning efforts (see, for example, van Jaarsveld *et al.* 1998; Moritz *et al.* 2001; Lund & Rahbeck 2002).

Even where the geographic pattern of species diversity is known or can be predicted from other taxa, species-based conservation plans may be ineffective at capturing genetic diversity within and across species (Crozier 1997; Moritz 2002). In this context, attention has been given to

using evolutionary trees to estimate the phylogenetic diversity (PD) (Faith 1992) represented by a given set of species or areas. Both simulations (Nee & May 1997; Chapter 5, this volume) and evidence (Polanski *et al.* 2001; Rodrigues & Gaston 2002) suggest that conservation priorities established though complementarity (dissimilarity) analysis of species are often effective at capturing phylogenetic diversity. However, Rodrigues *et al.* (Chapter 5, this volume) found that species-based approaches can under-represent PD where some areas have few, but phylogenetically divergent, endemic species and suggested that this situation could arise on small, long-isolated islands.

Much of the work on developing methods for conservation planning has focused on analysis of biodiversity *pattern*, with less attention to the underlying *process*, in particular the biogeographic and evolutionary processes that have shaped current patterns of diversity. Recent theory (Rosenzweig 1995; Hubbell 2001) demonstrates how spatial processes of speciation and extinction can affect the distribution of species diversity at varying geographic scales determined by a combination of environmental heterogeneity and intrinsic dispersal limitation. We suggest that phylogenetic analyses, both within and across species, can contribute directly to conservation planning by illuminating these processes, by identifying spatial surrogates for representing them in a conservation plan and by using this information to improve predictions of biodiversity pattern. Phylogenetic analyses also provide a richer perspective on diversity above and below the species level than do 'flat-field' lists of species (Avise 2000; Brooks & McLennan 2002).

One simple prediction from evolutionary biogeography is that the use of a few well-known taxa to predict taxonomically broader patterns of diversity will be most effective for areas that have been effectively isolated and subject to independent 'vicariant' evolution for long periods of time. Under these conditions, taxa with limited dispersal are expected to have spatially congruent phylogenies and patterns of species diversity. Applying this logic to a rainforest fauna with a well-understood vicariant history, Moritz *et al.* (2001) found that, although spatial patterns of community dissimilarity were congruent across insects, snails and vertebrates, the finer-grained insects and snails were effective surrogates for identifying conservation priorities for vertebrates, but not vice versa. Thus, we need to consider not just regional history but also the spatial scale at which various taxa respond to that history.

In this chapter we summarise patterns of species and phylogenetic diversity, primarily for reptiles and amphibians, across a strongly vicariant system: the tropical and sub-tropical rainforests of eastern Australia (Fig. 11.1). We consider species endemism and phylogenetic diversity at two spatial scales: (i) among the four major isolates along the Queensland
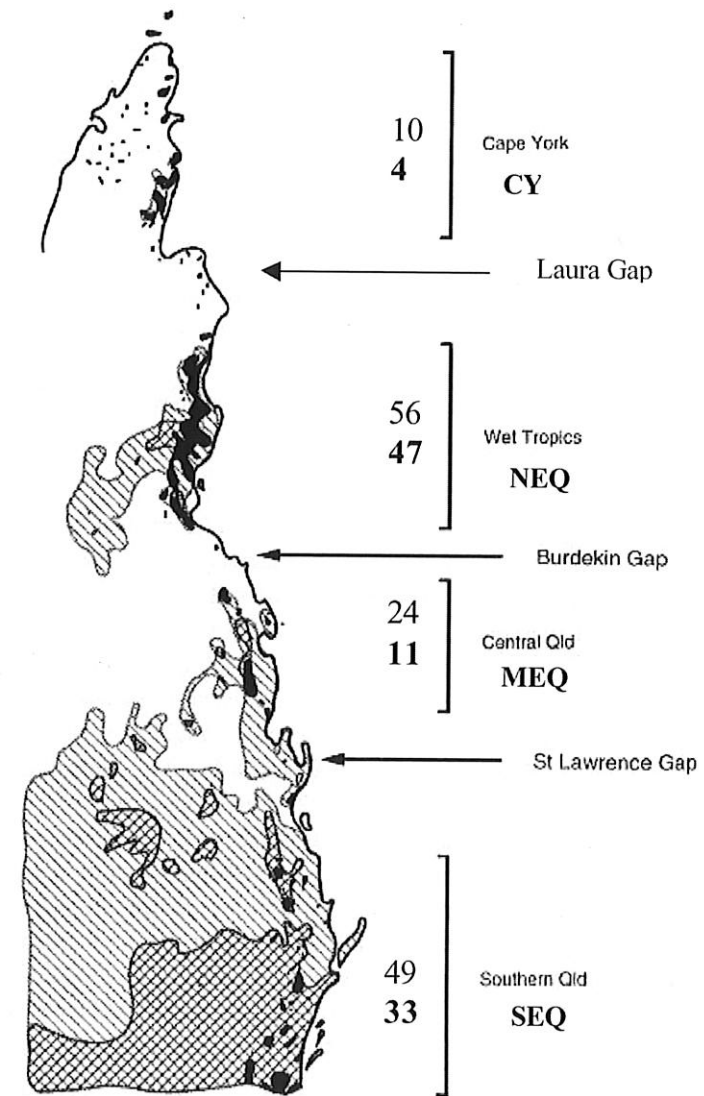

Figure 11.1. Distribution of the major areas of tropical and sub-tropical rainforest in north-eastern Australia (black areas) (adapted from Webb & Tracey, 1981; Nix 1991) and the location of recognised warm, dry corridors (marked with arrows). Cross-hatching indicates mesotherm-dominant climates; diagonal hatching indicates transitional mesotherm–megatherm climates. Numbers represent richness (upper) and endemism (lower, bold) of rainforest-associated species of frog and reptile within each area.

coast (southeastern Queensland (and adjacent northeast New South Wales) (SEQ), mid-east Queensland (MEQ), the Wet Tropics region of northeast Queensland (NEQ) and Cape York (CY)), and (ii) among topographically defined sub-regions within NEQ. A third scale, intraspecific phylogeographic diversity within NEQ, and its relation to species-level endemism, has been discussed elsewhere (Moritz 2002; Moritz & McDonald 2005). The backdrop to these studies is a long history of climate-induced contraction of rainforest habitats to refugia, and we use a combination of phylogeographic analysis and spatial modelling of rainforest-dependent snails to infer the location and extent of these refugia.

Current distribution and palaeoecology of east Australian rainforests

The tropical and sub-tropical rainforests of eastern Australia are patchily distributed in mesic, primarily upland areas on the coastal side of the Great Dividing Range (Fig. 11.1). Nix (1991, 1993) referred to this fragmented distribution as the 'mesotherm archipelago': a series of cool, moist 'islands' surrounded by a 'sea' of hotter and drier climates. Palaeobotanical studies of both macrofossils and pollen reveal that these rainforests represent a flora that was widespread on the continent until the early Miocene (Adam 1992; Greenwood & Cristophel 2005) and which contracted to the mesic east coast during the late Miocene through the Quaternary as the continental climate became more arid and increasingly seasonal. The most detailed palaeo-record is for NEQ, where pollen records from offshore drilling sites and mostly upland terrestrial sites indicate a relatively stable mosaic of angiosperm rainforests in wetter montane regions, surrounded by drier gymnosperm rainforests for much of the past ten million years, until replacement of the latter with fire-prone sclerophyll forests in the past few hundred thousand years (Kershaw 1994; Kershaw *et al.* 2005). For the last glacial period in particular, it is likely that angiosperm-dominated rainforests were restricted to relatively mesic coastal and upland refugia (Webb & Tracey 1981), although even these 'refugia' were themselves probably deeply dissected by sclerophyll vegetation (Hopkins *et al.* 1993). Application of temperature shifts, as estimated through bioclimatic analysis of pollen cores (Kershaw & Nix 1988), to spatially interpolated climate surfaces suggested that areas potentially suitable for rainforest were much reduced at the last glacial maximum (LGM) and then expanded rapidly under cooler wetter climates from about 7500 years ago (Nix 1991) (Table 11.1).

In contrast to the relatively detailed knowledge of vegetation dynamics within NEQ, the history of contact and isolation among the four major

Table 11.1. *Current and historical (LGM) rainforest area, and reptile and amphibian species-richness and endemism across the major east coast rainforest areas*

Abbreviations: Cape York (CY), Wet Tropics (NEQ), mid-east Queensland (MEQ) and southeast Queensland / northeast New South Wales (SEQ). Note that CY was not modelled explicitly for the LGM climate.

	CY	NEQ	MEQ	SEQ
Current (ha)	189 000	791 300	172 556	436 444
LGM (ha)	minimal	24 535	3382	44 308
Species-richness	10	56	24	49
Endemic species	4	47	11	33

rainforest isolates, SEQ, MEQ, NEQ and CY, is uncertain. The heterogeneity among regions has long been recognised in biogeographic studies (Keast 1961), although broad-scale analyses have tended to combine MEQ with either SEQ or NEQ (Schodde & Calaby 1972; Cracraft 1986; Crisp *et al.* 1995). In general, the four areas have quite different patterns of faunal diversity. NEQ, the most extensive and continuous of the rainforest areas (Table 11.1; Fig. 11.1), has the highest diversity of rainforest specialists, followed by SEQ, MEQ and CY. Winter (1988) noted that mammals present in SEQ rainforests are mostly ecotone specialists, whereas NEQ has a diverse community of rainforest specialist mammals, and suggested that this may reflect extreme fragmentation and reduction of rainforests in the former region at the LGM. For birds, SEQ and NEQ have similarly diverse rainforest assemblages, with over 50% of species shared between the two areas (Nix 1993). The MEQ rainforest avifauna is essentially an attenuated version of that in SEQ, with just a single endemic species (Nix 1993; Joseph *et al.* 1993). As for the birds, NEQ and SEQ have the highest diversity of rainforest reptiles and amphibians and MEQ lacks some lineages shared by SEQ and NEQ, e.g. rough-scale snakes (*Tropodechis*), forest dragons (*Hypsilurus*) and *Coeranoscincus* skinks. However, relative to birds and mammals, the rainforest herpetofauna shows much higher levels of local endemism within each of these units, including MEQ (Covacevich & McDonald 1991) (Fig. 11.1), presumably reflecting finer-grained geographic processes of speciation, local extinction and range expansion. Until recently, the lack of phylogenies for genera with substantial numbers of narrowly endemic species has precluded understanding of how these historical processes have operated within and among these rainforested regions.
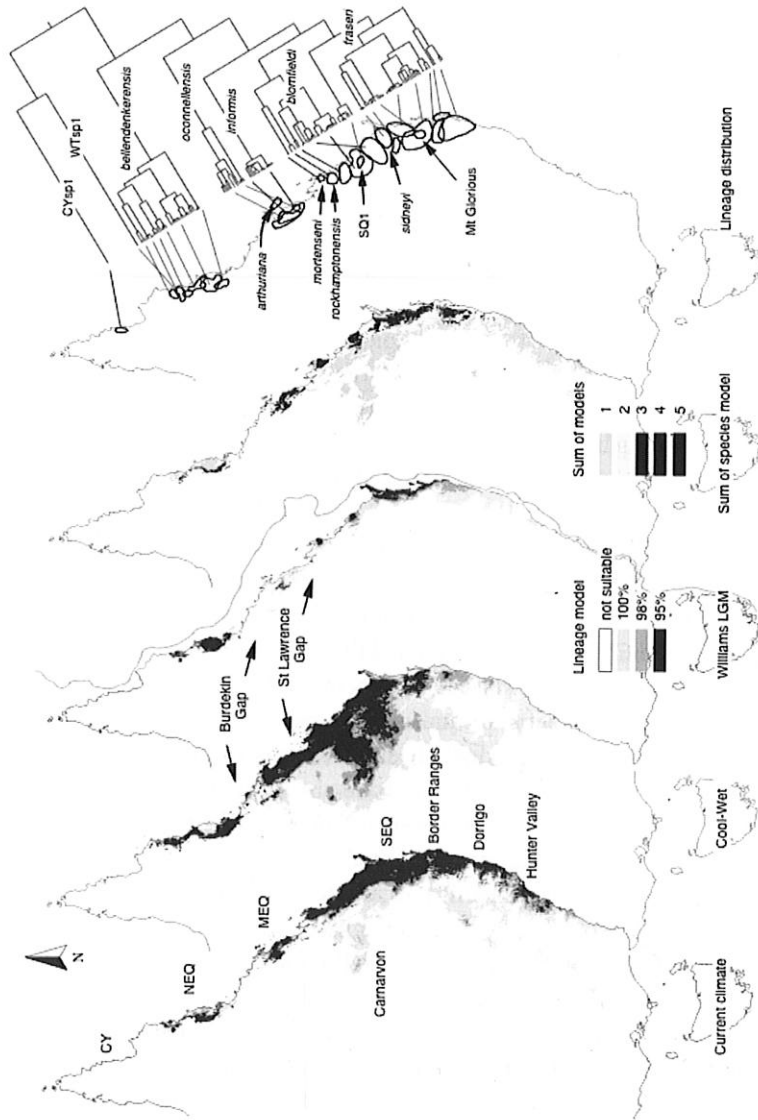
Figure 11.2. Phylogeographic and bioclimatic modelling of the 'Sphaerospira' lineage of snails from east coast Australia (modified from Hugall *et al.* 2003). Right to left: Ultrametric mtDNA phylogeny with schematic distribution of species and major phylogeographic lineages; sum of bioclimatic models of each species indicating core habitats for the species and lineage; combined lineage bioclimatic model for the cool and dry LGM scenario of Williams (Nix 1991) with estimated maximum palaeo-coastline indicated; combined lineage bioclimatic distribution model for cool wet phase of the early Holocene (Nix 1991); combined lineage bioclimatic model for current climate. Methods for modelling and phylogenetic analysis are described by Hugall *et al.* (2002, 2003). Note that the CY species were not included in the models.

INSIGHTS INTO HISTORICAL RAINFOREST DISTRIBUTIONS FROM SNAIL PHYLOGEOGRAPHY

Snails have exceptionally low vagility and, based on the presence of many species restricted to small mesic forest isolates (Stanisic 1994), are able to persist within small refugia. These attributes make snails especially effective as indicators of areas that retained rainforest under drier climates. In turn, the evolutionary biogeography of the snails provides a valuable backdrop for interpreting the historical dynamics of rainforest-dependent vertebrates, most of which are expected to require larger areas of habitat or have higher dispersal potential or both. As part of a broad analysis of the evolution and biogeography of east Australian camaenid snails, Hugall *et al.* (2002, 2003) combined mtDNA phylogeography with palaeoclimatic modelling to infer historical distributions of the 'Sphaerospira' lineage, a monophyletic group of eight species, and the rainforests that they inhabit (Fig. 11.2).

Phylogeographic analysis of the 'Sphaerospira' lineage, including extensive geographic sampling within lineages, revealed a strongly nested phylogeny with the earliest separations between NEQ and MEQ species, then between MEQ and species found in SEQ (Fig. 11.2). Overall, phylogeographic analysis indicates a history of southward expansion in the late Miocene followed by strong climate-induced vicariance within and among described species. Modelling of potential distributions under restrictive LGM (cool, dry) and permissive (cool, wet) early Holocene climates (by using NEQ paleoclimate estimates or modifications thereof) predicted refugial habitats within each of NEQ, MEQ and SEQ (note that CY was not modelled explicitly). NEQ and SEQ were predicted to have a substantially greater area of rainforest at the LGM, albeit fragmented, than did MEQ (Fig. 11.2; Table 11.1). Similarly, phylogenetic analysis of crayfish endemic to montane rainforests revealed a deep split between NEQ and MEQ/SEQ taxa, although in this case the relationships among the latter are less clear (Ponniah & Hughes 2004). For both MEQ and SEQ, comparative mtDNA phylogeography of herpetofauna indicates the retention of multiple refugia (McGuigan *et al.* 1998; Stuart-Fox *et al.* 2001), although genetic divergence among historical isolates is generally less than that observed within NEQ (Schneider *et al.* 1998).

Within NEQ, the same general approach revealed strong concordance between the spatial pattern of genetic diversity and the predicted location of LGM refugia for the NEQ representative of the Sphaerospira lineage, *Gnarosophia bellendenkerensis* (Hugall *et al.* 2002). Here, a major, probably

subdivided refuge was predicted for the central region (Atherton Uplands and mountains and lowlands to the east), whereas rainforest was severely fragmented (although evidently still able to support snails) in topographically complex areas of the northern and southern wet tropics (see also Fig. 11.5). The central and northern regions were strongly isolated by a break in predicted rainforest distribution: the Black Mountain Barrier (BMB). By contrast, the potential distribution of rainforest was considerably broader than at present under the cooler, wetter conditions that prevailed in the early–mid Holocene, even connecting rainforest areas that are now disjunct. The exceptions are the 'Burdekin Gap', the hot and dry barrier currently separating NEQ and MEQ, and the even more extreme 'Laura Gap' separating NEQ and CY (the latter including the Iron and McIlwraith Ranges). These barriers were still evident under the favourable cool–wet conditions of the early Holocene (Fig. 11.2), with substantially cooler and less seasonal climates being needed to bridge them (Hugall *et al.* 2003).

DIVERSITY OF THE RAINFOREST HERPETOFAUNA

Our knowledge of the diversity, distribution and genetic diversity of the rainforest herpetofauna has increased substantially over the past few years. This is exemplified by the leaf-tail geckos, which seem able to persist in small refugia, and for which the described diversity has expanded from one genus with four species to three genera and 12 species (Hoskin *et al.* 2003). Molecular phylogenetic studies have led to recognition of new species and major historical subdivisions within described species, and in some cases also reveal that currently recognised genera are paraphyletic or even polyphyletic (see, for example, O'Connor & Moritz 2003; Reeder 2003). However, we still have much to learn about how the historical fluctuations in rainforest habitats have influenced speciation, extinction and local ecological interactions, and thus the spatial patterns of diversity, in the fauna. Phylogenetic studies, especially if combined with population-level analyses, provide useful insights into these processes (Barraclough & Nee 2001; Moritz *et al.* 2000). Such analyses require that lineages be monophyletic and comprehensively sampled: we are confident of this for the genera examined below. In the following, we use new data on distributions and phylogeny of three taxa with high levels of local endemism: leaf-tail geckos and *Saproscincus* skinks, each of which is widely distributed across the east coast rainforests, and microhylid frogs of the genus *Cophixalus*, which in Australia is restricted to NEQ and CY and is the only vertebrate group to have radiated extensively within the NEQ. *Cophixalus* is also diverse

Table 11.2. *Number of rainforest-associated reptile and amphibian species shared between areas*

Numbers on diagonal represent total richness for rainforest-dependent frogs and reptiles for each area.

	CY	NEQ	MEQ	SEQ
CY	10			
NEQ	3	56		
MEQ	1	7	24	
SEQ	1	6	11	49

in New Guinea, but the available phylogenetic evidence indicates that the Australian species are monophyletic (Zweifel 1985; D. Bickford, personal communication).

Diversity, relationships and endemism among major rainforest isolates

Of the four regions studied, NEQ has the largest current rainforest area, the highest diversity of rainforest-associated species and the highest proportion of endemic rainforest species, despite a severe reduction in rainforest area at the LGM (Fig. 11.1; Table 11.1). Although more fragmented at present, the SEQ region is also predicted to have retained a relatively large area of rainforest at the LGM and currently has high species-richness and endemism. Despite the reduction of rainforest to a very small area in MEQ during the LGM, the number of rainforest species endemic to this area is relatively high. The currently small rainforest in the CY area is predicted to have almost completely disappeared at the LGM, and its species-richness and endemism are low relative to other regions.

In accord with the high levels of species endemism seen within NEQ, MEQ and SEQ, the number of reptile and amphibian species shared between these areas is very low (Table 11.2). Only one rainforest-associated species is distributed across all four areas and four species occur across NEQ, MEQ and SEQ. CY shares few species with the other areas. MEQ and SEQ share the largest number of species, a pattern also reflected in intraspecific phylogeography of rainforest birds (Joseph *et al.* 1993; J. Austin, unpublished data) and some open-forest frogs (Schauble & Moritz 2001). From these two lines of evidence, it could be predicted that most MEQ endemics will be related, perhaps closely, to rainforest species from SEQ.

To add a phylogenetic perspective to our understanding of lineage diversity, as well as the processes that gave rise to it, we have used mtDNA
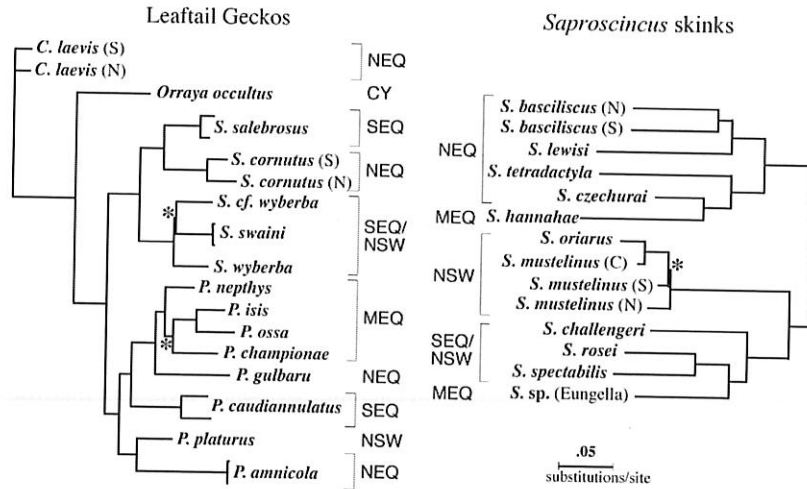
Figure 11.3. Molecular phylogenies of leaf-tail geckos (*Orraya*, *Saltuarius* and *Phyllurus*) (Hoskin *et al.* 2003) and *Saproscincus* skinks (Moussalli *et al.* 2005) from east Australian rainforests. The former is based on segments of 12S rDNA and cytochrome *b* and the latter on 16S rDNA and ND4 genes, all from mtDNA. Nodes for which Bayesian support is less than 95% are marked with asterisks. 'N', 'C' and 'S' refer to major phylogeographic lineages within the leaf-tail gecko *Saltuarius cornutus* (Schneider *et al.* 1998) and the skinks *Saproscincus basciliscus* and *S. mustelinus* (A. Moussalli, unpublished data).
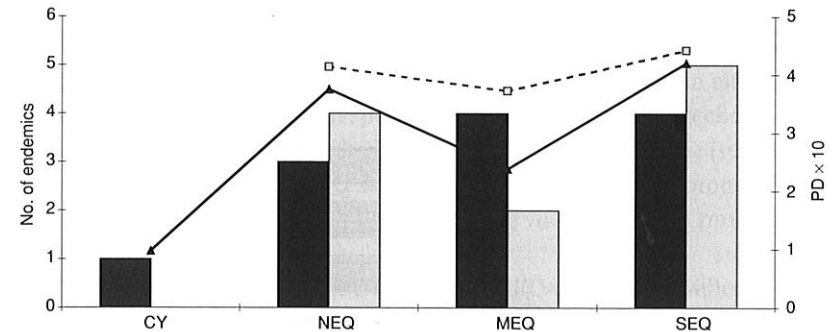

Figure 11.4. Phylogenetic diversity (PD-endemism) estimated from mtDNA phylogenies (lines; see Fig. 11.3) and numbers of endemic species (bars) across the four rainforest regions for leaf-tail geckos (solid bars and lines) and *Saproscincus* skinks (shaded bars; dotted lines).

sequencing to estimate phylogenies of the leaf-tail geckos (*Orraya*, *Saltuarius* and *Phyllurus*) (Hoskin *et al.* 2003) and skinks of the genus *Saproscincus* (Moussalli *et al.* 2005) (Fig. 11.3). The geckos have high richness within each region, with every species being endemic to a single area (SEQ 4 species, MEQ 4 species, NEQ 3 species, CY 1 species). Similarly, all species of *Saproscincus* are endemic to single regions (3 in SEQ (and adjacent NE NSW), 2 in MEQ and 4 in NEQ), with additional species found to the south of SEQ in wet forests of central-north coastal NSW.

Both the leaf-tailed gecko and *Saproscincus* phylogenies reveal high levels of sequence divergence between rainforest-associated species distributed along the east coast (mean divergence among sister taxa 14% in geckos, 19% for *Saproscincus*), implying late Tertiary divergences, but they differ in spatial patterns of diversification. For the geckos, the monotypic genus *Orraya* from Cape York is basal in the phylogeny, indicating a long history of isolation. The remaining species fall into two highly divergent clades: *Saltuarius*, in which most species are restricted to the SEQ area but one is

from NEQ, and *Phyllurus*, which is represented in NEQ, MEQ and SEQ, but includes an endemic radiation of four species within MEQ. Interestingly, the two NEQ representatives of *Phyllurus* are distantly related: *P. gulbaru* has close affinities to the MEQ radiation, whereas *P. amnicola* is related to the most southerly member of the genus, *P. platurus* from NSW. In comparison with the geckos, the major clades of *Saproscincus* are geographically confined: one clade is dominated by NEQ endemics and the other by species from SEQ and adjacent areas in NSW. For this genus, the MEQ rainforests include two phylogenetically remote species, one from the NEQ clade and another from the SEQ–NSW clade. The presence of phylogenetically divergent MEQ endemics is also evident among *Eulamprus* skinks (O'Connor & Moritz 2003), as well as in the Sphaerospira lineage of snails (Fig. 11.2).

The difference between the geckos and skinks in the spatial distribution of clades is reflected in the per-region estimates of PD (also referred to as PD-endemism) (Figure 11.4). To estimate PD-endemism we summed estimated branch lengths connecting the species or deeply divergent phylogeographic lineages contained within each area. For unique endemic species (e.g. *O. occultus*) or clades (e.g. the MEQ *Phyllurus* radiation), we included the branch to the common ancestor with species from other areas (see Rodrigues & Gaston 2002). For the geckos, there is four-fold variation in PD across areas, with CY having the lowest value and SEQ the highest. For the skinks, there is no representative in CY, but NEQ, MEQ and SEQ each have similarly high PD values. Comparison with the number of endemic
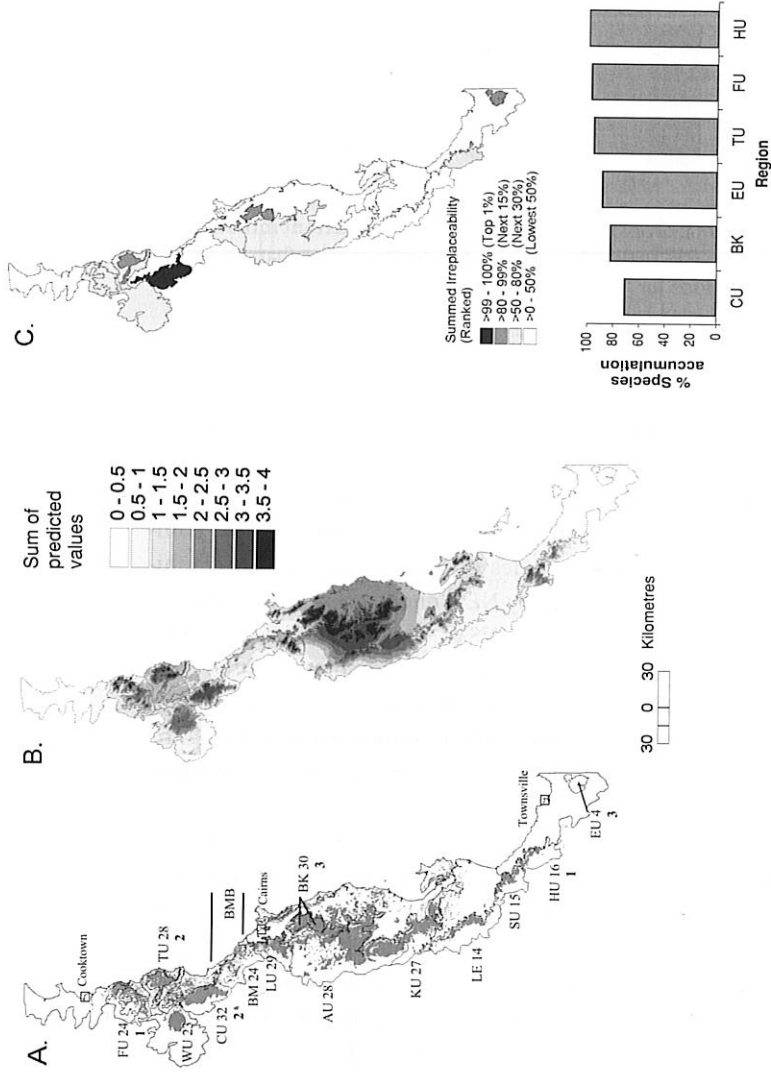
Figure 11.5. Maps of the Wet Tropics region of NEQ showing (a) the current distribution of rainforest and numbers of regionally endemic (upper) and sub-regionally endemic (lower, bold) reptile and amphibian species; (b) the stability surface for upland rainforest, created by overlaying prediction from logistic-regression models of upland rainforests in current, cool–wet, warm–wet and cool–dry periods of the late Pleistocene and Holocene (C. Graham, S.E. Williams & C. Moritz, in preparation), and (c) conservation ranking of sub-regions by using irreplaceability (Ferrier *et al.* 2000) with a target of representing each species in at least one sub-region. The inset at the bottom right shows the cumulative progress towards meeting his target as areas are added in the optimal order. Upland (> 300 m) sub-regions in (a) are as defined in previous biogeographic studies (Williams *et al.* 1996; Moritz *et al.* 2001; Yeates *et al.* 2002). From north to south, these are: Finnegan Uplands (FU), Thornton Uplands (TU), Windsor Uplands (WU), Carbine Uplands (CU), Black Mountain (BM), Lamb Uplands (LU), Bellenden Ker Range (BK), Atherton Uplands (AU), Kirrima Uplands (KU), Lee Uplands (LE), Spec Uplands (SU), Halifax Uplands (HU) and Elliot Uplands (EU).

species is instructive. For the geckos, PD per endemic species is similar across CY, NEQ and SEQ, but relatively low for MEQ. By contrast, for the skinks PD per endemic species is much higher in MEQ than in either SEQ or NEQ. This reflects different speciation histories. The MEQ geckos appear to have diverged *in situ* through vicariance among micro-refugia (see Stuart-Fox *et al.* 2001), whereas MEQ skinks have either been more prone to local extinction in the smaller regions, or diversified via vicariance at much larger spatial scales.

The northernmost isolate, CY, has lower PD-endemism, reflecting the presence of just one narrow endemic across these two groups of lizards, the gecko *Orraya occultus*. The phylogenetic distinctiveness of CY species is not restricted to the geckos: the same is evident for the snails (Fig. 11.2) and the microhylid frogs considered below (Figure 11.6). Thus, even though they inhabit a small area with limited richness, the species that do occur in the CY rainforests appear to represent a substantial component of the phylogenetic diversity within their respective higher taxa.

Diversity, relationships and endemism among sub-regions within NEQ

The endemic, rainforest-restricted fauna of NEQ is concentrated in the uplands (> 300 m) and is distributed across a latitudinal series of topographically defined sub-regions with varying levels of current connectivity (Fig. 11.5a) (Nix 1991). Patterns of richness and endemism across the topographically defined subregions of the Wet Tropics have been studied intensively (see, for example, Williams 1997; Williams & Pearson 1997; Williams & Hero 2001; Moritz *et al.* 2001; Yeates *et al.* 2002; Bouchard *et al.* 2005). Species diversity of the NEQ endemic herpetofauna is highest in the central (AU, BK, KU), and northern (CU, TU, FU) regions (Fig. 11.5a). Narrow endemics, i.e. species restricted to a single sub-region, occur on semi-isolated rainforest blocks in the northern (FU, TU, CU), central (BK) and southern (HU, EU) regions (Fig. 11.5a). For NEQ-endemic, rainforest-restricted vertebrates (Williams *et al.* 1996), variation in subregional species-richness is predicted by a combination of rainforest area and shape (independent of area), with the proportion of endemics per subregion being most affected by shape (Williams & Pearson 1997). Together with significant nestedness of assemblages among subregions (Williams & Hero 2001), these observations suggest strong effects of local extinction and recolonisation through the alternating climates of the late Pleistocene and Holocene, a hypothesis supported by genetic data for some of the widespread endemic species (Schneider *et al.* 1998; Schneider & Moritz

1999). There is also a qualitative correspondence between subregional rich-ness and the inferred location of LGM refugia: diverse areas such as AU, BK, CU, TU and FU are predicted to have retained reasonably substantial (> 2000 ha) areas of rainforest under the cool dry climates of the LGM, whereas low-diversity areas such as LE, SU and HU are predicted to have undergone severe rainforest contraction (Fig. 11.5*b*; see also Hugall *et al.* 2002). Geographic turnover of endemic vertebrate species (Moritz 2002) is strongest across the BMB, a currently tenuous connection between the northern and central areas of rainforest and the predicted location of a major gap in rainforest distribution during cool dry glacial maxima (Fig. 11.5*b*). As a further indication of the importance of biogeographic history in this system, sub-regional patterns of species-richness and turnover for endemic reptiles and microhylid frogs (but not birds, mammals or aquatic-breeding frogs) are better predicted by using rainforest area and among-area cost–distance estimated for restrictive paleoclimates than by using analogous parameters for the current environment (C. Graham, S. E. Williams and C. Moritz, in preparation).

Given the strong effect of historical rainforest contractions, can cur-rent patterns of species-richness be attributed to speciation dynamics, or is it more a consequence of local extinction and species sorting? For the majority of vertebrate species endemic to NEQ, the closest extant relatives occur outside the region (Moritz *et al.* 1997; O'Connor & Moritz 2003) (see, for example, Fig. 11.3), although some deeply divergent phylogeo-graphic lineages within morphologically defined species could also be con-sidered as distinct species (see, for example, Phillips *et al.* 2004). The NEQ *Saproscincus* are one example of local (though pre-Pleistocene) speciation, but the most prominent vertebrate radiation within NEQ involves the micro-hylid genus *Cophixalus*. Of the 14 species, 10 are restricted to single sub-regions (eight within NEQ), some to single mountain-tops, suggesting that the molecular phylogeny for this genus (Hoskin 2004) (Fig. 11.6*a*) should be highly informative about historical processes of diversification within NEQ. As with other rainforest fauna (Moritz *et al.* 2000), sequence diver-gences among sister taxa are substantial (minimum 5%, mean = 11% for 12*S* + 16*S* rDNA), again indicating pre-Pleistocene divergences. The phy-logeny is dominated by three major clades: (i) a group primarily distributed across the central to southern wet tropics, including both widespread (*C. ornatus* and *C. infacetus*) and localised (*C. neglectus* (BK), *C. mcdonaldi* (EU) and *C. zweifeli* (Cape Melville, north of NEQ)) species; (ii) the CY endemic *C. crepitans*; and (iii) a less well supported clade consisting of seven species, each of which has a restricted range among sub-regions north of the BMC. The latter includes two strongly supported sub-clades, each one containing
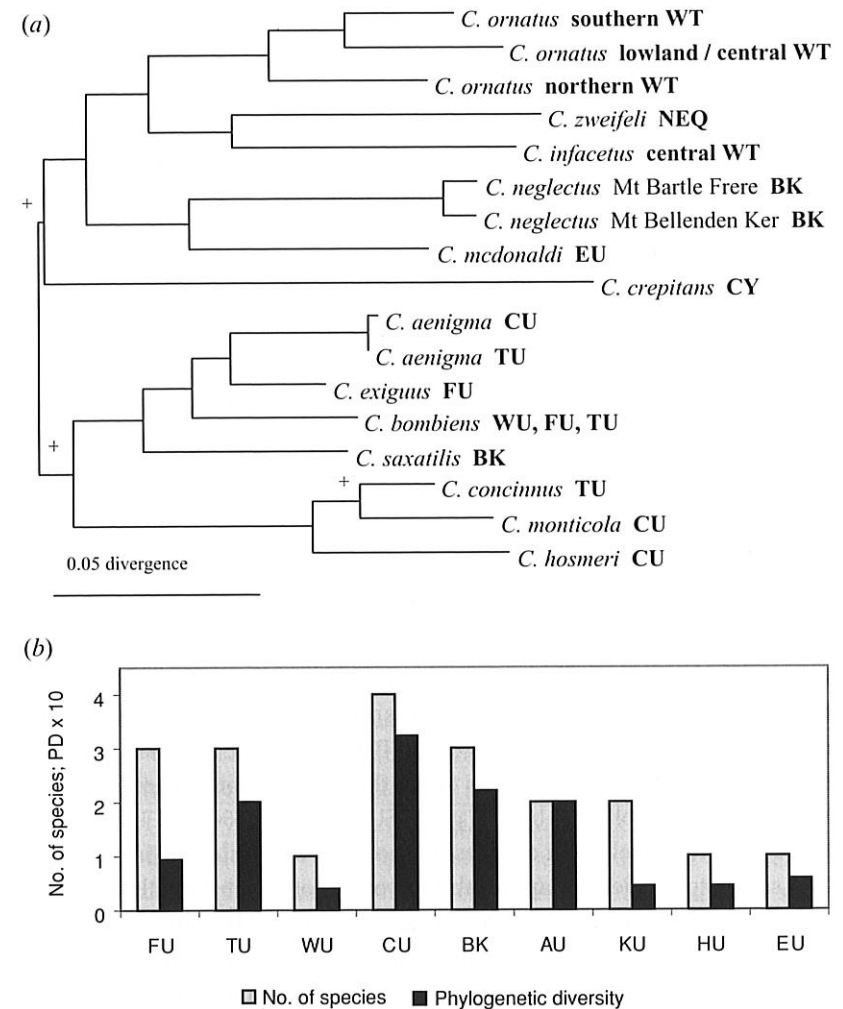

Figure 11.6. (*a*) Molecular phylogeny for NEQ microhylid frogs of the genus *Cophixalus* (Hoskin 2004) based on 12*S* + 16*S* rDNA. All nodes are strongly supported (> 0.95) in Bayesian analysis, except for those labelled with '+'. Abbreviations after species names refer to biogeographic subregions, as in Fig. 11.5*a*. (*b*) Species richness and phylogenetic diversity for *Cophixalus* frogs across the upland sub-regions of the Wet Tropics.

geographically adjacent sister species, e.g. (*C. concinnus* (TU), *C. monticola* (CU)), and (*C. exiguus* (northern FU), *C. aenigma* (CU, TU, southern FU)).

For the southern-central assemblage, the speciation processes are unclear because of large gaps between distributions of the narrow endemics and overlapping ranges of the more widely distributed species. However,

for the northern clade the geographic adjacency of narrowly endemic sister lineages is consistent with expectations of allopatric divergence. This is analogous to the diversification of leaf-tail geckos (*Phyllurus*) among small rainforest isolates within MEQ (see above). Sub-regional patterns of species and PD-endemism for *Cophixalus* are summarised in Fig. 11.6*b*. Both measures, but PD in particular, reflect the distribution of inferred LGM refugia (Fig. 11.5*b*), with the highest PD values at CU, BK, AU and TU.

Implications for conservation

For the NEQ herpetofauna, there is strong consistency across conservation priorities assessed on the basis of irreplaceability analysis (Ferrier *et al.* 2000) of species distributions (Fig. 11.5*c*) and phylogenetic diversity of *Cophixalus*. For the former, with a target of representing every species in at least one sub-region, CU has the highest summed irreplaceability, followed by BK, EU, TU, FU and HU; inclusion of all of these areas is essential to meet the target. The most species-poor area is HU, but the presence of a recently discovered and narrowly endemic gecko, *Phyllurus gulbaru* (Hoskin *et al.* 2003), means that this area must be included. The Wet Tropics rainforest species of *Cophixalus* collectively represent 74% of the total PD for the Australian clade; the more northern species (*C. saxatilus, C. zweifeli, C. crepitans*) capture the remaining 26% of PD. To capture the maximum PD of Wet Tropics *Cophixalus*, CU is again the most important area (44% of Wet Tropics PD), followed by BK (37%), FU (9%), EU (8%) and TU (2%), in that order. Thus, selection of areas on the basis of reptile and frog species also serves to efficiently capture the PD of the only substantial vertebrate radiation within the region. Interestingly, the large AU subregion, which was the highest ranked in irreplaceability analysis of total fauna and total vertebrates (Moritz *et al.* 2001), does not contain any unique herpetofauna and therefore was not ranked highly in any of these analyses. In addition, as in previous analyses of these systems, the high-priority areas selected by irreplaceability or PD analysis do not include the major suture zone (BM to LU), within which divergence phylogeographic lineages within multiple species meet and interact (Phillips *et al.* 2004). Elsewhere (Moritz 2002), we have argued that these subregions should be protected to maintain evolutionary processes.

At the broader geographic scale, the combined analyses of species and phylogenetic diversity clearly reinforces the high conservation value of the major rainforest areas of NEQ and SEQ; both regions have substantial National Parks and have special status as World Heritage Areas. However,

recent discoveries of new species (see, for example, Hoskin *et al.* 2003; Hoskin & Couper 2004), together with the phylogenetic (PD) analyses, also emphasise the significance of the MEQ and CY rainforests, as well as of geographically marginal areas in NEQ (e.g. EU, HU) for protection of reptile and amphibian diversity. Thus, we support previous calls (Covacevich & McDonald 1991; Nix 1993; Couper *et al.* 2000; Moritz 2002; Hoskin *et al.* 2003) for enhanced protection of these areas and urge that small, peripheral rainforest isolates in the region also be surveyed and included in biodiversity analyses. Fortunately, recent assessments of biodiversity values for the SEQ region as part of a Regional Forest Agreement process have led to a substantial expansion of National Parks, affording increased protection for the phylogenetically divergent and narrowly endemic reptiles and amphibians of this region.

In relation to evolutionary processes, two themes recur across the studies presented here. One is the importance of long-term refugial areas, as predicted by snail phylogeography, for protecting the species and phylogenetic diversity that has accumulated via mostly ancient speciation in the frogs and reptiles. Even the smaller areas of CY and MEQ retain phylogenetically divergent endemic species, enhancing our appreciation of their biodiversity value. The second theme is that there are substantial differences among taxa in the geographic scale of evolutionary response to a common history of climate-driven habitat change. This was evident in the differing geographic scales of diversification of microhylids versus lizards within NEQ, and of *Phyllurus* geckos versus *Saproscincus* skinks within MEQ. In some cases the ecological correlates of persistence within, and divergence among, small refugial areas are evident; examples include small body size of *Cophixalus* and persistence of *Phyllurus* in mesic boulder microhabitats. A better understanding of how lineage-specific ecology predicts responses to historical rainforest contractions is needed to develop strategies for protecting such diverse biotas in the face of future fluctuations in rainforest distributions.

Recent declines of amphibian species, most within National Parks, are a stark reminder that habitat protection alone does not guarantee persistence. Overall, six species have disappeared (two from SEQ, one from MEQ and three from NEQ) and several more have declined precipitously, especially from montane areas (Richards *et al.* 1993). To complicate matters further, spatial modelling of both critical habitats (e.g. high-elevation rainforest (Hilbert *et al.* 2001)) and individual species (Williams *et al.* 2003) suggests that future climate change could lead to substantial extinction of high-elevation endemics, especially those that have persisted through the

Quaternary in coastal montane refugia (FU, TU, BK, EU). If these projections are even close to accurate, they represent a major challenge to conserving this diverse and phylogenetically deep fauna. Priority should be given to refinement and testing of these models, including monitoring of abundance across altitudinal transects and testing of species' physiological limits, and also to developing conservation strategies (e.g. protection and/or restoration of altitudinal gradients) that will minimise the loss of diversity.

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