



Arthropods of Australia's subtropical and tropical rainforests: rich and unique hotspots of biological diversity?

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Received: 17 May 2022 / Accepted: 26 June 2022
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Abstract

The tropical and subtropical rainforests of eastern Australia are a major component of the Forests of East Australia global hotspot. Australian rainforests are maintained orographically and are embedded within vast tracts of pyrogenic open forest and woodland. Australian tropical and subtropical forests stretch over 24° of latitude from Cape York, Queensland, to south of Sydney, New South Wales. Since European colonization in 1788 these rainforests have been reduced in extent by about 30%. The most abundant and functionally significant animal species within these forests are arthropods. These have attracted the attention of western science since before formal colonization. Through the twentieth century this focus increased and comparative biogeographic studies began to emerge. Some taxa have received much more attention than others. Selected butterflies and beetles plus economically important species stand out in this respect. From the late 1980s mass sampling approaches developed. Recent research foci have included tropical and subtropical elevational transects, latitudinally diverse multi-method one-hectare surveys, and use of canopy knockdown as a way of sampling the canopy. Important and distinct patterns reflecting latitude, altitude and vertical position have emerged. A focus on moths in remnant and elevational studies has led to the identification of indicator sets of species which may be most useful for tracking the impacts of environmental degradation and global warming. Arthropods are increasingly being nominated on lists of rare, threatened and endangered species; a range of species of insects, particularly butterflies, have been so identified in Australia but few of these are rainforest species. The vulnerable Richmond Birdwing butterfly, a species of subtropical rainforests, has become an icon of how recovery methods can be applied to invertebrate species. Regarding the entire rainforest community—microbiota, plants, vertebrates and invertebrates—as the ‘object’ to be conserved is an essential and much more realistic mindset for future conservation efforts. Most of Australia’s tropical and subtropical rainforests are held in National Parks and they are defining features of two of Australia’s largest World Heritage Areas. Growing impacts of global warming means they cannot be regarded as ‘safe’ from a conservation point of view. Increasing frequency of wildfires impinging upon rainforest areas is having a devastating effect on some of these fire-sensitive forests.

Implications for insect conservation Most of Australia’s tropical and subtropical rainforests are held in National Parks and they are defining features of two of Australia’s largest World Heritage Areas. Nevertheless the growing impacts of global warming means they cannot be regarded as ‘safe’ from a conservation point of view. Increasing frequency of wildfires impinging upon rainforest areas is having a devastating effect on these fire-sensitive forests. Regarding the entire rainforest community—microbiota, plants, vertebrates and invertebrates—as the ‘object’ to be conserved is an essential and much more realistic mindset for future conservation efforts.

Keywords Arthropoda · Rainforest · Australia · Diversity · Lepidoptera · Conservation · Richmond birdwing · Hotspot · Forests of East Australia

Introduction

The ‘Forests of East Australia’ were added to the global list as the ‘35th hotspot’ of biodiversity in 2011. This vast region of over 250,000 square km encompasses both tropical and subtropical rainforest as well as the surrounding

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eucalyptus-dominated dry forests. The case for the listing as put forward by Williams et al. (2011) was based on the overall richness of the flora and vertebrate fauna, the levels of endemism, and the area lost since European colonisation in 1788.

Forests generally contain high levels of invertebrate, particularly arthropod, diversity and, globally, rainforests are considered particular foci of arthropod diversity (Basset et al. 2012; Hammond 1990; Novotny et al. 2006). Since 1987 a research group based first at the University of New England, New South Wales, and, since 1992, at Griffith University, Queensland, under the leadership of RLK, have investigated this arthropod biodiversity in Australian tropical and subtropical rainforests (as well as carrying out comparable studies in New Guinea, Vietnam and China). All of these studies on the Australian mainland now fall within the Forests of East Australia hotspot. Here we describe and review this work and place it in context with other knowledge of the arthropod fauna of the hotspot. In particular we make the case that the entire arthropod assemblage of the rainforest component should be a conservation target.

Most definitive work on rainforests globally has been generated in one of the three major blocs of wet tropical forest: the Amazon/Orinoco basins of the Neotropics; the Congo/Guinea/Niger basins of Central and West Africa; and, the tropical south-east Asian forests of Indo-China, Malaysia and Indonesia. The great rainforested island of New Guinea, biogeographically Australasian, completes the global set. Although there is ecological variety within each of these vast blocks, nevertheless the expanse of forest in each case is recognisable 'rainforest' and any particular location is likely to be surrounded by or adjacent to not dissimilar forest types.

Beyond these major, tropical rainforest regions, however, are many outliers: the Western Ghats of India, the East African highlands, Madagascar, the Atlantic areas of Brazil, and the eastern coastal regions of Australia, to note just a few. In most of these locations the rainforests are maintained by local orographic conditions reflecting their topography rather than continental climatic conditions over vast, largely flat, areas (Stork et al. 2008). In each of these cases, even before human degradation took its toll, the rainforests, although undeniable in character, are adjacent to, interdigitating with or, even, surrounded by drier forest and woodland types. In these cases interpreting the biological diversity and dynamics within the 'rainforests' needs, also, to take account of the adjacent forests which carry their own characteristic biotas.

Nowhere is this more true than in Australia where the rainforests have been perceptibly described as 'islands of green in a land of fire' (Bowman 2008).

Tropical and subtropical rainforests in Australia

Rainforests in Australia are distributed as patches from Tasmania (*ca* 41° S) to the tip of Cape York (*ca* 11° S) along the East Coast with scattered monsoonal forests across the northern coastal areas of the Northern Territory and the Kimberley Region of Western Australia (Fig. 1). The forest patches vary from a few hectares to the hundreds of thousands of hectares of the Wet Tropics of Queensland. Forests designated as subtropical to tropical occur from just south of Sydney (*ca* 35° S) northwards and those from Cooktown (15.5° S) southwards fall within the Forests of East Asia hotspot.

Until the 1970s these subtropical and tropical forests were generally thought of as outliers of the great Papuan and south-east Asian rainforests. They received little serious attention from Australian ecologists for whom the pyrogenic eucalypt-dominated forests and woodlands were the 'true' Australian ecosystems. All this changed with increasing understanding of both vegetation history and plant phylogeny (Webb and Tracey 1981). Current understanding is that the Australian rainforests encountered by humans over the last 60 or more millennia are considerably less extensive than the vast expanse of Gondwanan, Miocene forests. Many of the classical 'Australian' plant genera including *Eucalyptus* and its relatives may well have had their evolutionary origins in these earlier extensive rainforests (Sytsma et al. 2004). The Miocene forests gradually diminished as the continent dried and shifted northwards. Nevertheless rainforests are generally supposed to have increased in area reflecting increased rainfall regimes following the last glacial maximum (16–25 K bp) (Kershaw and Nanson 1993). Gondwanan elements diminish northwards where, indeed, Malesian elements are prominent.

The recent patchwork of rainforests then is the product of both climate change and human impact. Australia's first peoples, arriving on the continent from the north somewhere before 60 thousand years ago undoubtedly increased the frequency of fire on the continent and, indeed, probably largely avoided the rainforests as dwelling places. This increased fire frequency accompanying human invasion (sometimes described as 'firestick farming', Bird et al. 2008) no doubt favoured the pre-existing fire-driven forests and woodlands dominated by eucalypts and other scleromorphic genera. This human impact over millennia also encompassed the waxing and waning of the Younger Dryas glaciation so any human impact added to global scale climatic changes.

When Europeans arrived in the late eighteenth century the extent of rainforest (of all kinds) in Australia is estimated to have been 43,500 km². According to a 2001 audit about 30,200 km² remain (Stork et al. 2008).

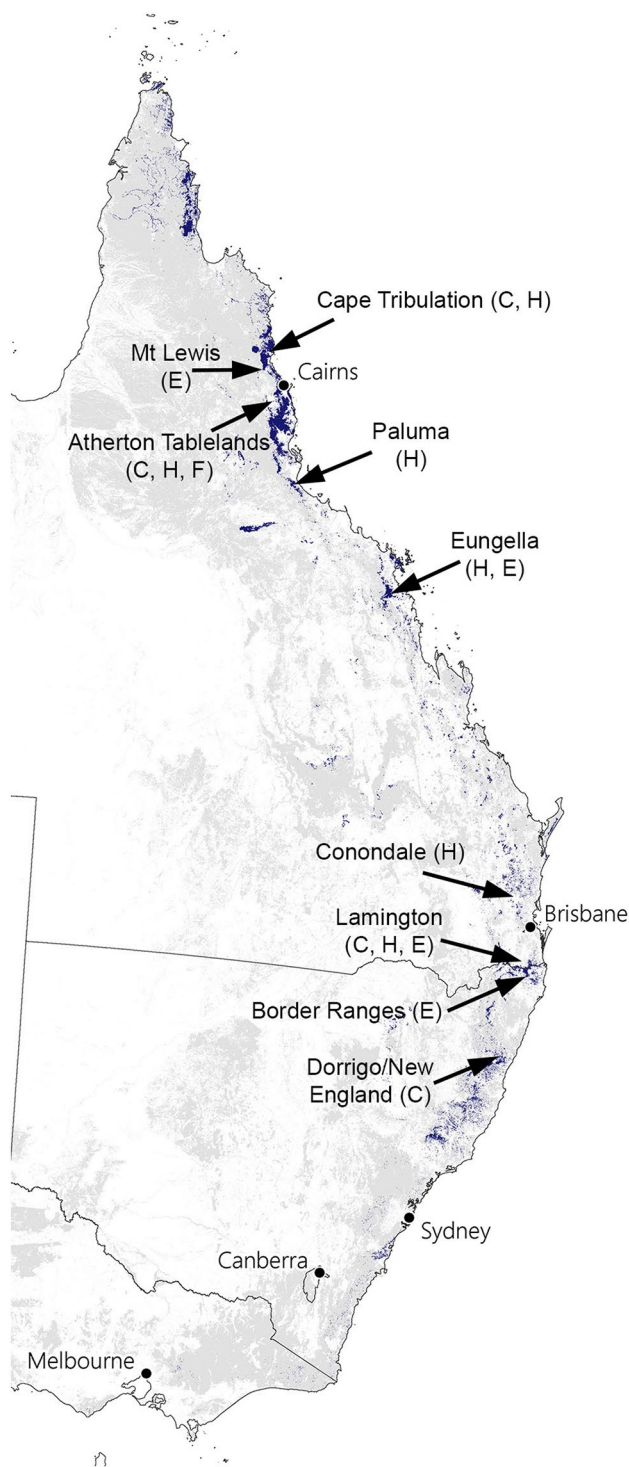


Fig. 1 Subtropical and tropical rainforest in mainland eastern Australia (blue areas), grey areas represent other forest types. Arrows indicate the studies discussed in this article. KEY: C—canopy knock-down studies; H—one-hectare plot studies; E—Elevational transects; F—Atherton fragmentation study. Base-map is modified from the website of Forests Australia and used with their permission. (www.awe.gov.au/abares/forestsaustralia/profiles/rainforest-2019)

Turning to subtropical and tropical rainforests, eastern Australia is currently dominated by three large areas of such forest. In south-east Queensland and north-eastern New South Wales are the subtropical forests of the Border and McPherson Ranges. These more or less contiguous forests (with associated cooler and drier forests) encompass Main Range, the Tweed Caldera and Focal Peak groups of National Parks totalling over 100 thousand hectares (Kitching et al. 2010) located at about 28° S. This block would also have connected to the celebrated ‘Big Scrub’: an area of about 75,000 ha of subtropical lowland forest to the south of the current forests. These forests were cleared for agriculture in the late nineteenth century leaving just a few tiny remnants amounting to about 320 ha (Parkes et al. 2012). These remnants include some of the richest survivals of Gondwanan plant taxa (Kooyman et al. 2020).

Heading north, the next large block of intact rainforest is located in the Clarke Range centred on Eungella National Park. This reserved area comprises just under 60 thousand hectares of which substantial areas are subtropical and tropical rainforest (Kitching 2020; Anon 2021). These forests are located at about 21° S, inland from the city of Mackay. Together with some rather smaller patches of rainforest on northern Cape York the Eungella forests are the only extensive rainforests in Australia not protected by World Heritage status (a third WHA encompasses the cool rainforests of Tasmania).

Finally, from 15.5° S to 19° S, are the Wet Tropics rainforests comprising genuine lowland rainforest merging up to high elevation forests at over 1000 m asl. The Wet Tropics forests comprise just under 900 thousand hectares stretching from the Paluma Ranges and Mt Spec in the south to Cooktown, on Cape York Peninsula, to the north. Almost all of these forests are preserved as National Parks. There are significant areas of lowland and upland rainforest on Cape York to the north of the Wet Tropics but these remain as isolated blocks and are separated from the more southerly forests by substantial dry forest ‘gaps’ (Lavarack and Godwin 1987).

Arthropods in rainforests: diversity, history and role

It is well established that arthropods (and other invertebrates) play crucial roles in the functioning of forest (and, indeed, any terrestrial or freshwater) ecosystems. E. O. Wilson’s trope that they are the ‘little things that run the world’ is often quoted (Wilson 1987) and never refuted. Perhaps only greater insight into the roles and pervasiveness of, on the one hand, even smaller organisms, the microbiota (Staley and Reysenbach 2002) and, on the other, the heterotrophic fungi (Sheldrake 2020), might challenge this truism, and add further insight and complexity to our understanding.

So this is not the place to review the many and crucial interconnecting functional roles played by arthropods in rainforests. Indeed, we have discussed this at length elsewhere in recent commentaries (Kitching et al. 2020a, b; Kitching 2006). Suffice it to say that the intricate web of interactions that make up the rainforest foodweb is, at least at the level of multi-celled organisms, largely populated by arthropods. In that earlier commentary the roles of insects (and other terrestrial arthropods) in both ‘green’ foodwebs (that is those based directly on plants and other primary producers) and so-called ‘brown’ foodwebs (based on decomposing organic material) were identified and discussed. Other forms of webs that do not involve trophic interactions also engage insects in rainforests. Webs based on animal:animal and animal:plant mutualisms are critical here. Williams (2020), for example, discusses pollination interactions in rainforests.

Studies of arthropods in Australian rainforests

Early days

Formal Western entomological studies began in Australia even before Europeans formed permanent settlements on the continent. The *Endeavour* under the indefatigable Captain James Cook sailed up the East Coast in 1770 and the expedition naturalist, Joseph Banks (among others), collected insects whenever landfall was made. The last and longest landfall was in the region of what is now Cooktown on southern Cape York peninsula where the damaged *Endeavour* was beached, careened and repaired. Many of the very first insects, principally butterflies, described from Australia came from there—and that is an area where abundant tropical rainforest and rainforest/sclerophyll edges are dominant. Shortly after permanent European settlements were established resident entomologists began work documenting the fauna. Early volumes describing the Australian fauna, principally but not exclusively of Lepidoptera, included Donovan (1805), Lewin (1805) and Scott (1864).

Once permanent collections were established serious collecting began and considerable focus was placed on rainforested locations where professional and amateur collectors got the ‘best’ return on effort. So significant public collections grew. The Australian Museum in Sydney was established in 1845, the Melbourne Museum in 1854 and the Queensland Museum in 1862.

The middle years

From the late nineteenth century until the late twentieth century and beyond, arthropod work in Australian

rainforests was done principally by museum taxonomists (or associated amateurs) in expedition mode. It is probably fair to say that the vast numbers of rainforest arthropods that were added to collections over that period greatly exceeded the taxonomic expertise available to sort and describe them, let alone achieve biogeographical or ecological syntheses. Many groups await attention. There are, however, a few exceptions: higher taxa for which there was popular interest, immediate economic benefit, or where particular groups just happened to coincide with the special interests and passions of the available taxonomists. Not surprisingly the Lepidoptera, particularly the butterflies, received most attention but other groups that attracted significant taxonomic attention included the Odonata, the cicadas (and other auchenorrhynchs), termites, ants, carabid, tenebrionid, buprestid, cerambycid, curculionid and scarabid beetles, Neuroptera and mosquitoes (and other Diptera of medical and veterinary importance). Of particular and lasting importance was the extensive and well documented work of the coleopterist, Philip Darlington, who not only made extensive collections of carabids in Australia and New Guinea but also synthesised these into insightful biogeographical analyses that have seldom if ever been surpassed (see, e.g., Darlington 1961, 1965). These studies in no small part stimulated later scientists and remain relevant to any current analysis. Among non-insectan arthropods, the spiders received the greatest share of attention, partly because of the venomous nature of a small number of them, partly out of intrinsic interest.

Reviews and overviews of this productive museum-based work are rare. Williams (1995, 2002, 2020) provides exhaustive syntheses of arthropods (and other invertebrates) from the subtropical and cooler rainforests of the CERRA WHA (now the Gondwana Rainforests of Australia WHA). A few other syntheses appeared principally as a response or adjunct to the conservation debates of the day (e.g. Monteith 1980; Walter et al. 1998).

Mass sampling approaches 1988–2020

In 1982 Terry Erwin published the first of a series of papers (Erwin 1982) on the diversity of arthropods in tropical forest canopies. He collected data on beetles in Neotropical canopies using insecticide knockdown techniques—effectively directing a cloud of insecticide into the forest canopy and collecting the many arthropods that fell to the ground subsequently. Erwin encountered very large numbers of unknown species of beetles and then used crude extrapolation techniques to make new predictions about global levels of terrestrial arthropod species richness. These estimates were an order of magnitude greater

than any preceding estimates. This has led to decades of debate (see Stork 2018 for a recent assessment) but did divert many insect ecologists to this sampling methodology and an approach to the entire assemblage¹ of insects within a block of canopy rather than a focus on single taxa. One of the most successful of these follow-up studies was carried out in Sulawesi, Indonesia, in 1985 as part of the Royal Entomological Society's centenary expedition (Hammond 1990; Stork and Brendell 1990). Two of us (RLK and AGO) participated in that expedition. RLK observed and assisted with the canopy fogging and resolved to bring this technique to bear on the canopy of Australia's rainforests. This proved to be the serendipitous beginning of a 35 year focus on measuring and understanding the diversity of arthropods in Australian rainforests, initially focussing on the canopy but, subsequently, widening that to all components of the rainforest ecosystem.

Canopy studies—latitudinal and tree species comparisons

Initial studies focussed on subtropical (Lamington NP) and tropical (Cape Tribulation NP) canopies with additional sites in cool temperate forest in northern New South Wales. (Dorrigo/New England NP)(sites labelled 'C' in Fig. 1). This last forest type is dominated by *Nothofagus moorei*, the Antarctic beech. In each case 10×10 m blocks of forest canopy were sampled using pyrethrum-knockdown techniques. Each sample was accompanied by a vegetation profile of the sites targeted. Generally, analysis of results was restricted to ordinal profiles although more detailed taxonomic analyses were performed in selected cases reflecting the availability of appropriate specialists. General results are presented in Kitching et al. (1993). More focussed, taxon-specific results included; Tipulidae (Kitching and Theischinger 1996a), ants (Majer et al. 2001), beetles (Hammond et al. 1997), mites (Walter et al. 1998) and flies (Kitching et al. 2004). Fundamentally these studies confirmed the general patterns observed elsewhere. Australia's rainforest canopies contain an abundant and species-rich assemblage of arthropods which, for those taxa investigated further, contains substantial levels of novelty and hitherto unknown taxa.

Subsequent Australian canopy studies by this group of researchers focussed on individual species of trees. A set of species in the lowland Daintree region of North Queensland was examined by Kitching and Zalucki (1996b). These authors showed that individual species of trees carried different arthropod profiles even at the ordinal level. A more

extensive study focussed on a family-level analysis of Coleoptera from a set of tree species in the mid-altitude, subtropical rainforests of Lamington National Park (SE Queensland) (Kitching et al. 2003). This last contribution is interesting for two reasons. First it demonstrates that when examining the similarity of arthropod assemblages from co-occurring tree species then the phylogeny of the tree species must be taken into account. Second, fogging tree canopies generates a mixed sample of species and feeding guilds of insects (even *within* a large order such as the Coleoptera). Differentiating between species actually associated with that tree and the larger group that just happen to have been intercepted by sampling that tree (the so-called 'tourists') is impossible without deep knowledge of the biology of individual species (which is seldom available in rainforest situations). This is complicated further by the many species that represent higher trophic levels within the food-web. It was for this reason that several of our later studies focussed on leaf-miners (Maunsell et al. 2015, 2016a, b) and galling insects (Hall et al. 2015) where a much more direct association with the host plant can be assumed.

One hectare multi-method surveys

By the mid-nineties it was clear that the focus on the 'unknown' canopy was delivering a rather one-sided view of arthropod biodiversity in Australian rainforests. Accordingly we developed a multi-method approach to assessing arthropod diversity in forests using a range of standard (and not-so-standard) trapping methods focussing on the arthropod assemblages from the ground-zone leaf litter to the canopy (Kitching et al. 2005). Undisturbed one-hectare plots were established in each targeted location. Within each hectare all trees and other woody plants with a breast-height diameter of 5 cm or above were recorded, mapped, measured and identified. Arthropods were sampled intensively within this one-hectare. The ground dwellers (the 'epigeal' fauna) were sampled using Tullgren funnels, pitfall traps and yellowpan (water) traps. The water traps also sampled a rich fauna of low-flying micro-Hymenoptera and Diptera. Tree-trunk dwellers (the 'corticolous' fauna) were sampled using hand-held insecticide sprays. Free-flying insects in the understorey were sampled using Malaise, light and window traps. The canopy fauna was examined using canopy knockdown (as before) and canopy located Malaise and light traps.

In this fashion we established six permanent plots in Australia: Lamington National Park (NP) (28.2° S), Conondale NP (26.4° S), Eungella NP (21° S), Paluma NP (19° S), the Atherton Tablelands (ca 17.3° S) and Cape Tribulation (16.1° S) (sites marked 'H' in Fig. 1). Additional sites were established using the same protocol in Papua New Guinea (2 sites), Brunei and Vietnam. A critical assessment of this approach focussing on four sites from south-east Queensland

¹ We avoid using the term 'community' here deliberately. We regard a taxonomically defined subset of the rainforest community as an 'assemblage'. We appreciate this is a purist view!

Table 1 An ecological templet summarising hypotheses about the generation and maintenance of arthropod diversity (from Kitching et al. 1997)

| | | SPATIAL AND CURRENT FACTORS | | | | |
|---|----------|--------------------------------------|----------------------------|--|---|---|
| | | Processes | Geological/ Pedological | Synoptic Climate | Fragmentation/ Patch pattern | Co-evolution Co-ecology |
| T E M P O R A L S C A L E | Far Past | Tectonic | Basic biogeographic sets | | Evolutionary radiation | |
| | | Glaciation-related climatic change | | | Species 'pumps' | Food-web dynamics trophic mutualistic structural |
| | Recent | Island biogeographical dynamics | Topographic effects | | Gamma-diversity | Guild structures |
| | | Cyclones Clearing Exploitation | Recovery processes | Seasonality Anthropogenic extinctions | Levels of endemism Assemblage heterogeneity | Establishment facilitation by predecessor species |
| | | | | | Impacts of exotic biota | |

to Borneo was made by Kitching et al. (2001). That article, among other things, identified which of our sampling methods and target taxa gave the most information-rich results most efficiently. For constancy across all sites then Malaise traps and pitfall traps gave the best results. If identifying contrasts across sites was a primary goal then bark-spraying (of tree trunks) and canopy knockdown using pyrethrum insecticide were the most useful. Collembola, ants and the hemipteroids showed the greatest site-to-site contrasts. Overall, however, the analysis concludes that a shopping-basket approach using multiple methods and target taxa is to be preferred if sufficient resources are available.

These one-hectare, multi-method surveys produced an almost overwhelming amount of data—as collections, as field-collected data and as data-sets enriched by subsequent sorting in the laboratory. It is certainly true to say that the anticipated interest and follow-up by other entomologists and taxonomists was not as forthcoming as anticipated (perhaps hoped for is a better phrase). Some significant analyses however did follow focussing principally on two groups of arthropods that are seldom targeted in assemblage-level work: the Collembola and the Diptera.

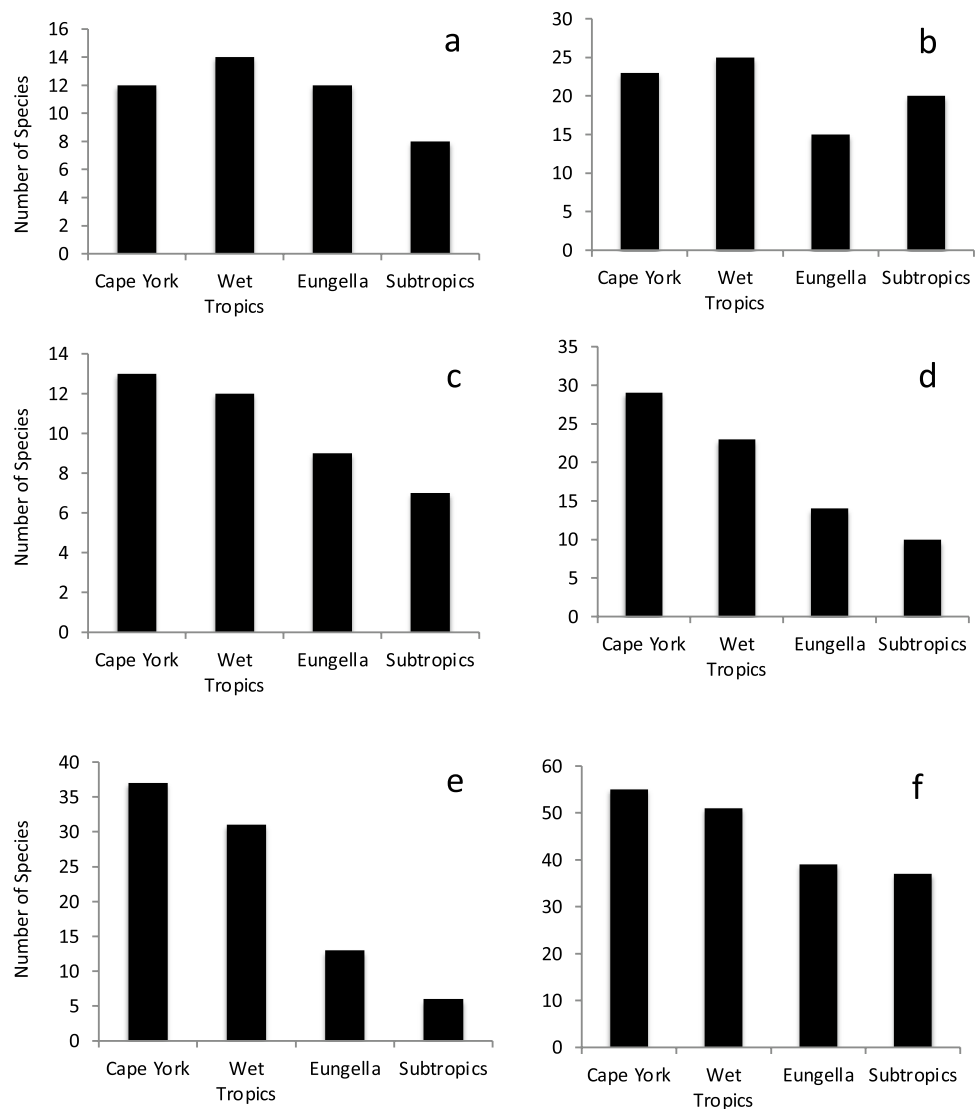
The Collembola, springtails, are key decomposers in rainforest ecosystems. Not only are they a major component of the ground zone leaf-litter community, they are also tree-trunk and canopy dwellers. The canopy fauna of Collembola in Australian (and other) rainforests is strongly associated with the 'perched' leaf litter held in basket ferns (*Asplenium* spp. in the Australian flora). A preliminary study of the fauna of these aerial communities was made by Christophe Thébaud who compared the entire leaf litter fauna in *Asplenium* ferns in the canopy with that in the ground-zone leaf litter beneath. From volumetrically standard-sized samples the perched litter was considerably richer than that on the ground across all higher taxa except the Amphipoda (Kitching et al. 1997). This work was followed up in the doctoral studies of Denis Rodgers which focussed on the Collembola and which was carried out on our one-hectare plot in the subtropical forests

of Lamington NP (Rodgers and Kitching 1998, 2011). Rodgers showed, *inter alia*, three key things. First there were a few collembolan species more or less restricted to the perched leaf litter in the canopy. Second, for the majority of species, there was a dynamic exchange of individuals by tree-trunk dispersal connecting the ground and canopy collembolan assemblages. Third, he demonstrated that the principles of island biogeography could be applied to the 'islands' represented by individual fern rosettes in the canopy with species richness being determined in large part by the size of the fern 'basket' and its height from the ground—the 'mainland'.

Our parallel focus on the Diptera examined samples collected by canopy knockdown, Malaise traps and water-filled yellow pans. We focussed on the collections from four sites along the east coast of Australia (Lamington, the Conondale Range, Eungella and Cape Tribulation as well as our New Guinea plots. A total of 28,647 Diptera were sorted to family-level and the results subject to a variety of multivariate statistical analyses (Kitching et al. 2004). Essentially these showed that the lowland tropical sites in Australia had affinities, at the family pattern level, with the New Guinean sites. The subtropical sites (Lamington and the Conondale Ranges) similarly clustered together in n-space. The Eungella sites clustered only with themselves underlining previous hypotheses that this large, isolated block of forest had unique features. In later work this led us to pay much more attention to this region (see below).

Biodiversity surveys of this kind record the diversity of particular sites. Comparing results across sites demands the erection of hypotheses explaining why particular assemblages of taxa occur in particular places and what generates site to site contrasts and similarities. Such sets of hypotheses can be combined to generate a 'templet' (sensu Southwood 1977) which then stands as a general explanatory model for diversity generation and maintenance. We attempted to construct such a templet in Kitching et al. (1997) (Table 1). We identified and ordered spatial processes and observed patterns from the continental to the local, temporal processes

Fig. 2 Butterfly and hawkmoth richness in Australian tropical and subtropical rainforests. **a** Papilionidae, **b** Hesperidae, **c** Pieridae, **d** Nymphalidae, **e** Lycaenidae, **f** Sphingidae. **a–e** were collated from distribution maps in Orr and Kitching (2010), **f** from the maps in Moulds et al. (2020)



from the tectonic to very recent impacts such as cyclones, clearing and forestry. This conceptual model remains a useful scaffold for explaining biodiversity patterns although it predated current acute concerns about anthropogenic climate change (see below and Steffen et al. 2002).

A focus on the Lepidoptera

The butterflies (Papilionidae) and selected families of larger moths are sufficiently well known that distribution and habitat analyses can be carried out using available distribution maps (Fig. 2). If a much greater component of the lepidopteran fauna is the target then mass sampling using light traps is the approach of choice. ‘As discussed, part of our one-hectare survey protocols was the use of light traps to sample night-flying insects, principally moths. Lepidoptera are not sampled well by canopy knockdown or any other techniques in which the catches end as mixed and

preserved in liquid (although molecular methods based on metabarcoding may eliminate this shortcoming—see Ji et al. 2013). Traditionally adult Lepidoptera are pinned, set (‘spread’ in North American parlance) and preserved as dry mounted specimens. This is what we did with all of our light trap samples focussing on all individuals with a forewing length of 1 cm or more (plus a few targeted ‘micro-‘families). Among the Australian fauna the Lepidoptera have the advantage of being relatively well known compared with most other insect Orders, although there remain large numbers of species awaiting description. Further, the entire known Australian fauna, held in the National Collection, has been CO1 bar-coded and is accessible through the BOLD website (Hebert et al. 2013). For those carrying out biodiversity surveys this means that assessments and comparisons can be done at the species-level—initially as so-called morphospecies, subsequently, if necessary and where possible, as named taxa.

Experience with the moths processed from the one-hectare plots discussed above led to a whole research programme in which moth surveys have been used to examine dimensions of spatial change in assemblage structure. The work of relevance here was carried out in the three major blocks of Australian rainforest—the Border Ranges of south-east Queensland (and north-eastern NSW), the Eungella area of central Queensland and the fully-tropical Wet Tropics in the far north, with parallel projects elsewhere in the world. This work is on-going.

Remnant quality and moth diversity

The first of these independent moth studies was an examination of the way in which the age and condition of rainforest fragments on basaltic soils affect the moth assemblages occurring within them (Kitching et al. 2000a, b; Orr and Kitching 1999, 2003). Our focus for this study were the remnant rainforests of the Atherton Tablelands in the Wet Tropics (indicated as ‘F’ in Fig. 1). Three levels of disturbance were identified: uncleared remnants of previously extensive rainforest, remnants of regrowth following clearing 40 to 60 years earlier, and newly cleared ‘scramblerlands’. This last category described recently cleared land, vegetated by invasive creepers and herbaceous plants. Highly characteristic assemblages of moths were encountered in each forest type with small sets of families or sub-families typifying each remnant type. At the crudest level some very simple ratios using the most abundant of families could be used to classify remnants in a post hoc fashion. The key article (Kitching et al. 2000a, b) informed a subsequent global literature on the use of moths (or subsets of them) as indicators of ecological changes. Unpublished parallel work on moth assemblages in rainforests at similar altitude but on metamorphic substrates yielded quite different but comparably rich moth assemblages.

Elevational transects

Altitudinal transects have always been attractive to ecologists interested in species turnover and high elevation adaptations and endemism. The tropical rainforests of Australia provide particular opportunities in this regard as, in places, forest stretches, uninterrupted, from sea level to as much as 1500 m asl. Geoff Monteith of the Queensland Museum led early expeditions explicitly to sample the invertebrates of two such transects in the Australian Wet Tropics (Monteith 1985; Monteith and Davies 1991; Yeates and Monteith 2009). Extensive and long-term work by Steve Williams and his group at James Cook University focussed principally on vertebrates although more recently has considered selected groups of insects as well (Wilson et al. 2007, Staunton et al. 2016). Two other transects were established by Wardhaugh

et al. (2018) in the Queensland Wet Tropics (at Paluma at ca 19° S, and on the Atherton Tablelands at ca 17.5° S) and used these to examine diversity and phenology of Coleoptera using ground-based interception traps.

In 2003 Dr Yves Basset instigated and led the IBISCA-Panama project (Investigating Biodiversity of Soil and Canopy Arthropods) (Basset et al. 2007). That project examined the arthropods in an area of undisturbed lowland tropical forest in Panama with particular reference to the diversity in the canopy compared with ground level. The project brought together a team of researchers from around the globe each of whom focussed on a particular higher taxon and/or methodology within the larger protocol designed by Basset. The ‘IBISCA approach’ has been used as a model for several subsequent projects including the IBISCA-Queensland Project led by Kitching in 2003–2004 (Kitching et al. 2011). That project examined how arthropod and plant diversity changed over a 1000 m elevational transect in subtropical rainforest within Lamington National Park in south-east Queensland driven by the question of how animal biodiversity changes over adjacent (elevation-driven) climates in the hope that particularly sensitive taxa could be identified for subsequent monitoring as global change occurs. Over 40 scientists from 17 countries participated. As part of that project a team examined moth diversity over five different elevations and two seasons. That team subsequently replicated the moth study in a second subtropical transect in northern New South Wales, in the Eungella NP in central, tropical Queensland and at Mt Lewis in the Wet Tropics of far north Queensland (all sites labelled ‘E’ in Fig. 1). The Australian results have been comprehensively analysed and presented in a series of papers (Ashton et al. 2011, 2015, 2016a, b, 2020; Odell et al. 2016; Kitching et al. 2013, 2020a, b). Comparable transects were also established in south-western China (Ashton et al. 2016a, b) and the French Pyrénées (Dale et al. 2019). In summary all of these transects showed clear elevation to elevation turnover with characteristic sets of indicator species driving turnover. Generally these changes occurred in a clear stepwise fashion. At Eungella the elevation-specific assemblages clustered into upland and lowland faunas. In all cases a unique set of higher elevation species was identified which we deemed to be of highest conservation risk under a warming climate. This last result was especially notable in the subtropical transects where the uppermost elevations comprise relictual *Nothofagus*-dominated ‘cool temperate’ rainforest which we showed contained distinctive invertebrate assemblages over a range of insect taxa (Kitching et al. 2013).

Taxonomically-informed follow-ups

The altitudinally and latitudinally organised studies of moths at these Australian sites each generated permanent

reference collections. This presents the opportunity for a more leisurely and in-depth look at particular taxa based on species-level identifications. This work is open-ended and on-going. Currently attention is focussed on the large superfamily, the Pyraloidea. Eungella-focussed results have already been published (Kitching et al. 2020a, b) showing that, for one large clade of these ubiquitous moths the unique rainforests of the Eungella massif represents the southern limits of species known from moister, more tropical locations to the North. A smaller but not insignificant group of essentially subtropical species reach their northern limits in the Eungella forests. These analyses continue and underline the advantage of a long sequence of collections across a substantial portion of the Australian continent using identical methodologies.

Turnover, specialization and endemism: how unique are rainforests?

In studying any biodiversity ‘hotspot’ there is an a priori expectation that the biota will exhibit high levels of species richness, have spatially unique features and show high levels of endemism. So is this true of the tropical and subtropical arthropods? The answer must remain ‘probably’ and ‘as far as we know’. A vast knowledge gap remains.

Our studies bear out the first of these expectations in general. The arthropod fauna of these forests is indeed very rich. This richness, however, needs to be interpreted in the broader context of the Australian fauna as a whole and needs continent-wide analyses which seldom exist.

Our studies were often made at supra-species levels and, where species level analyses were carried out these were on a subset of the arthropod fauna and a subset of our sampling sites only. Among our results perhaps the most striking answers emerged from studies of the Arachnida. In our first analyses of canopy faunas it was also noteworthy that across latitudes ordinal profiles differed significantly. For example, more southerly canopies were dominated numerically by mites, fully tropical ones by spiders (Kitching et al. 2003).

Subsequently, Walter et al. (1998) examined the parasitiform mites from 18 samples collected by canopy fogging in the subtropical rainforest of Lamington National Park, Queensland. These were compared with samples collected from a variety of other ground and canopy habitats *in the same patch of subtropical forest*. A total of 185 species were distinguished, 80% of which were new to science. There were very high levels of complementarity suggesting that habitat to habitat turnover was very high. Indeed, using standard extrapolation methods these authors estimated that more than 2000 species of Acari occupied this particular forest and concluded that on the basis of these results the term hyperdiverse could

be applied confidently to the Australian rainforest mites. In other unpublished results from but nine of the same canopy-knockdown samples 49 species of spider were identified, 48 of which were, at the time, undescribed (R. Raven, Queensland Museum, *pers. comm.*).

Other taxa also show very high levels of species richness in Australian rainforests both from our studies and those of others (see, e.g., Hancock 2013, on Tephritidae; Reid 2016, on Chrysomelidae; Nowrouzi et al. 2016, on ants) although each major taxon exhibits unique biogeographic patterns reflecting the history and radiation of particular subtaxa. It must be stressed however that few other whole assemblage studies have been carried out and, even from our limited samples, many taxa were sorted only to Order or Family. As already noted our studies of Dipteran families showed clear south to north patterns with the lowland, northern assemblages having New Guinean affinities. Substantially similar patterns are evident at the family level in our samples of Coleoptera from light trapping surveys (R. L. Kitching, unpublished results).

Contrasting rainforest faunas with those of the surrounding sclerophyllous ecosystems is fraught with difficulty. First, there have been few studies of the canopy fauna of eucalypts (but, see Majer et al. 2000, Recher et al. 1996) and where these do exist they have not been adjacent to rainforests. Undoubtedly many major faunal radiations in Australian forests have little connection to rainforests. Notable examples include the Oecophorinae, a vast group of micromoths that have co-evolved with the drier Myrtaceae-dominated flora of Australia (see Common 1994). Other notable examples are found among the acridid Orthoptera (Rentz et al. 2003) and cicadas (Marshall et al. 2016). Comparative analyses across rainforest/sclerophyll boundaries using comparable survey methodologies would repay attention. These would be especially pertinent to the Forests of East Australia hotspot given it is defined by both classes of ecosystems.

It is also noteworthy that some taxa, abundant and diverse in rainforests to the north are poorly represented in such forests in Australia. A relatively small proportion of the odonate fauna, for example, occurs regularly in rainforest and only a few species are confined to rainforest, in stark contrast with New Guinea and Southeast Asia (Orr 2006). Australian rainforests contain lower termite diversity than those in Asia, Africa and South America (Jones et al. 2010) with declining diversity along a precipitation gradient from arid ecosystems to rainforest (Clement et al. 2021). Australia lacks major termite groups that dominate other biogeographical realms – the fungus and soil feeding termites. This has been linked to the biogeographical isolation of Australia and nutrient poor Australian soils (Jones et al. 2010).

Conservation issues

There is little doubt that the eastern Australian rainforests are justifiably included within a global hotspot of diversity—both in the original sense of Myers (1988)—who did not include them in his original ten designations—and in the later designation of 35 (later 36) sites by Conservation International (see, e.g., Habel et al. 2019 for a list and discussion of current status of 33 of these sites). This faunal richness was noted in the original analysis of Williams et al. (2011) based on the vertebrate fauna only. We can now confidently add the terrestrial invertebrates of Australia's eastern rainforests to this justification. For many taxa it seems likely that they contribute disproportionately to arthropod diversity within the overall forest biome. Where there is adequate taxonomic information high levels of endemism occur, including many narrow range species. These are biogeographically unique locations although the northernmost lowland forests do display strong biogeographic connections with the New Guinea fauna.

A second original criterion for hotspot status for the regions concerned is that they or the biota they contain are under threat. The loss of rainforest cover in the modern era seems an obvious reason to perceive Australia's rainforests as being under threat yet their largely conserved status (in the National Park system and World Heritage Areas) may mitigate this threat. It is in this context that we discuss the conservation of rainforest invertebrates. Consider first individual species and, then, whole assemblages.

Invertebrates as pseudo-vertebrates

Most conservation theory and practise has been built, nationally and internationally, at the species level. With few exceptions the criteria, standards and bureaucracy that has built up around these actions (or promises of action) have been targeted at vertebrates and higher plants. Transferring these standards to the invertebrates has been done and is continuing but, in most cases, presents significant issues.

As with most invertebrates threats to the well-being and continued health of populations of rainforest arthropods are seldom if ever species-specific. It is threats to the existence and integrity of the ecosystem itself which represent dangers to the insects that are associated with the forest type. Indeed, the IPBES (2012) report identifies a decline in ecosystem services, many of which are driven by invertebrate

assemblages, as a critical problem globally. Accordingly it is debatable whether the philosophy and bureaucratic infrastructures that has grown up around 'endangered species' should be applied to the conservation of insects in general.

Of course for well-known and ecologically well understood groups like the butterflies, a few moth and beetle families, cicadas and odonates, the species-specific ideas of vulnerability do more or less fit. Even then, setting numerical thresholds for categories of endangerment may be nonsensical. A remnant population of 2000 butterflies may represent more likelihood of local extinction than a herd of 20 black rhinoceros. Nevertheless, there is no doubt we should continue to use these approaches, making selected insects 'honorary vertebrates' if for no other reason that it keeps public and political attention on them and, more important, the places they live. It is also the case that species-level assessments for invertebrates will become more powerful as our knowledge of their distributions improves. The automated data-bases now growing in popularity through platforms such as GBIF and iNaturalist facilitate this approach but are long-term solutions to conservation problems which are often urgent and time-limited. Such platforms also rely on the availability of a body of taxonomic and ecological service providers which is limited, even diminishing, as demand for such services continues to expand (Wilson 2017).

For a very few insect species, specific vertebrate-style conservation interventions work and are valuable both scientifically and politically. Recent work in Australia has identified 26 species of butterfly which are of conservation concern (Geyle et al. 2021). Of those 26 only one is a rainforest insect. One other rainforest species, the Richmond Birdwing, however, has previously been classified as vulnerable and has been the subject of one of the most successful recovery efforts certainly in Australia, and which stands as a model for such efforts globally (Box 1).

Examples such as the Richmond Birdwing remain extremely important as flagship species for the entire national and global conservation effort. Any conservation effort is an active interaction between nature and humanity at large. Without popular support no conservation effort will work. Charismatic species such as the birdwing butterflies, vertebrates like koalas or giant pandas, and plants like Wollemi pines or California redwoods create dramatic stories as examples of nature that can and must be conserved. The more abstract concept of conservation of rainforest invertebrate assemblages and the associated ecosystem services that they represent then builds on public and political sympathy generated by the aforementioned species-specific stories.

Box 1 Illustration. A male Richmond Birdwing**Box 1 The Richmond Birdwing**
Ornithoptera richmondia

The Richmond Birdwing, *Ornithoptera richmondia* is the smallest of the three Australian species of birdwings. At the time of European incursion it had a distribution in subtropical rainforests from Maryborough, Queensland (25.5° S) to Grafton, New South Wales (29.7° S). This spanned the area which became the greater Brisbane conurbation. Gallery rainforests along creeks originally provided habitat and connectivity. Its food-plants are two species of the *Pararistolochia* vines: *praevensa* in the lowlands and *laheyana* in the uplands. By the late twentieth century the distribution of the species had been reduced through development and habitat destruction to two clusters of rainforest remnants, one north of the city and one to the south. Inbreeding depression was beginning to occur. Further threats included exotic weeds including toxic food-plant relatives, and inappropriate fire-regimes. The species was declared as ‘vulnerable’ in Queensland in the 1990s and



given protected status. A major recovery effort began following drafting of a recovery plan in 1996. This was subsequently enacted with State and private funding. The following actions were critical to the programme’s success.

Biological Understanding Simply knowing the species is vulnerable was not enough. Details of its behaviour, genetics, food-plant relations and seasonality were an essential first step in the conservation programme.

Community Engagement The Richmond Birdwing relies on scattered patch of food-plant often in tiny remnants of rainforest on private land. So engaging with the community from the beginning was essential. The spectacular appearance of the species helped in this respect.

Captive Breeding A captive breeding programme was established founded on collections of live material from both extremes of the species’ remaining range. Releases were made in areas where inbreeding had been detected.

Food-plant Propagation & Planting A nursery propagating many thousands of food-plants was established. Planting programmes engaged schools, tourist facilities and households to re-establish connectivity.

Long-term commitment The programme is on-going.

This account is based on Sands and New (2013) *Conservation of the Richmond Birdwing Butterfly in Australia*, Springer, Dordrecht. Opinions and errors of interpretation rest with the current authors.

Conservation at the assemblage level

As we have noted effective conservation of entire forest assemblages of insects depends on the health of the forests they occupy. For all but small remnants of Australian rainforests this has been achieved through their declaration as National Parks. The first such Parks in Queensland were declared to preserve patches of rainforest in the Mt Tamborine area in 1908. Shortly afterwards, in 1915, the vast Lamington NP was gazetted (McDonald 2010). The Eungella rainforests are now wholly conserved within the National Park estate. This has been a stepwise process which began in 1936 (Ogilvie 2006). The Wet Tropics region of far north Queensland now contains a network of rainforest parks. The history of conservation in this region is complex and was, in its day, highly contentious. Most parks in the region have been established only since the 1970s and

‘80 s. Many of these areas had previous status as State Forests which gave them a semi-protected status while allowing exploitation for timber and other forest products. In the 1980s they were the focus of major disputes between the Australian federal and Queensland state governments which were finally resolved by the declaration of the Wet Tropics as a World Heritage area in 1988, immediately after the defeat of the anti-conservation Bjelke-Petersen Government in December 1987.

So the northern tropical forests gained a doubly protected status as both National Parks and parts of a World Heritage area. The subtropical parks close to the Queensland/New South Wales border also enjoy World Heritage status as the northernmost parts of the Gondwana Rainforests of Australia WHA (originally the Central Eastern Rainforest Reserves of Australia). Lamington and the Queensland subtropical parks joined this World Heritage area upon its renomination

and listing in 1994. (Cavanaugh et al. 2010). They had been excluded from the original 1986 listing because of the objections and refusal to cooperate of the same state government which opposed the Wet Tropics nomination.

Eungella National Park does not have World Heritage status.

The preservation of these subtropical and tropical rainforests within National Parks and World Heritage areas protects them from many of the threats that reduced the larger rainforest estate in former times. Proximal threats remain—weed invasions, feral predators, human overuse, cyclones, inappropriate fire regimes—but these are anticipated by Park Management Plans and are, at least in principle, under control. The entire National Park estate and the underlying philosophy of preserving pristine and characteristic examples of vegetation types has been designed and assembled under an assumption of climatic stability. Such an assumption is, of course, no longer valid.

Global warming is now an established reality (Reisinger et al. 2014). Australia's east coast will gradually warm to the end of the twenty-first century with greater increases further from the coast. The subtropical regions currently show a drying trend but the future trajectory of rainfall is uncertain. Extreme events, such as cyclones, are likely to get more severe. Sea levels are predicted to continue to rise over the next several centuries. Perhaps most important from a rainforest viewpoint, the number of severe 'fire days' each year will continue to increase.

So what might this mean for the subtropical and tropical rainforests? The entire biota will experience higher environmental temperatures placing many at risk of heat stress. This could well be more severe in the Tropics where animals and plants live closer to their thermal limits than further south. Higher elevation areas will be under greatest pressure especially those that depend upon occult precipitation for their dry season survival (Narsey et al. 2020). The high elevation assemblages at all latitudes will be at greatest risk in this regard having limited ability to shift upwards as microclimates change. Increased risk of wild fires, though, are undoubtedly the greatest immediate risk to fire-averse ecosystems such as rainforests. Already hot and damaging fires in adjacent sclerophyll forests have spread into rainforests. The Eungella region for example lost over 11,000 ha of rainforest to fire in 2018 (Hynes et al. 2020). In a similar fashion areas of remnant subtropical rainforest in New South Wales were lost to fire in 2019 (Kooyman et al. 2020). These areas are very unlikely to return as rainforest in the post-fire period. The sometimes tiny remnants of Gondwanic rainforest in the south are particularly vulnerable. In addition the predicted increased severity (but not frequency) of cyclones will inevitably create a greater fuel load and enhance the risk of more severe fires. Parenthetically this also facilitates invasion by exotic weeds and feral predators.

Elsewhere in Australia inappropriate fire regimes have been fingered as having substantial impacts on particular species of butterflies (see, for example, Sands and New 2013; Geyle et al. 2021). In drier ecosystems fire regimes and management run the risk of destroying most patches of the restricted habitats of rare and endangered species. The risk for the rainforest biota as a whole is commensurately greater with the entire ecosystem being at risk: a true 'tipping point' in climate change parlance.

Anthropogenic fire regimes are also implicated in areas which buck the continental trend and show significant expansion in the rainforest estate. Wet sclerophyll forests are defined as having a eucalypt overstorey and an understorey of 'wet' grassy, fern and rainforest elements. Perhaps ironically, lowered fire frequencies in the Wet Tropics (from where, hereto, few fire-driven losses of rainforest have been reported) are likely drivers of rainforest expansion into these adjacent areas of wet sclerophyll forest threatening the unique biotas of those eucalypt-dominated ecosystems (Harrington and Sanderson 1994). In an unpublished study of moths in the subtropics these wet sclerophyll forests showed a higher diversity than co-occurring patches of rainforest possibly reflecting the fact that wet sclerophyll samples contain both rainforest and sclerophyll associated species. The transition from rainforest to adjacent wet sclerophyll will reward further entomological study.

Rainforest expansion is also occurring in the monsoonal Northern Territory of Australia driven by a combination of increasing temperatures and atmospheric carbon dioxide mediated by changing fire regimes (Banfai and Bowman 2006).

In spite of these rare exceptions (which may themselves threaten the ecosystems adjacent to them), we conclude there is no room for complacency with respect to the futures of Australia's rainforests even when they are located, as most are, in designated National Parks. Global warming and associated climate change will increase the risk of fire, impose heat stress especially on climate-sensitive species, and lead to shrinkage of the high elevation assemblages and their associated vegetation. Australia's rainforest estate, as discussed at the outset, is a series of islands in drier pyrogenic ecosystems. This enhances speciation and species diversity through isolation but also increases the vulnerability of these patches under a regime of global climate change. Some species will have some adaptive capacity by shifting their ranges upwards but for the many mountaintop endemics this is not an option. Extensive latitudinal shifts are unlikely given the major dry gaps between the various rainforest regions.

Acknowledgements Our work on the arthropod faunas of Australia's rainforests has been funded by many different organisations. Detailed acknowledgements of these are to be found in individual data-based papers. We acknowledge and thank major donors without whom the overarching approach would have been impossible: the Australian

Research Council, the Rainforest Cooperative Research Centre, Earthwatch (Australia), the Queensland Government, the Wet Tropics Management Authority, the Mackay Regional Council, the Queensland Museum, the Chinese Academy of Sciences and Griffith University have all been major contributors to one or more projects over the years. Again individual advisees and contributors are acknowledged elsewhere. We are however particularly grateful to Dr Dan Bickel, Dr Chris Burwell, Mr Ted Edwards, Dr Penny Greenslade, Dr Melinda Laidlaw, Dr Meg Lowman, Dr Bill Macdonald, Dr Sue McIntyre, Dr Heather Proctor, Dr Chris Reid, Emeritus Professor Nigel Stork, Prof Christophe Thébaud, Mr G. Theischinger, Dr Dave Walter and Prof Doug Yu for key inputs and advice across the years. A legion of doctoral and other research students worked within the projects described. Those not mentioned elsewhere include Drs Francois Beaulieu, Darren Bito, Francesca Dem, Peter Grimbacher, Casey Hall, Florian Menzel, Geoff Morse, Denis Rodgers, Tang Yong and Jacinta Zalucki. Able and essential research assistance on one or more projects has been provided by Heather Mitchell, Genevieve Carruthers, Elizabeth Baker, Karen Hurley, Sarah Boulter, Guy Vickerman, David Putland and many, many student and community volunteers. We thank them all. We are grateful to Emeritus Professor Tim New, Dr Jorge L. León-Cortés and Dr Christine Haaland for the invitation to contribute to this Special Issue. We thank, also Professors New and Stork for reading and commenting on earlier drafts.

Author contributions RLK conceived and drafted the paper. LA, SM, AN, EO and AO provided editorial input. All authors were involved in data collection and analysis in the projects that are reviewed. RLK and LA revised the article following revision and input from other authors.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Declarations

Conflict of interest None of the authors have any conflicts of interest with respect to the publication of this article.

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