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Biogeographic influences on the evolution and historical dispersal of the Australo-Pacific Dacini fruit flies (Tephritidae: Dacinae)

Melissa L. Starkie[1] ![ORCID] | Stephen L. Cameron[2] | Matt N. Krosch[3] | Andrew D. Sweet[4] | Anthony R. Clarke[5]

[1]Biosecurity Queensland, Department of Agriculture and Fisheries, Brisbane, Queensland, Australia

[2]Department of Entomology, Purdue University, West Lafayette, Indiana, USA

[3]Forensic Services Group, Queensland Police Service, Brisbane, Queensland, Australia

[4]Department of Biological Sciences, Arkansas State University, Jonesboro, Arkansas, USA

[5]School of Biology and Environmental Science, Queensland University of Technology, Brisbane, Queensland, Australia

Correspondence
Melissa L. Starkie, Biosecurity Queensland, Department of Agriculture and Fisheries, Brisbane, QLD, Australia.
Email: melissa.starkie@daf.qld.gov.au

Abstract

Fruit flies (Tephritidae: Dacini) are a frugivorous insect group that exhibit high endemic diversity in the rainforests of Australia and the western Pacific. In this region, biogeography has been influenced by tectonic plate movements and cycles of isolation and re-connection of landmasses and rainforest habitats during glacial periods. However, how such factors have influenced the speciation and historical dispersal of the regional Dacini is largely unknown. To address this, we use a dated phylogeny to reconstruct the biogeographical history of the tribe. We found the Dacini radiated eastward into the Pacific islands largely from sources in New Guinea. We also found evidence for historical dispersal from both Australia and New Guinea into New Caledonia, a pathway unique to this island compared with neighbouring islands. There was also evidence for multiple, bidirectional dispersal events between Papua New Guinea and Australia, likely facilitated by the cyclically exposed Torres Strait land bridge. Cape York in far northern Australia was likely the only entry point for species dispersing into Australia; there was no evidence for entry of flies into Australia directly from West Papua or Wallacea. Several lineages radiated after entering Australia, such as members of the *Bactrocera dorsalis* species group. Within Australia, speciation was not associated with the biogeographic barriers known to have impacted other rainforest fauna in eastern Australia. Overall, we demonstrate that isolation between islands and large landmasses is important in the evolution of the Australo-Pacific Dacini, but the reason for their extensive radiation within Australia and Papua New Guinea remains unclear.

KEYWORDS
ancestral range reconstruction, *Bactrocera*, BioGeoBEARS, *Dacus*, *Zeugodacus*

1 | INTRODUCTION

The tribe Dacini (Diptera: Tephritidae) is a diverse and relatively widespread clade of frugivorous flies, consisting of over 900 recognised species in four genera: *Bactrocera* Macquart, *Dacus* Fabricius, *Zeugodacus* Hendel and *Monacrostichus* Bezzi (Doorenweerd et al., 2018). The tribe is distributed throughout the Mediterranean, Afrotropical, Asia-Pacific regions (Doorenweerd et al., 2018). *Zeugodacus* and *Monacrostichus* are present only in the Asia-Pacific, whereas *Dacus* is most diverse in Africa, while *Bactrocera* is spread throughout the entire range (Doorenweerd et al., 2018; Drew & Hancock, 1999). In the Asia-Pacific region, the Dacini are largely restricted to breeding in the fruit of native rainforest host species, except for ~10% of the dacines that are pestiferous and attack cultivated crops (Doorenweerd et al., 2018; Drew & Romig, 2013; Hancock et al., 2000). Given the Dacini is one of the most speciose tribes within the Insecta (White & Elson-Harris, 1992), understanding the reasons for its extensive radiation may offer general insights into the hyper-diversity of tropical herbivore systems (Novotny et al., 2006).

Drew (2004) suggested that dacines, while older than the tropical and subtropical rainforest species they utilise as their hosts, extensively radiated alongside these plants during the Tertiary Period (~66 mya). Within *Bactrocera*, rapid radiations are suspected to have been highly influenced by the expansion of the rainforests of south-east Asia (Drew & Romig, 2013) and New Guinea (Drew, 2004). Host plant choice was identified to be closely associated with monophyletic clades in the African *Dacus*, which are tightly associated with Cucurbitaceae (melons) and Asclepiadoideae (milkweeds) (Virgilio et al., 2009). However, countering this close association between plants and Dacini species is the fact that many *Bactrocera* are not host-specific (Drew, 2004; Novotny et al., 2005) and that recent radiations of *Bactrocera* have tended to involve polyphagous species (Starkie, Cameron, et al., 2022). This suggests that vicariance and allopatric evolution caused by biogeographic barriers may have been relatively more important for speciation in *Bactrocera* than host-driven factors.

The biogeographic history of south-east Asia and the Pacific is complex but offers clues to the dispersal of fauna in the region. This region is situated at the juncture of multiple geological plates: the Pacific, Australian, Indian, Philippine and Eurasian; the precise history of which are still debated in the literature (Turner et al., 2001). One of the more important events in the region was the collision of the Australian plate with the Asian plate in the Late Oligocene (23–33 mya) (Axelrod & Raven, 1982). This collision caused the uplift of

New Guinea and scattered islands, such as Fiji, to form during the Eocene (47–56 mya), which are now present on the outer arc of the plates (Axelrod & Raven, 1982; Karig, 1974). Other island groups, such as the Solomon Islands and New Hebrides, are later archipelago formations, suspected to span the Eocene-Pleistocene (2–23 mya) (Carney & MacFarlane, 1982; Coleman & Packham, 1976). Factors such as volcanic activity, plate collisions, sea-floor spreading and sea-level fluctuations have resulted in rapid changes in topography (Hall, 2001) and influenced the evolution of flora and fauna in the region. Of particular note is New Caledonia, the only landmass on earth that contains the two main clades of flowering plants (Heads, 2019), but for which it has a unique and highly debated geological history in the region (Grandcolas, 2017; Heads, 2023). Furthermore, Hall (2001) argues that there is no easy explanation as to how Australian and Asian taxa have 'mixed' in this region. Because taxa of different origins overlap (or do not overlap), this has prompted the proposal of numerous biogeographic "lines" or barriers by various authors (Hall, 2001; van Welzen et al., 2011).

The influence of biogeographic barriers on the Dacini at the population and genus-levels has been widely discussed. Based on modern distribution patterns of the Dacini, Hancock and Drew (2015) recognised six biogeographic regions with high degrees of *Bactrocera* species endemism in South-east Asia and the Pacific (Indian subcontinent, South-east Asia, Wallacea, New Guinea, Australia, and South Pacific) and concluded speciation within the genus to be a result of geographic separation. At the species level, *Bactrocera umbrosa* Fabricius was found to be native to the West Pacific but had colonised west of Wallace's Line via a pre-historic incursion event (Krosch et al., 2019). In that study, the major split (both genetically and morphologically) between Asian and Pacific *B. umbrosa* populations was associated with Lydekker's Line (Krosch et al., 2019). In contrast, the Isthmus of Kra, a known biogeographic barrier located on the Thai/Malay peninsula, was found to have minimal impact on population structuring of within what is now recognised as *Bactrocera dorsalis* (Hendel) (formerly *Bactrocera papayae* Drew and Hancock) (Krosch et al., 2013) or within *Zeugodacus cucurbitae* (Coquillet) (Boontop et al., 2017). Despite this, differentiation in climate, vegetation, and terrain along the Thai peninsula was found to significantly influence population structuring of *Z. cucurbitae* (Boontop et al., 2017), suggesting that regional-scale factors may impact on recent structuring within Dacini species.

To better understand the potential impact of biogeographic barriers on Dacini diversification, we carried out the first detailed study of the western Pacific Dacini fauna. New Guinea is considered to be one centre of Dacini

diversity (Drew, 2004; Drew & Hancock, 1999), with the greatest species diversity occurring in West Papua and Papua New Guinea (411 known species) (Drew, 2004; Drew & Romig, 2022), with particularly high levels of endemism recorded in the Morobe and Central provinces (Clarke et al., 2004; Novotny et al., 2005). Australia has its own large endemic Dacini fauna of 113 species, with the highest species diversity in the tropical far-northern rainforests, decreasing further southward (Hancock et al., 2000; Huxham & Hancock, 2002; Huxham et al., 2006; Royer & Hancock, 2012). The Dacini fauna of the other Western Pacific islands is smaller, with diversity declining from west to east, but high levels of island endemicity (Drew, 2004).

Regional morphological cladistic analysis found the Australian Dacini to form close relationships with those from the Solomon Islands, Bismarck Archipelago and mainland New Guinea (the northern limit of the Australian craton) (Michaux & White, 1999). Based on species distribution data, Clarke et al. (2004) demonstrated high levels of endemism in the island provinces of Papua New Guinea (e.g., Bougainville, New Britain), but minimal biogeographic structuring of species distributions throughout mainland Papua. Molecular dating studies, such as Krosch et al. (2012), corroborated the out-of-India hypothesis (proposed by Drew and Hancock (1999)), for the origin of the dacines' ancestors, and in contrast to Drew and Hancock (1999), proposed more refined timelines and dispersal pathways into Asia. Similarly, Zhang et al. (2022) also investigated the biogeography of the Dacinae at a larger scale, and achieved similar divergence time estimates as Starkie, Cameron, et al. (2022), but did not widely sample the Australian fauna. At present, no biogeographic studies have investigated pathways into Australia and the Pacific, or the effects biogeographic barriers have had on historical dispersal. There is a priori reason to predict that biogeographic barriers may have influenced Dacini distribution and speciation given the otherwise largely contiguous east coast Australian rainforests are interrupted several times by dry lowland forests, which create biogeographical barriers to dispersal for many taxa (Bell et al., 2007; Bryant & Fuller, 2014; Bryant & Krosch, 2016; Kershaw, 1994; Nicholls & Austin, 2005; Williams & Pearson, 1997). These isolated rainforest regions are centres of endemism that have remained stable and highly diverse for at least the past 120,000 years (Weber et al., 2014). Given that the Dacini are intimately associated with rainforests and are not found in seasonally dry savannah regions (such as the Carpentaria Basin that separates northern NT and Queensland [Hancock et al., 2000]), the rainforest regions between the drier-zone barriers may have played an important role in diversification of the endemic Australian Dacini.

The aim of this research was to investigate how biogeographic barriers and historical movement have influenced the current diversity and distribution of species using a time-scaled molecular phylogeny. The focus was primarily on movement and dispersal in the Australo-Pacific region, rather than inferring ancestral ranges. Crucially, the phylogeny included approximately 80% of the Australian Dacini species, strong representation from Papua New Guinea and Melanesia faunas, and a small number of Polynesian taxa. Specific questions tested were as follows: (i) was the movement of the Dacini into the Pacific from New Guinea only, or were smaller landmasses colonised from both New Guinea and Australia? (ii) was movement of the Dacini into Australia predominantly via the land bridge between New Guinea and northern Queensland? (iii) was movement between landmasses unidirectional or bidirectional? and (iv) can sister-clades or species-pairs of endemic Australian species be associated with rainforest segments isolated by known biogeographic barriers?

2 | MATERIALS AND METHODS

2.1 | Data preparation

We conducted two main analyses that focussed on the influence of biogeography on fruit flies in (i) the Pacific region and (ii) Australia. We used modified dated tree topologies prepared from the tree produced in Starkie, Cameron, et al. (2022). Specifically, we used R v4.3.0 in RStudio v2022.12.0.353 (R Core Team, 2003; RStudio Team, 2019) to run the 'drop.tip' function in the package ape (Paradis & Schliep, 2019) to trim outgroups, undescribed species and multiples, and *Bactrocera oleae* (Rossi) (European native distribution), retaining a total of 142 species for the Pacific analysis. For the Australian analysis, we also removed species restricted to the Pacific Islands of Melanesia, Polynesia and New Caledonia, retaining 121 species.

The native distribution range was scored for each taxon, with known human introductions and recent range expansions removed from the dataset as per Royer et al. (2016) and Krosch et al. (2019). Range data were collated from Smith et al. (1988), Drew (1989), Osborne et al. (1997), Drew and Hancock (1999), Raganath and Veenakumari (1999), White and Evenhuis (1999), Hancock et al. (2000), Huxham and Hancock (2002), Hollingsworth et al. (2003), Drew et al. (2011), Leblanc et al. (2012), Royer and Hancock (2012), Drew and Romig (2013), Leblanc et al. (2014), Royer (2015), Hancock and Drew (2017), Linda et al. (2018), Royer et al. (2018) and Starkie, Strutt, et al. (2022).

For the Pacific focussed analysis, areas were grouped into six ranges: north and west of Wallacea; Australia;
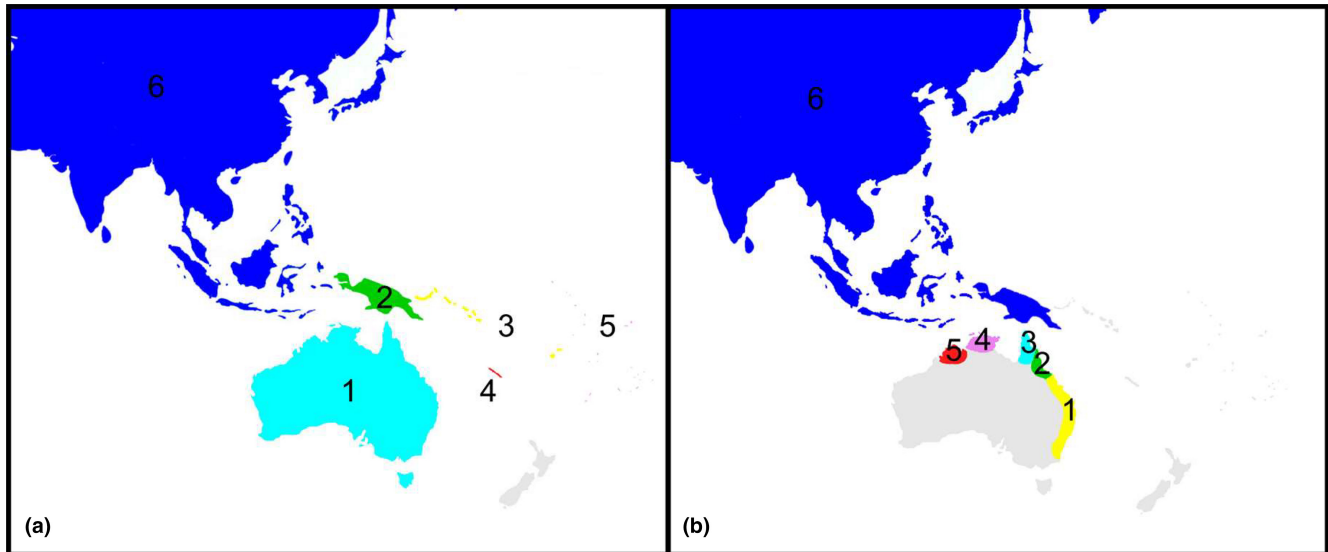
FIGURE 1 Biogeographic regions scored in two analyses in this study. A: 1. Australia; 2. Papua New Guinea mainland; 3. Melanesia (including Bismarck Archipelago); 4. New Caledonia; 5. Polynesia; and 6. north and west of Wallacea. B: 1. Eastern Queensland and New South Wales; 2. Atherton Plateau; 3. Cape York; 4. Kimberley Plateau; 5. Arnhem Land; and 6. outside Australia.

Papua New Guinea; Melanesia; New Caledonia; and Polynesia (Figure 1a). To aid in hypothesis testing, New Caledonia and Papua New Guinea were included as independent ranges due to the high levels of endemic fauna, unique geological history, and suspected dispersal pathways (Drew, 1989, 2004; Mortimer et al., 2017). The Torres Strait islands were included in the Papua New Guinea range due to the large number of species that are either endemic to the Torres Strait or are also distributed in Papua New Guinea and not Australia (Hancock, 2013). The Bismarck Archipelago of Papua New Guinea was included as part of Melanesia due to the differences in species composition previously recognised to exist there (Clarke et al., 2004).

For Australian subregions, we followed the ranges identified by Bryant and Krosch (2016) and Ebach et al. (2015). This resulted in six ranges: outside Australia; Cape York; Atherton Plateau; Eastern Queensland and New South Wales; Kimberley Plateau; and Arnhem Land (Figure 1b). The Eastern Queensland and New South Wales range combined three accepted biogeographic regions (as referred to by Ebach et al. (2015)): the McPherson-Macleay overlap, the Southern Transition Zone and Eastern Queensland, because the native distributions of all species found in this range spanned all three regions. Data files for both analyses are shown in Tables S1 and S2.

2.2 | Analysis

Both analyses were run in RStudio using the package BioGeoBEARS (Matzke, 2013) and its dependencies. We followed the example script provided at: http://phylo.

wikidot.com/biogeobears#toc29 (accessed October 10, 2019) and ran six models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. Note, while there has been criticism of the DEC+J model (Ree & Sanmartin, 2018), we include it here in our analysis following the justification provided in Matzke (2022). For the Pacific data, we also ran a time-stratified analysis using additional inputs to restrict dispersal to certain time periods (see Data S1 for analysis inputs). We assigned time periods based on the review by Hall (2001). Due to the debate that still surrounds the biogeographic history of some areas in the Pacific; a good example being New Caledonia (Grandcolas, 2017; Heads, 2019), we opted to present the model with the least number of priors in our results to avoid a biased outcome. For the Australian dataset, we did not use the time-stratified approach due to the small time slices required for this approach.

3 | RESULTS

3.1 | Pacific analysis

Of all six models, the DEC+J model was the best fit for the Pacific data in both the time-stratified and un-stratified analyses (Table 1). Across both analyses, the +J parameter models were the best fit, with the next best (without the J parameter) identified to be the DEC models. There were only small incongruences identified between the DEC and DEC+J model outputs, with the largest differences observed in proportions in Melanesian and Polynesian ancestral states; however, the regions remained largely the

TABLE 1 Models estimated in BioGeoBEARS for ancestral range estimation of Dacini species included in the Pacific analysis. Best fit models are bolded.

Model	d	e	j	LnL	AIC
DEC	0.0068	4.58E-03	0	−421.45	846.986
DEC + J	**0.0048**	**1.00E-12**	**0.0461**	**−392.83**	**791.825**
DIVALIKE	0.0082	2.75E-03	0	−440.83	885.749
DIVALIKE + J	0.0058	1.00E-12	0.0382	−416.8	839.767
BAYAREALIKE	0.0032	3.98E-02	0	−441.3	886.682
BAYAREALIKE + J	0.003	1.05E-02	0.082	−408.18	822.527
DEC time stratified	0.0082	4.61E-03	0	−410.26	824.602
DEC + J time stratified	**0.0058**	**1.00E-12**	**0.0614**	**−379.05**	**764.274**
DIVALIKE time stratified	0.0098	2.67E-03	0	−428.85	861.784
DIVALIKE + J time stratified	0.0068	1.00E-12	0.051	−401.74	809.644
BAYAREALIKE time stratified	0.0045	3.89E-02	0	−437.48	879.05
BAYAREALIKE + J time stratified	0.003	1.27E-02	0.0527	−391.78	789.738

Note: In bold are the best fitting models for each analysis.

same across all analyses (see Figures S1–S3). From here on, we discuss the DEC + J model without time stratifications applied.

We found species dispersed into the Pacific Islands from west to east. This dispersal was found to be unidirectional, with no evidence of westward movement. This eastward movement occurred primarily out of New Guinea (Figure 2). The one exception was New Caledonia, where our analysis also showed movement of ancestral species from Australia. There was strong evidence that the ancestor of Melanesian species also originated out of New Guinea.

The New Caledonian fauna is composed of multiple radiations onto the landmass from both Australia and New Guinea. Divergence between New Caledonian and Australian species occurred recently, with divergence of *Bactrocera curvipennis* (Froggatt) from Australian and New Guinean ancestors 2.42 mya (95% CI = 1.39–3.77). New Caledonian species with New Guinean and Melanesian origins were also quite young, with *Bactrocera caledoniensis* Drew diverging 0.9 mya (95% CI = 0.32–1.9) and *Bactrocera mucronis* (Drew) 8.37 mya (95% CI = 4.71–13.1). Melanesian species were polyphyletic across the tree, suggesting multiple lineages have moved into the region independently. There were very young species such as *Bactrocera atramentata* (Hering), diverging 0.4 mya (95% CI = 0.16–1.0) and *Zeugodacus triangularis* (Drew) which diverged 5.35 mya (95% CI = 3.26–8.56), and clades across the tree that contain species endemic to Melanesia and other adjacent eastern regions. For example, this includes but is not limited to a clade containing *Bactrocera unitaeniola* Drew and Romig and *Bactrocera distincta* (Malloch), which are present in Melanesia and Polynesia. This is a common trend across the dataset, which suggests that

some ancestors moved easterly to outer Pacific islands, while other sister species remained and diversified in Melanesia. There is no evidence of eastern Pacific species moving westward.

There were only four species native to Polynesia included in this analysis; *Bactrocera passiflorae* (Froggatt), *Bactrocera xanthodes* (Broun), *Bactrocera facialis* (Coquillet) and *B. distincta*. *Bactrocera passiflorae* and *B. facialis* formed a monophyletic clade, with stem groups present in New Guinea and Melanesia. *Bactrocera xanthodes* and *B. distincta* formed clades with their sister species from New Caledonia and Melanesia respectively, providing further evidence towards an east-ward radiation of species in the Pacific.

3.2 | Australian analysis

The DEC + J model was the best fit model for the Australian data (AIC = 863.7170; Table 2). There is evidence of multiple incursions of species into Australia via Papua New Guinea (Figure 3). Species have dispersed across the Carpentarian barrier from either Cape York, Atherton, or both (*Dacus bellulus* (Drew and Hancock) and *Dacus newmani* (Perkins) are examples). Species endemic to eastern Queensland and those found in Atherton, the Kimberley Plateau and Arnhem Land have undergone very recent speciation within the last 5 mya. There are no clades restricted to a single biogeographic region within Australia, instead the species endemic to each region are polyphyletic across the tree. The biogeographical barriers down the eastern coast of Australia, south of the Burdekin Gap do not appear to have had any impact on speciation and movement of the Dacini.
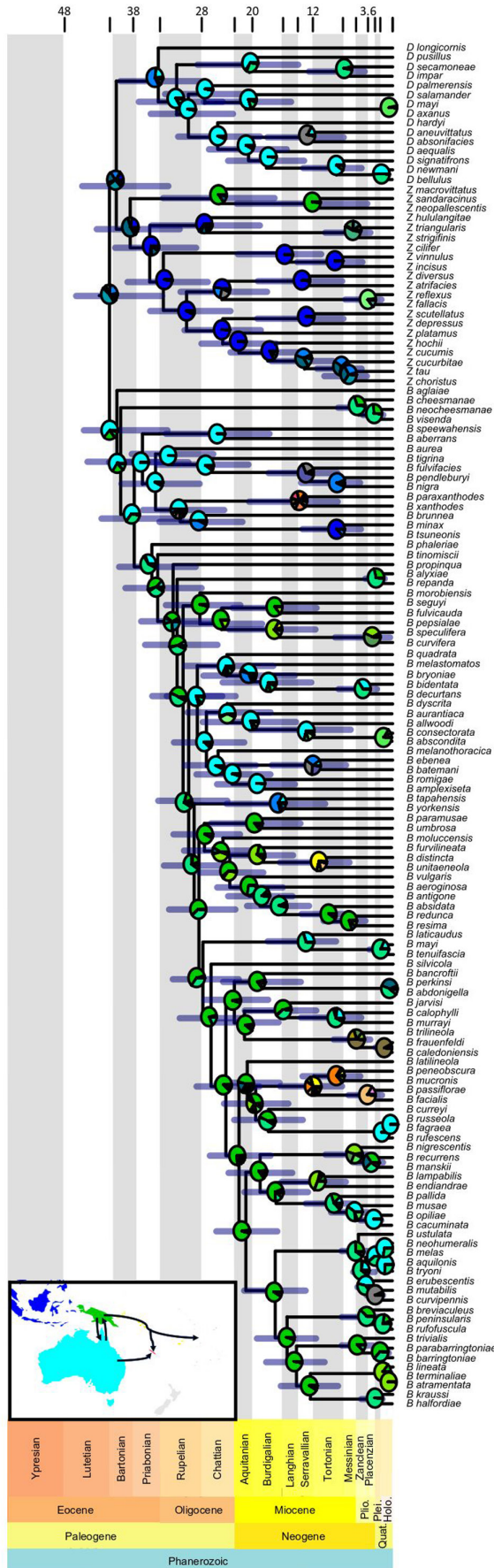
FIGURE 2 Dated biogeographical cladogram of Pacific Dacini fruit flies produced using the BioGeoBEARS DEC + J model. Pies on nodes represent the maximum likelihood of that ancestor inhabiting a region, and blue bars represent the 95% confidence interval of the divergence time estimates. Inset: pathways identified by the analysis and colour legend. Note: If a species is present in more than one range, this is represented by a third colour, i.e., presence in New Caledonia (red) and Melanesia (yellow) would be represented as orange in the ML pie.

4 | DISCUSSION

We investigated the biogeographic influences on dispersal pathways of the dacines in the Australo-Pacific region. This study identified unidirectional movement of Dacini species into the Pacific predominantly via New Guinea and only rarely from Australia. There was no movement of species back into Australia from the Pacific. Australia appears to have been colonised exclusively via New Guinea and there were multiple occurrences of species moving back and forth between the two landmasses over historical time. Evidence supported a single entry point for the ancestors of Australian species via the Torres Strait land bridge between Papua New Guinea and Cape York, with species subsequently spreading west into Arnhem Land and the Kimberley Plateau as well as south along the east coast of Queensland and New South Wales. Cape York and New Guinea share a large number of species in common, adding further evidence to this region being the main point of entry for the ancestors of modern-day species. Additionally, there is little evidence to suggest that biogeographic boundaries within Australia have contributed to speciation of the *Bactrocera*, due to the presence of close sibling species in sympatry in the identified biogeographic regions, but there is some evidence for *Dacus*; differences between genera could be linked to dispersal ability or host use.

4.1 | New Caledonia

New Caledonia is considered to harbour high levels of endemic fauna (Bauer & Sadlier, 1993), and this is especially true for the Dacini (Michaux & White, 1999). We identified the earliest radiation from New Guinea and Melanesia into New Caledonia represented in our tree was *B. umbrosa* 20 mya (95% CI = 13.45–26.46). Radiations through Melanesia were found for multiple clades of the phylogeny, where some species have remained and diversified within Melanesia, and others have dispersed and diversified in New Caledonia and Polynesia. The eastward dispersal of New

TABLE 2 Models estimated in BioGeoBEARS for ancestral range estimation of Dacini species included in the Australian analysis. The best fit model is bolded.

Model	d	e	j	LnL	AIC
DEC	0.105	3.054e-02	0	−433.3633	870.7267
DEC + J	**0.107**	**1.000e-12**	**0.010**	**−428.8585**	**863.7170**
DIVALIKE	0.113	1.000e-12	0	−450.5623	905.1247
DIVALIKE + J	0.122	1.000e-12	0.005	−449.1837	904.3674
BAYAREALIKE	0.063	3.420e-01	0	−466.0740	936.1480
BAYAREALIKE + J	0.05294947	2.493e-01	0.013	−430.8524	867.7048

Guinean species is evident in two clades in the phylogeny, the *B. unitaeniola* and *B. distincta* clade diversified 19.82 mya (95% CI = 14.52–24.86), and the clade containing *Bactrocera peneobscura* Drew and Romig, *B. mucronis*, *B. passiflorae* and *B. facialis* 19.93 mya (95% CI = 15.19–24.54). These dates coincide with those proposed for the existence of several Melanesian island arcs between New Guinea and New Caledonia during the Eocene–Oligocene (Heads, 2010). These island arcs not only explain the dispersal patterns seen here in the dacines but also of diving beetles (Toussaint et al., 2015), lichen (Galloway, 2007), fruit bats (Simmons, 2005) and a number of plant species (Govaerts et al., 2001; Swenson et al., 2007).

Our analysis indicates that divergence dates between Australian and New Caledonian species are much younger than geological events might suggest; the New Caledonian landmass being submerged until 34–37 mya (Cluzel et al., 2001). This is similar to the results found by Nattier et al. (2017), which conducted a meta-analysis of New Caledonian biota and found that clades were younger than the islands they inhabit; and dispersal from nearby landmasses is a likely explanation for present day species compositions. Using the New Caledonian species *Bactrocera ebenea* (Drew) and *Dacus aneuvittatus* Drew as examples, these species diverged from Australian fauna approximately 11.77 mya (95% CI = 6.81–17.61) and 12.3 mya (95% CI = 7.14–18.26), respectively. This is consistent with many studies that have investigated the radiation of other species from Australia into New Caledonia and New Zealand (for in-depth discussion see Condamine et al. (2017)); for example, Lucky (2011) investigated the biogeography of spider ants and found similar divergence times for their New Caledonian clade: 4.12 mya (95% HPD: 1.3–7.7). They suggested New Caledonian taxa may have reached New Caledonia via long distance dispersal (Lucky, 2011). Similarly, transoceanic dispersal was considered to be the primary explanation for colonisation of New Caledonia by chironomids from Australia, with divergence occurring around 8 mya (95% HPD = 1.5–13) (Krosch et al., 2020). Alternatively, Condamine et al. (2017) found that conifer diversification in the Pacific is best explained by the existence of ancient Pacific islands which acted as refugia for species during the Oligocene and Miocene, which allowed for species to move from Australia to New Caledonia and New Zealand. Either of these explanations are plausible for our group, as the Dacini are known to be able to travel long distances over water (Otuka et al., 2016).

4.2 | Australian and Papua New Guinean fauna

Our findings indicate there were multiple movements of species between Australia and Papua New Guinea at various time periods. The analysis suggests that there was a single point of entry for species into Australia, and this was Cape York via Papua New Guinea. Possible dispersal mechanisms include the possibility of wind-assisted dispersal (as discussed above), but a more supported theory is a land bridge which connected Cape York and the Northern Territory in Australia with Papua New Guinea in the north (Burbidge, 1960; Hall, 2001; Mirams et al., 2011). This land bridge was present for millions of years, first forming sometime around the Carboniferous (358 mya) and was submerged intermittently throughout the Pleistocene (0.012–2.58 mya) (Doutch, 1972). The land connection was severed for the final time around 7000 years ago (Reeves et al., 2008; Voris, 2000). Some species, such as the Australian *Dacus* clade, moved between the two landmasses relatively early, corresponding with earlier land bridge connections, and the collision of Australia + southern Papua New Guinea with the accreted terranes of northern Papua New Guinea. Additionally, other species such as those in the *Bactrocera tryoni* (Froggatt) species complex have clearly undergone very recent exchange due to their close genetic affinity to each other and geographic polyphyly. Similar Mid-Pleistocene divergence has been observed in pademelons as a result of the intermittent presence of the Torres Strait land bridge (Macqueen et al., 2010); while similar pathways of divergence have also been reported for honeyeaters (Norman et al., 2007). The absence of Australian species at basal nodes of the tree, combined with an isolated geological history, and similar patterns of dispersal for other taxa, suggests that species colonised from Papua
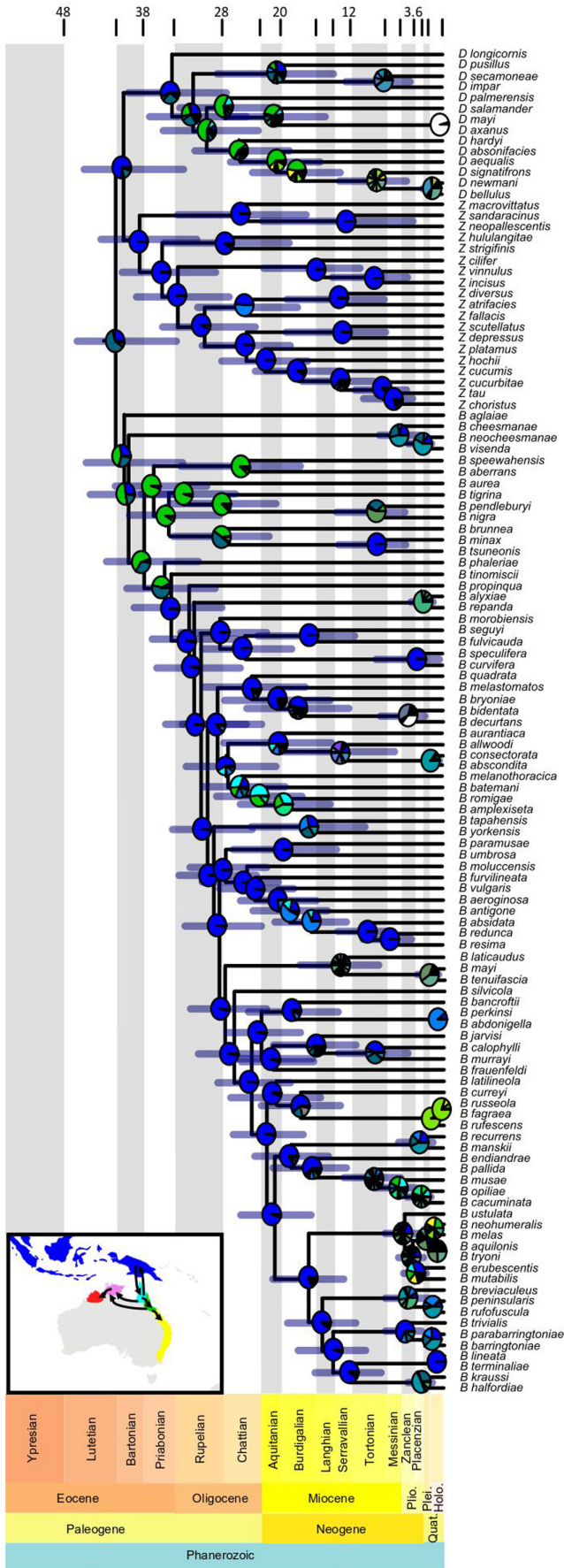
FIGURE 3 Dated biogeographical cladogram of Australian Dacini fruit flies produced using the BioGeoBEARS DEC + J model. Pies on nodes represent the maximum likelihood of that ancestor inhabiting a region, and blue bars represent the 95% confidence interval of the divergence time estimates. Inset: pathways identified by the analysis and colour legend. Note: If a species is present in more than one range, this is represented by a third colour, i.e., presence in New Caledonia (red) and Melanesia (yellow) would be represented as orange in the ML pie.

New Guinea and adds to the mounting evidence that Australia is not the origin of the Dacini tribe.

The Australian analysis found some impact of biogeographic barriers on species movement, but the extent to which barriers have influenced diversification in the group is unclear. Many species are found in both the Cape York and Atherton Plateau regions, which suggests that the barrier between these regions (the Laura Basin) has not restricted movement. The Laura Basin may have contributed to the divergence of *Bactrocera mutabilis* (May) from close sibling species *Bactrocera erubescentis* (Drew and Hancock); however, this could also be due to other factors such as climate and host plant distribution (Drew, 2004). The Burdekin Gap (south of the Atherton Plateau) has restricted southern movement of species such as *Bactrocera aurantiaca* (Drew and Hancock), *Bactrocera barringtoniae* (Tryon) and *Bactrocera antigone* (Drew and Hancock). Moussalli et al. (2005) noted that divergence in rainforest skinks was influenced by the Burdekin Gap in the mid-late-Miocene (~5–15 mya). Formation of the Burdekin Gap may be responsible for the divergence of *Dacus signatifrons* (May) from its northerly distributed siblings, but there appears to be little, if any influence on divergence in *Bactrocera*. For species such as *Bactrocera jarvisi* (Tryon) and *B. tryoni*, their wide distribution range could be attributed to their ability to utilise many host fruits, but for species such as *Bactrocera aurea* (May) which are recorded from a single host (Hancock et al., 2000) it seems that is has been no barrier to dispersal.

5 | CONCLUSION

Our study is the first comprehensively sampled biogeographic analysis of dacines in the Pacific. We identified key divergence pathways and areas where biogeographical barriers have, and have not, influenced divergence in the Dacini. An investigation into other influential factors such as climate and host availability could further our understanding of the drivers of diversification of this group. Furthermore, Australian species diverged from

Papua New Guinean ancestors, a region with some of the highest diversity of dacines. With additional sampling in the Papua New Guinean region and adjacent regions in South-east Asia, we could further expand our understanding of the dacines' pathways into the Pacific.

ORCID

Melissa L. Starkie 🔟 https://orcid.org/0000-0002-4240-0032

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