JSE Journal of Systematics and Evolution

doi: 10.1111/jse.12299

Research Article

Historical biogeography of *Melicope* (Rutaceae) and its close relatives with a special emphasis on Pacific dispersals

Marc S. Appelhans[1,2]*, Jun Wen[2], Marco Duretto[3], Darren Crayn[4], and Warren L. Wagner[2]

[1]Department of Systematics, Biodiversity and Evolution of Plants, Albrecht-von-Haller Institute of Plant Sciences, University of Goettingen, Untere Karspuele 2, 37073 Goettingen, Germany
[2]Department of Botany, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA
[3]National Herbarium of New South Wales, Royal Botanic Gardens & Domain Trust, Mrs Macquaries Rd, Sydney NSW 2000, Australia
[4]Australian Tropical Herbarium, James Cook University, PO Box 6811, Cairns QLD 4870, Australia
*Author for correspondence. E-mail: marc.appelhans@biologie.uni-goettingen.de

Received 17 October 2017; Accepted 22 December 2017; Article first published online 8 February 2018

Abstract The genus *Melicope* (Rutaceae) occurs on most Pacific archipelagos and is perfectly suited to study Pacific biogeography. The main goal was to infer the age, geographic origin and colonization patterns of *Melicope* and its relatives. We sequenced three nuclear and two plastid markers for 332 specimens that represent 164 species in 16 genera of Rutaceae. Phylogenetic reconstruction, molecular dating, ancestral area reconstruction and diversification analyses were carried out. The two main clades (*Acronychia-Melicope* and *Euodia*) originated in Australasia and their crown ages are dated to the Miocene. Diversification rates differed among the subclades and were lowest in the *Euodia* lineage and highest in the Hawaiian *Melicope* lineage. The Malagasy and Mascarene species form a clade, which split from its SE Asian relatives in the Pliocene/Pleistocene. At least eight colonizations to the Pacific islands occurred. The timing of all colonizations except for the Hawaiian group is congruent with age of the island ages. Australia, New Guinea and New Caledonia have been the source of colonizations into the Pacific islands in the *Melicope* clade. *Melicope* shows high dispersability and has colonized remote archipelagos such as the Austral and Marquesas Islands each twice. Colonization of islands of the Hawaiian-Emperor seamount chain likely predates the ages of the current main islands, and the initial colonization to Kaua'i occurred after the splitting of the Hawaiian lineage into two subclades. Wider ecological niches and adaptations to bird-dispersal likely account for the much higher species richness in the *Acronychia-Melicope* clade compared to the *Euodia* clade.

Key words: *Acronychia*, dispersal, *Euodia*, *Melicope*, Pacific biogeography, Rutaceae.

1 Introduction

Due to their geographic isolation, mostly recent volcanic origin and their high endemicity, Pacific archipelagos are particularly interesting for biogeographic and evolutionary studies. Most Pacific islands are of volcanic origin and have never been in direct contact with continental landmasses (Neall & Trewick, 2008). Pacific islands that consist of continental crust – e.g., New Caledonia and New Zealand – have long been separated from other continental landmasses and elements of their floras and faunas arrived after their isolation (Sharma & Wheeler, 2013). Colonizers of Pacific islands most likely arrived by means of long-distance dispersal (LDD) events (Nathan et al., 2008). Different vectors facilitating LDD have been identified; the most common being birds, wind, ocean currents, and driftwood rafts (Donlan & Nelson, 2003; Cowie & Holland, 2006; Wenny et al., 2016). A 'standard vector' of dispersal has been proposed for many species based on morphological characters (Carlquist, 1967). However the relationship between morphology and dispersal is difficult to quantify and it has been proposed that multiple or non-standard vectors might account for LDD events (Higgins et al., 2003; Nathan et al., 2008). Molecular phylogenetic studies have identified examples of single LDD events across thousands of kilometers (Le Roux et al., 2014), as well as shorter distance events as stepping-stone dispersals (Harbaugh et al., 2009). Since only a small percentage of the Pacific region consists of exposed land, successful colonizations, especially of the more remote islands, can be considered to be extremely rare. Many lineages once thought to represent independent colonizations on a particular archipelago have been shown to be the result of an extensive radiation after a single colonization event. The most notable example being the Hawaiian Lobeliads (Campanulaceae), the largest island radiation of angiosperms (Givnish et al., 2009). Pacific lineages are mostly of Asian, Australasian or American origin and only a few examples of an African origin are known (Baldwin & Wagner, 2010; Keeley & Funk, 2011).

Melicope J.R.Forst. & G.Forst. (Rutaceae; *Citrus* family) and its close relatives (hereinafter the *Acronychia-Euodia-Melicope* group) occur on most Pacific archipelagos and the group is therefore perfectly suited to study Pacific biogeography and dispersal routes. Recent phylogenetic studies have demonstrated that *Melicope* is not monophyletic and several genera need to be merged into it or into *Acronychia* J.R.Forst. & G.Forst. and *Euodia* J.R.Forst. & G.Forst. to ensure monophyly of each genus (Appelhans et al., 2014a, 2014b; Holzmeyer et al., 2015). *Melicope* (~240 spp.) is the largest genus in Rutaceae and occurs in Madagascar and the Mascarene Islands, throughout SE Asia, Malesia, Australasia, and on most Pacific archipelagos. Its centers of species richness and endemicity are the Hawaiian Islands and New Guinea (Hartley, 2001). *Acronychia* (49 spp.) is the second largest genus of the *Acronychia-Euodia-Melicope* group and is mainly confined to eastern Australia and New Guinea with two species extending west to Java and India, and two eastward to the Solomon Islands and New Caledonia (Hartley, 1974, 2013; Holzmeyer et al., 2015). *Euodia* (7 spp.) is more restricted and is present in eastern Australia, New Guinea and the South Pacific from New Britain and New Caledonia to Samoa and Niue (Hartley, 2001).

The *Acronychia-Euodia-Melicope* group consists of 15 genera and about 360 species (Kubitzki et al., 2011; Appelhans et al., 2014a). Of these, *Comptonella* Baker f., *Dutaillyea* Baill., *Picrella* Baill. (all New Caledonia), *Platydesma* H.Mann (Hawaii) and *Sarcomelicope* Engl. (Australia to Fiji) are nested within *Melicope* while *Maclurodendron* T.G.Hartley (Malay Peninsula to the Philippines and Hainan) is nested within *Acronychia*. *Platydesma* has recently been merged into *Melicope* (Appelhans et al., 2017). *Medicosma* Hook.f (New Guinea, E Australia, New Caledonia) and *Tetractomia* Hook.f (Malay Peninsula to the Solomon Islands) are consecutive sister groups of the *Acronychia-Melicope* clade. *Brombya* F. Muell. (Australia), *Pitaviaster* T.G.Hartley (Australia), along with *Melicope vitiflora* (F.Muell.) T.G.Hartley, group with *Euodia*, and this clade is sister to *Perryodendron* T.G.Hartley (Moluccas to New Britain) (Appelhans et al., 2014a). The monotypic *Dutailliopsis* T.G.Hartley (New Caledonia) is a potential member of the *Melicope* clade based on morphological characters (Hartley, 1997, 2001; Bayly et al., 2013), but it has not been sampled in any molecular phylogenetic study. Unpublished results (M. Duretto) indicate *Zieria* Sm. (Australia & New Caledonia), *Neobyrnesia* J.A.Armstr. and *Boronia* Sm. section *Cyanothamnus* (Lindl.) F.Muell. (Australia) classify within the *Acronychia-Euodia-Melicope* group but are separated from other genera by long branches. These last three taxa are not included in this analysis. Even though the *Acronychia-Melicope* clade and the *Euodia* clade occupy similar habitats, they differ largely in terms of distributional range and species richness.

The main goal of this study is to establish a dated molecular phylogeny with an ancestral area reconstruction and a diversification analysis of the *Acronychia-Euodia-Melicope* group to (1) infer the geographic origin and the temporal diversification history of the group; (2) reconstruct major dispersal routes in the Pacific region; and (3) evaluate if there are different diversification rates among subclades.

2 Material and Methods

2.1 Taxon sampling & datasets

The taxon sampling of this study was largely based on that of Appelhans et al. (2014a, 2014b) and Holzmeyer et al. (2015) with several additional species mainly from Pacific archipelagos sampled. A total number of 332 specimens, representing 164 species and 16 genera, were included in this study (Table 1): *Melicope* (118 out of 235 species and 12 unidentified specimens), *Acronychia* (24/48), *Brombya* (1/2), *Comptonella* (4/8), *Dutaillyea* (1/2), *Euodia* (4/6), *Maclurodendron* (1/6), *Medicosma* (1/25), *Perryodendron* (1/1), *Picrella* (2/3), *Pitaviaster* (1/1), *Sarcomelicope* (1/9), *Tetractomia* (1/6). *Dutailliopsis*, *Boronia* section *Cyanothamnus*, *Neobyrnesia* and *Zieria* were the only putative relatives that were not sampled. We sampled throughout the distributional range of *Melicope* and its relatives with particularly comprehensive sampling of the Pacific species (72/111). One specimen of *Boronia* (section *Boronella* (Baill.) Duretto & Bayly) and three specimens of *Myrtopsis* O.Hoffm. were included as outgroups based on previous phylogenetic studies (Bayly et al., 2013; Appelhans et al., 2014a).

For the ancestral area reconstructions (AAR) and diversification analyses, a reduced dataset containing only a single specimen for each species was used. For species found to be polyphyletic, one specimen for each evolutionary lineage was included. This dataset contains 166 species/specimens (Table 1, specimens in bold type).

2.2 Molecular lab work and phylogenetic analyses

Our datasets included nuclear markers ETS, ITS and NIAi3 and plastid markers *psbA-trnH* and *trnL-trnF*. DNA extraction, PCR amplification, contig assembly, construction of alignments and model selection followed Appelhans et al. (2014b). All sequences were deposited at EMBL/Genbank (Table 1). Alignment was straightforward except for the *psbA-trnH* region which contained many, often large (ca. 100 bp) indels. After excluding bases that could not be aligned with confidence, the *psbA-trnH* alignment was reduced from 1101 to 509 bp. Phylogenetic reconstructions were conducted with mrbayes 3.2.5 (Ronquist et al., 2012) using the best-fit models of sequence evolution for each marker (Table 2) and applying the settings described by Appelhans et al. (2014b). We checked if effective sample sizes (ESS) were above 200 for all parameters using Tracer 1.6.0 (Rambaut et al., 2014) and discarded 10% of the trees as burnin before calculating a 50% majority rule consensus tree in MrBayes. Clades with posterior probabilities (pp) of $\geq$0.95 were considered statistically supported.

2.3 Molecular dating analyses

Molecular dating analyses were performed using BEAST v.1.8.4 (Drummond et al., 2012). The dated maximum clade credibility consensus tree from the reduced dataset was used in the downstream analyses (AAR, diversification analyses).

While Rutaceae have a good fossil record (Appelhans et al., 2012), no fossils suitable for molecular dating are known for the *Acronychia-Euodia-Melicope* clade. The oldest fossils possibly belonging to this clade are from the Miocene-Oligocene boundary in Australia and New Zealand ("aff. *Acronychia*, aff. *Euodia*" [Blackburn & Sluiter, 1994] and "? *Melicope*" [Conran et al., 2014]) but since they are of uncertain affinity they were not considered further. Other *Melicope* (sub)fossils (Burney et al., 2001; Kershaw et al., 2007) were not suited because of their young age (Late Pleistocene or Holocene). Fossils formerly assigned to *Euodia* (Tiffney, 1980,

Table 1 Voucher information, area codes for biogeographic analyses and Genbank numbers of all individuals used in this study

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
A. acronychioides	*Forster PIF30987* (L)	Australia, Queensland	D	LN849177	LN849136	LN849220	–	–
A. acuminata	*Ford 3997* (CNS)	Australia, Queensland	D	LN849178	LN849137	LN849221	LN849160	LN849199
A. baeuerlenii	*Beesley 1080a* (NSW)	Australia, NSW	D	LN849179	LN849138	LN849222	LN849161	LN849200
A. baeuerlenii	*Rossetto ABNIG1* (NSW)	Australia, NSW	D	LN849180	LN849139	LN849223	LN849162	LN849201
A. brassii	*Appelhans 454* (LAE, US)	Papua New Guinea	D	HG971153	HG971304	HG971458	HG971025	HG971612
A. brassii	*Appelhans 466* (LAE, US)	Papua New Guinea	D	HG971154	HG971305	HG971459	HG971026	HG971613
A. brassii	*Appelhans 467* (LAE, US)	Papua New Guinea	D	HG971155	HG971306	HG971460	HG971027	HG971614
A. cartilaginea	*Takeuchi 23857* (A)	Papua New Guinea	D	–	LN849140	LN849224	–	–
A. chooreechillum	*Telford 11393* (NSW)	Australia, Queensland	D	LN849181	LN849141	LN849226	LN849163	LN849202
A. eungellensis	*Forster PIF25513* (CNS)	Australia, Queensland	D	–	–	LN849228	LN849164	LN849203
A. imperforata	*Forster PIF30952* (L)	Australia, Queensland	D	LN849182	LN849143	LN849231	–	LN849204
A. laevis	*Forster PIF30953* (L)	Australia, Queensland	D	LN849183	LN849144	LN849232	–	–
A. ledermannii	*Appelhans 426* (LAE, US)	Papua New Guinea	D	HG971156	HG971307	HG971461	HG971028	HG971615
A. ledermannii	*Appelhans 448* (LAE, US)	Papua New Guinea	D	HG971157	HG971308	HG971462	HG971029	HG971616
A. ledermannii	*Appelhans 458* (LAE, US)	Papua New Guinea	D	HG971158	HG971309	HG971463	HG971030	HG971617
A. littoralis	*Rossetto ALBAL1* (NSW)	Australia, NSW	D	–	AY588597	LN849233	LN849165	LN849205
A. littoralis	*Rossetto ALAB1* (NSW)	Australia, NSW	D	LN849184	–	LN849234	LN849166	LN849207
A. littoralis	*Rossetto ALSC2* (NSW)	Australia, NSW	D	LN849185	–	LN849235	LN849167	LN849206
A. murina	*Utteridge 542* (A)	Papua New Guinea	D	LN849186	LN849145	LN849236	–	–
A. murina	*Regalado 1023* (A)	Papua New Guinea	D	LN849187	LN849146	LN849237	LN849168	LN849209
A. murina	*Takeuchi 24793* (A)	Papua New Guinea	D	LN849188	LN849147	LN849238	–	LN849208
A. oblongifolia	*Winsbury 97* (CBG)	Australia, NSW	D	EU493242	EU493185	HG971464	EU493204	–
A. octandra	*Forster PIF34176* (MEL)	Australia, Queensland	D	LN849190	LN849149	LN849240	LN849170	–
A. parviflora	*Ford 4434* (CNS)	Australia, Queensland	D	LN849191	LN849150	LN849241	–	LN849211
A. pauciflora	*Rossetto APAWIL1* (NSW)	Australia, NSW	D	LN849192	LN849151	LN849242	LN849171	LN849212
A. pedunculata	*de Wilde 6834* (L)	Thailand	B, C, D	HG002754	HG002398	HG002527	HG002652	HG002957
A. pedunculata	*Brambach 1503* (GOET)	Indonesia, Sulawesi	B, C, D	LN849193	LN849152	LN849243	–	LN849214
A. pedunculata	*Wen 12364* (US)	Indonesia, Java	B, C, D	–	LN849153	LN849244	LN849172	LN849213
A. pubescens	*Rossetto APUWIL1* (NSW)	Australia, NSW	D	LN849194	LN849154	–	LN849173	LN849215
A. pullei	*Appelhans 460* (US)	Papua New Guinea	D	HG971159	HG971310	HG971465	HG971031	HG971618
A. reticulata	*Coode 8081* (L)	Indonesia, Papua	D	HG971160	HG971311	HG971466	–	–
A. suberosa	*Forster PIF28797* (L)	Australia, Queensland	D	LN849195	LN849155	LN849246	–	–
A. suberosa	*Rossetto ASNIG1* (NSW)	Australia, NSW	D	LN849196	LN849156	LN849247	LN849174	LN849216
A. trifoliolata var. microcarpa	*James 459* (LAE, BISH, GOET)	Papua New Guinea	C, D	HG971161	HG971312	HG971467	HG971032	HG971619
A. trifoliolata var. *microcarpa*	*Appelhans 416* (LAE, US)	Papua New Guinea	C, D	HG971162	HG971313	HG971468	HG971033	HG971620

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
A. vestita	*Forster PIF27548* (L)	Australia, Queensland	D	–	LN849157	LN849248	–	LN849217
A. wilcoxiana	*Rossetto AWIL1* (NSW)	Australia, NSW	D	LN849197	LN849158	LN849249	LN849175	LN849218
Bo. spec.	*Lowry 6481* (MO)	New Caledonia	D	HG971285	HG971314	HG971469	–	HG971621
Br. platynema	*Ford 4819* (L)	Australia	D	HG971163	HG971315	–	HG971034	HG971622
C. baudouinii	*MacKee 29450* (L)	New Caledonia	D	HG971165	HG971317	HG971471	–	–
C. microcarpa	*Munzinger 679* (MO)	New Caledonia	D	HG971274 + HG971286	HG971318	HG971472	HG971035	HG971623
C. microcarpa	*Lowry 5734* (MO)	New Caledonia	D	HG971275 + HG971287	HG971319	HG971473	HG971036	HG971624
C. oreophila	*McPherson 18544* (MO)	New Caledonia	D	HG971166	HG971320	HG971474	HG971037	HG971625
C. sessilifoliola	*McPherson 18023* (MO)	New Caledonia	D	HG971276 + HG971288	HG971322	HG971475	HG971038	HG971626
C. sessilifoliola	*Van Balgooy 7053* (L)	New Caledonia	D	HG971167	HG971323	HG971476	HG971039	–
D. spec.	*Munzinger 790* (MO)	New Caledonia	D	HG971277	HG971324	HG971477	HG971040	HG971627
E. hortensis	*Appelhans 398* (US)	Singapore Botanical Garden (2007 0570*C)	D, F	HG971168	HG971325	HG971478	HG971041	HG971628
E. hortensis	*Drake 235* (US)	Polynesia, Tonga	D, F	HG002786 + HG002862	HG002399	HG002528	HG002653	HG002958
E. hylandii	*Forster 25754* (L)	Australia, Queensland	D	HG971169	HG971326	HG971479	HG971042	HG971629
E. montana	*James 381* (LAE, BISH, GOET)	Papua New Guinea	D	HG971170	HG971327	HG971480	HG971043	HG971630
E. pubifolia	*Sankowsky 1711* (QRS)	Australia	D	EU493243	EU493186	HG971481	EU493205	HG971631
M. accedens	*Beaman 7360* (L)	Borneo	B, C	HG971173	HG971331	HG971485	HG971046	HG971632
M. accedens	*Wen 10990* (US)	Vietnam	B, C	HG971174	HG971332	HG971486	HG971047	HG971633
M. accedens	*Kato 20120218182* (MAK)	Malaysia	B, C	AB766301	AB766300	–	AB766303	–
M. adscendens	*Oppenheimer 40001* (US)	USA, Hawaii, Maui	G	HG002787 + HG002863	HG002400	HG002529	HG002654	HG002959
M. adscendens	*Oppenheimer 40002* (US)	USA, Hawaii, Maui	G	HG002788 + HG002864	HG002401	HG002530	HG002655	HG002960
M. adscendens	*Wood 7672* (PTBG)	USA, Hawaii, Maui	G	HG002789 + HG002865	HG002402	HG002531	HG002656	HG002961
M. albiflora	*Whistler 2004* (B)	Samoa	F	*MG668986	*MG595154	*MG668941	–	*MG668968
M. aneura	*Appelhans 418* (LAE, US)	Papua New Guinea	D	HG971175	HG971333	HG971487	HG971048	HG971634
M. aneura	*Appelhans 439* (LAE, US)	Papua New Guinea	D	HG971176	HG971334	HG971488	HG971049	HG971635
M. aneura	*Appelhans 441* (LAE, US)	Papua New Guinea	D	HG971177	HG971335	HG971489	HG971050	HG971636
M. anisata	*Wagner 6892* (US)	USA, Hawaii, Kaua'i	G	HG002790 + HG002866	HG002403	HG002532	HG002657	HG002962

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. anisata	*Wood 5844* (PTBG)	USA, Hawaii, Kaua'i	G	HG002791 + HG002867	HG002404	HG002533	HG002658	HG002963
M. anomala	*Uttridge 359* (L)	Indonesia, Papua	D	HG971178	HG971336	HG971490	HG971051	HG971637
M. balgooyi	*Wood 9698* (BISH, NY)	Austral Islands	F	HG971246	HG971418	HG971571	HG971117	HG971710
M. balgooyi	*Wood 9727* (BISH, NY)	Austral Islands	F	HG971247	HG971419	HG971572	HG971118	HG971711
M. balloui	*Wood 7685* (PTBG)	USA, Hawaii, Maui	G	HG002792 + HG002868	HG002405	HG002534	HG002659	HG002964
M. barbigera	*Wagner 6896* (US)	USA, Hawaii, Kaua'i	G	HG002793 + HG002869	HG002406	HG002535	HG002660	HG002965
M. bonwickii	*Wen 10286* (US)	Indonesia, Sulawesi	C, D	HG971179	HG971337	HG971491	HG971052	HG971638
M. borbonica	*Adersen 5564* (C)	La Réunion	A	HG971180	HG971338	HG971492	HG971053	–
M. brassii (cf)	*Appelhans 436* (LAE, US)	Papua New Guinea	D	HG971181	HG971339	HG971493	HG971054	HG971639
M. broadbentiana	*Telford 9474* (CANB)	Australia, Queensland	D	HG971278 + HG971290	HG971340	HG971494	–	–
M. broadbentiana	*Gray 435* (L)	Australia, Queensland	D	–	HG971341	HG971495	HG971055	–
M. capillacea	*Smith 4992* (NY)	Fiji	F	HG971291	HG971342	–	–	HG971640
M. christophersenii	*Wood 7894* (PTBG)	USA, Hawaii, O'ahu	G	HG002794 + HG002870	HG002407	HG002536	–	HG971641
M. clemensiae	*Pearce 96017* (L)	Borneo	C	HG971292	HG971343	HG971496	–	–
M. clusiifolia	*Wagner 6894* (US)	USA, Hawaii, Kaua'i	G	HG002755	HG002408	HG002537	–	HG002966
M. clusiifolia	*Wagner 6900* (PTBG)	USA, Hawaii, O'ahu	G	EU493235	EU493178	HG002538	EU493197	HG002967
M. clusiifolia	*Wagner 6908* (US)	USA, Hawaii, O'ahu	G	HG002795 + HG002871	HG002409	HG002539	–	HG002968
M. clusiifolia	*Wagner 6912* (US)	USA, Hawaii, Maui	G	HG002796 + HG002872	HG002410	HG002540	HG002661	HG002969
M. clusiifolia	*Wood 12406* (PTBG)	USA, Hawaii, Hawai'i	G	HG002797 + HG002873	HG002411	HG002541	HG002662	HG002970
M. clusiifolia	*Wood 8151* (PTBG)	USA, Hawaii, Kaua'i	G	HG002798 + HG002874	HG002412	HG002542	HG002663	HG002971
M. clusiifolia	*Wood 8253* (PTBG)	USA, Hawaii, Kaua'i	G	HG002799 + HG002875	HG002413	HG002543	–	HG002972
M. coodeana	*Larsen 52* (C)	La Réunion	A	HG971182	HG971345	HG971498	HG971057	HG971642
M. cornuta	*Wood 2776* (PTBG)	USA, Hawaii, O'ahu	G	HG002936	HG002504	HG002644	–	–
M. crassifolia	*Soejarto 8054* (L)	Philippines	C	–	HG971452	HG971610	–	–
M. cravenii	*Regaldo 1027* (NY)	Papua New Guinea	D	HG971293	HG971346	HG971499	–	HG971643
M. cravenii	*Appelhans 432* (LAE, US)	Papua New Guinea	D	HG971183	HG971347	HG971500	HG971058	HG971644

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. cruciata	*Wood 13777* (PTBG)	USA, Hawaii, Kaua'i	G	HG002800 + HG002876	HG002414	HG002544	HG002664	HG002973
M. cruciata	*Wood 8146* (PTBG)	USA, Hawaii, Kaua'i	G	HG002801 + HG002877	HG002415	HG002545	HG002665	HG002974
M. cruciata	*Wood 8188* (PTBG)	USA, Hawaii, Kaua'i	G	HG002802 + HG002878	HG002416	HG002546	HG002666	HG002975
M. cucullata	*Kuruvoli 16067* (NY)	Fiji	D, F	HG971294	HG971348	–	–	HG971645
M. degeneri	*Wood 12137* (PTBG)	USA, Hawaii, Kaua'i	G	HG002803 + HG002879	HG002417	HG002547	HG002667	HG002976
M. degeneri	*Wood 7442* (PTBG)	USA, Hawaii, Kaua'i	G	HG002756	HG002418	HG002548	HG002668	HG002977
M. degeneri	*Wood 7445* (PTBG)	USA, Hawaii, Kaua'i	G	EU493236	EU493179	HG002549	EU493198	HG002978
M. degeneri	*Wood 7662* (PTBG)	USA, Hawaii, Kaua'i	G	HG002757	HG002419	HG002550	HG002669	HG002979
M. denhamii	*Appelhans 486* (GOET)	cultivated Hortus Botanicus Leiden	C, D, E, F	HG971184	HG971349	HG971501	HG971059	HG971646
M. denhamii	*Takeuchi 16796* (L)	Papua New Guinea	C, D, E, F	HG971185	HG971350	HG971502	HG971060	HG971647
M. denhamii	*Utteridge 266* (L)	Papua New Guinea	C, D, E, F	HG971186	HG971351	HG971503	HG971061	HG971648
M. denhamii	*Appelhans 401* (LAE, US)	Papua New Guinea	C, D, E, F	HG971187	HG971352	HG971504	HG971062	HG971649
M. denhamii	*Appelhans 402* (LAE, US)	Papua New Guinea	C, D, E, F	HG971188	HG971353	HG971505	HG971063	HG971650
M. denhamii	*Appelhans 419* (LAE, US)	Papua New Guinea	C, D, E, F	HG971189	HG971354	HG971506	HG971064	HG971651
M. denhamii	*Appelhans 428* (LAE, US)	Papua New Guinea	C, D, E, F	HG971190	HG971355	HG971507	–	HG971652
M. denhamii	*Appelhans 453* (LAE, US)	Papua New Guinea	C, D, E, F	HG971191	HG971356	HG971508	HG971065	HG971653
M. denhamii	*Appelhans 464* (LAE, US)	Papua New Guinea	C, D, E, F	HG971192	HG971357	HG971509	HG971066	HG971654
M. denhamii	*Appelhans 468* (LAE, US)	Papua New Guinea	C, D, E, F	HG971193	HG971358	HG971510	–	HG971655
M. denhamii	*Appelhans 396* (US)	cultivated SING (Nr. 20100535*A)	C, D, E, F	HG971194	HG971359	HG971511	HG971067	HG971656
M. durifolia	*Appelhans 424* (US)	Papua New Guinea	D	HG971195	HG971360	HG971512	HG971068	HG971657
M. durifolia	*Appelhans 455* (LAE, US)	Papua New Guinea	D	HG971196	HG971361	HG971513	HG971069	HG971658
M. durifolia	*Appelhans 465* (LAE, US)	Papua New Guinea	D	HG971197	HG971362	HG971514	HG971070	HG971659

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. elleryana	*Lorence 6602* (PTBG)	cultivated NTBG	D	EU493241	EU493184	HG002551	EU493203	HG002980
M. elleryana	*Weiblen WS4C-0692* (MIN)	Papua New Guinea	D	HG971198	HG971363	HG971515	HG971071	HG971660
M. elleryana	*Weiblen WS5C-0774* (MIN)	Papua New Guinea	D	HG971199	HG971364	HG971516	HG971072	HG971661
M. elleryana	*Appelhans 403* (LAE, US)	Papua New Guinea	D	HG971200	HG971365	HG971517	HG971073	HG971662
M. elleryana	*Appelhans 404* (LAE, US)	Papua New Guinea	D	HG971201	HG971366	HG971518	HG971074	HG971663
M. elleryana	*Appelhans 405* (LAE, US)	Papua New Guinea	D	HG971202	HG971367	HG971519	HG971075	HG971664
M. elleryana	*Appelhans 406* (LAE, US)	Papua New Guinea	D	HG971203	HG971368	HG971520	HG971076	HG971665
M. elleryana	*Appelhans 407* (LAE, US)	Papua New Guinea	D	HG971204	HG971369	HG971521	HG971077	HG971666
M. elleryana	*Appelhans 411* (LAE, US)	Papua New Guinea	D	HG971205	HG971370	HG971522	HG971078	HG971667
M. elleryana	*Appelhans 412* (LAE, US)	Papua New Guinea	D	HG971206	HG971371	HG971523	HG971079	HG971668
M. elleryana	*Appelhans 413* (LAE, US)	Papua New Guinea	D	HG971207	HG971372	HG971524	HG971080	HG971669
M. elleryana	*Appelhans 414* (US)	Papua New Guinea	D	HG971208	HG971373	HG971525	HG971081	HG971670
M. elleryana	*Appelhans 395* (LAE, US)	cultivated SING (Nr. 20103854*A)	D	HG971209	HG971374	HG971526	HG971082	HG971671
M. elliptica	*Wagner 6906* (US)	USA, Hawaii, Oʻahu	G	HG002758	HG002420	HG002552	HG002670	HG002981
M. elliptica	*Wagner 6907* (US)	USA, Hawaii, Oʻahu	G	HG002804 + HG002880	HG002421	HG002553	HG002671	HG002982
M. feddei	*Perlman 16139* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002805 + HG002881	HG002422	HG002554	HG002672	HG002983
M. feddei	*Wood 7514* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002806 + HG002882	HG002423	HG002555	HG002673	HG002984
M. feddei	*Wood 8263* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002807 + HG002883	HG002424	HG002556	HG002674	HG002985
M. forbesii	*Curry 1616* (L)	Vanuatu	D	HG971210	HG971375	HG971527	HG971083	HG971672
M. frutescens	*Laman 936* (L)	Borneo	C, D	–	HG971344	HG971497	HG971056	–
M. frutescens	*Brambach 464* (GOET)	Indonesia, Sulawesi	C, D	*MG668987	*MG595156	*MG668943	*MG668958	*MG668969
M. glabra	*Ambri AA1575* (L)	Indonesia, Borneo	B, C	*MG668988	*MG595157	*MG668944	*MG668959	*MG668970
M. glabra	*Kato 20120215152* (MAK)	Malaysia	B, C	AB766293	AB766292	–	AB766295	–
M. glabra	*Kato 20120215148* (MAK)	Malaysia	B, C	AB766297	AB766296	–	AB766299	–
M. glomerata	*Wen 5856* (US)	Vietnam	B	HG971211	HG971376	HG971528	HG971084	HG971673
M. goilalensis	*James 494* (LAE, BISH, GOET)	Papua New Guinea	D	HG971295	HG971377	HG971529	HG971085	HG971674
M. grisea	*404826* (MAK)	Japan, Chichijima Island	E	AB766345	AB766344	–	AB766347	–
M. grisea var. *crassifolia*	*404821* (MAK)	Japan, Chichijima Island	E	AB766349	AB766348	–	AB766351	–
M. grisea* var. *crassilfolia	*Katok M620* (MAK)	Japan, Chichijima Island	E	AB766353	AB766352	–	AB766355	–

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. haleakalae	*Oppenheimer 60141* (US)	USA, Hawaii, Maui	G	HG002808 + HG002884	HG002425	HG002557	HG002675	HG002986
M. haupuensis	*Wood 7724* (PTBG, US)	USA, Hawaii, Kauaʻi	G	HG002809 + HG002885	HG002426	HG002558	HG002676	HG002987
M. haupuensis	*Wood 7725* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002810 + HG002886	HG002427	HG002559	HG002677	HG002988
M. hawaiensis	*Oppenheimer 60151* (US)	USA, Hawaii, Maui	G	HG002811 + HG002887	HG002428	HG002560	HG002678	HG002989
M. hawaiensis	*Wood 12102* (PTBG)	USA, Hawaii, Maui	G	HG002812 + HG002888	HG002429	HG002561	HG002679	HG002990
M. hivaoaensis	*Meyer 826*	Marquesas Islands	F	EU493230	EU493173	HG002562	EU493192	HG002991
M. hookeri	*Riswan 61* (L)	Borneo	B, C	HG971212	HG971378	HG971530	–	–
M. hosakae	*Wagner 6903* (US)	USA, Hawaii, Oʻahu	G	HG002813 + HG002889	HG002430	HG002563	HG002680	HG002992
M. inopinata	*Meyer 887*	Marquesas Islands	F	EU493233	EU493176	HG002564	EU493195	HG002993
M. jonesii	*Ford 4684* (L)	Australia, Queensland	D	HG971213	HG971379	HG971531	HG971086	HG971675
M. kavaiensis	*Wood 12270* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002814 + HG002890	HG002431	HG002565	HG002681	HG002994
M. kavaiensis	*Wood 8182* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002759	HG002432	HG002566	HG002682	–
M. knudsenii	*Perlman 19411* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002815 + HG002891	HG002433	HG002567	HG002683	HG002995
M. knudsenii	*Wagner 6891* (US)	USA, Hawaii, Kauaʻi	G	EU493225	EU493168	HG002568	EU493187	HG002996
M. knudsenii	*Wood 12455* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002816 + HG002892	HG002434	HG002569	HG002684	HG002997
M. knudsenii	*Wood 15101* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002760	HG002435	HG002570	HG002685	HG002998
M. knudsenii	*Wood 7667* (PTBG)	USA, Hawaii, Maui	G	HG002817 + HG002893	HG002436	HG002571	HG002686	HG002999
M. knudsenii	*Wood 7678* (PTBG)	USA, Hawaii, Maui	G	HG002818 + HG002894	HG002437	HG002572	HG002687	HG003000
M. knudsenii	*Wood 7696* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002761	HG002438	HG002573	HG002688	HG003001
M. knudsenii	*Wood 7697* (PTBG)	USA, Hawaii, Kauaʻi	G	HG002819 + HG002895	HG002439	HG002574	HG002689	HG003002
M. lasioneura (cf)	*Munzinger 939* (P)	New Caledonia	D	HG971296	HG971380	–	–	HG971676
M. latifolia	*Polak 1044* (L)	New Guinea	C, D	HG002820 + HG002896	HG002440	HG002575	HG002690	HG003003
M. latifolia	*Lorence 10298* (PTBG)	cultivated NTBG (Nr. 990589)	C, D	HG971214	HG971381	HG971532	HG971087	HG971677

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. latifolia	*Davis 639* (L)	Indonesia, Papua	C, D	HG971215	HG971382	HG971533	–	HG971678
M. latifolia	*Curry 1314* (L)	Vanuatu	C, D	HG971216	HG971383	HG971534	HG971088	HG971679
M. lauterbachii	*Whistler 1148* (B)	Samoa	F	*MG668989	*MG595158	*MG668945	–	–
M. lucida	*Meyer 808*	Tahiti	F	HG971217	HG971384	HG971535	HG971089	HG971680
M. lucida	*Florence 11461* (US)	Tahiti	F	–	*MG595168	*MG668946	–	–
M. lunu-ankenda	*Stone 16055* (US)	Malaysia	B, C	HG971218	HG971385	HG971536	–	–
M. macrocarpa	*Kato 20120215150* (MAK)	Malaysia	B, C	AB766285	AB766284	–	AB766287	–
M. madagascariensis	*Ramananjanakary 410* (MO)	Madagascar	A	HG971219	HG971386	HG971537	HG971090	HG971681
M. madagascariensis	*Schatz 4057* (MO)	Madagascar	A	HG971220	HG971387	HG971538	HG971091	HG971682
M. makahae	*Wagner 6904* (US)	Hawaii, O'ahu	G	HG002821 + HG002897	HG002441	HG002576	HG002691	HG003004
M. mantellii	*Pelser 3122* (GOET)	New Zealand	D	*MG668990	*MG595159	*MG668947	*MG668960	*MG668971
M. mantellii	*Gardner 670* (L)	New Zealand	D	*MG668991	*MG595160	*MG668948	*MG668961	*MG668972
M. margaretae	*Meyer 1003* (NY)	Austral Islands	F	HG971221	HG971388	HG971539	HG971092	HG971683
M. margaretae	*Perlman 17954* (NY)	Austral Islands	F	HG971222	HG971389	HG971540	HG971093	HG971684
M. maxii	*Brambach 1916* (GOET)	Indonesia, Sulawesi	C	*MG668992	*MG595161	*MG668949	*MG668962	*MG668973
M. micrococca	*Carroll 941* (CANB)	Australia	D	HG971223	HG971390	HG971541	–	HG971685
M. molokaiensis	*Oppenheimer 60150* (US)	USA, Hawaii, Maui	G	HG002822 + HG002898	HG002442	HG002577	HG002692	HG003005
M. molokaiensis	*Oppenheimer 80023* (US)	USA, Hawaii, Maui	G	HG002823 + HG002899	HG002443	HG002578	HG002693	HG003006
M. molokaiensis	*Wagner 6911* (US)	USA, Hawaii, O'ahu	G	HG002762	HG002444	HG002579	HG002694	HG003007
M. mucronata	*Takeuchi 19705* (L)	Papua New Guinea	D	HG971297	HG971391	HG971542	–	–
M. mucronata	*Appelhans 442* (LAE, US)	Papua New Guinea	D	–	–	HG971543	–	HG971686
M. mucronata	*Appelhans 443* (US)	Papua New Guinea	D	HG971224	HG971392	HG971544	–	–
M. mucronulata	*Wood 7041* (PTBG)	USA, Hawaii, Moloka'i	G	HG002824 + HG002900	HG002445	HG002580	HG002695	HG003008
M. munroi	*Wood 12749* (PTBG)	USA, Hawaii, Lāna'i	G	HG002763	HG002446	HG002581	HG002696	HG003009
M. nishimurae	*404831* (MAK)	Japan, Anijima Island	E	AB766373	AB766372	–	AB766375	–
M. nishimurae	*404832* (MAK)	Japan, Anijima Island	E	AB766377	AB766376	–	AB766379	–
M. nishimurae	*404829* (MAK)	Japan, Anijima Island	E	AB766365	AB766364	–	AB766367	–
M. nishimurae	*404830* (MAK)	Japan, Anijima Island	E	AB766369	AB766368	–	AB766371	–
M. novoguineensis	*Takeuchi 24615* (LAE)	Papua New Guinea	D	–	HG971453	HG971611	–	–
M. nukuhivensis	*Meyer 889*	Marquesas Islands	F	EU493232	EU493175	HG002582	EU493194	HG003010
M. oahuensis	*Wagner 6899* (US)	USA, Hawaii, O'ahu	G	HG002825 + HG002901	HG002447	HG002583	HG002697	HG003011

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. oahuensis	*Wagner 6902* (US)	USA, Hawaii, O‘ahu	G	HG002826 + HG002902	HG002448	HG002584	HG002698	HG003012
M. oahuensis	*Wagner 6910* (US)	USA, Hawaii, O‘ahu	G	HG002764	HG002449	HG002585	HG002699	HG003013
M. oblanceolata	*Appelhans 461* (LAE, US)	Papua New Guinea	D	HG971279	HG971393	HG971545	HG971094	HG971687
M. oblanceolata	*Appelhans 462* (LAE, US)	Papua New Guinea	D	–	HG971394	HG971546	HG971095	HG971688
M. obscura	*Larsen OBS1* (C)	La Réunion	A	HG971225	HG971395	HG971547	HG971096	HG971689
M. obtusifolia	*Olsen s.n.* (C)	La Réunion	A	HG971226	HG971396	HG971548	HG971097	HG971690
M. orbicularis	*Oppenheimer 60087* (US)	USA, Hawaii, Maui	G	HG002827 + HG002903	HG002450	HG002586	HG002700	HG003014
M. orbicularis	*Wood 14762* (PTBG)	USA, Hawaii, Maui	G	HG002765	HG002451	HG002587	HG002701	HG003015
M. orbicularis	*Wood 2739* (PTBG)	USA, Hawaii, Maui	G	HG002766	HG002452	HG002588	HG002702	HG003016
M. ovalis	*Wood 13724* (PTBG)	USA, Hawaii, Maui	G	HG002828 + HG002904	HG002453	HG002589	HG002703	HG003017
M. ovalis	*Wood 7682* (PTBG)	USA, Hawaii, Maui	G	EU493226	EU493169	HG002590	EU493188	HG003018
M. ovata	*Perlman 15244*–Seed and DNA collection without voucher	USA, Hawaii, Kaua‘i	G	HG002767	HG002454	HG002591	HG002704	HG003019
M. ovata	*Wagner 6897* (US)	USA, Hawaii, Kaua‘i	G	HG002768	HG002455	HG002592	HG002705	HG003020
M. ovata	*Wood 13850* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002829 + HG002905	HG002456	HG002593	HG002706	HG003021
M. pachyphylla	*Kato 20120216163* (MAK)	Malaysia	B	AB766289	AB766288	–	AB766291	–
M. pachypoda	*James 326* (LAE, BISH, GOET)	Papua New Guinea	D	HG971227	HG971397	HG971549	HG971098	HG971691
M. pachypoda	*Appelhans 417* (LAE, US)	Papua New Guinea	D	HG971228	HG971398	HG971550	HG971099	HG971692
M. pachypoda	*Appelhans 447* (LAE, US)	Papua New Guinea	D	HG971229	HG971399	HG971551	HG971100	HG971693
M. pallida	*Wood 7366-A* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002830 + HG002906	HG002457	HG002594	HG002707	HG003022
M. pallida	*Perlman 19410* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002831 + HG002907	HG002458	HG002595	HG002708	HG003023
M. paniculata	*Perlman 18693* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002832 + HG002908	HG002459	HG002596	HG002709	HG003024
M. paniculata	*Wood 13686* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002833 + HG002909	HG002460	HG002597	HG002710	HG003025
M. paniculata	*Wood 7340* (PTBG)	USA, Hawaii, Kaua‘i	G	EU493228	EU493171	HG002598	EU493190	HG003026
M. paniculata	*Wood 8234* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002834 + HG002910	HG002461	HG002599	HG002711	–
M. peduncularis	*Wagner 6905* (US)	USA, Hawaii, O‘ahu	G	HG002769	HG002462	HG002600	HG002712	HG003027
M. peduncularis	*Wagner 6909* (US)	USA, Hawaii, O‘ahu	G	HG002835 + HG002911	HG002463	HG002601	HG002713	HG003028

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. polyadenia	*Appelhans 438* (LAE, US)	Papua New Guinea	D	HG971230	HG971400	HG971552	HG971101	HG971694
M. polyadenia	*James 661* (BISH, GOET)	Papua New Guinea	D	HG971231	HG971401	HG971553	HG971102	HG971695
M. polybotrya	*Hutton 284* (CANB)	Lord Howe Island	D	EU493240	EU493183	HG971554	EU493202	HG971696
M. ponapensis	*Tangalin 1182* (PTBG)	Caroline Islands, Pohnpei	E	HG971232	HG971402	HG971555	–	–
M. ponapensis	*Tangalin 1208* (PTBG)	Caroline Islands, Pohnpei	E	HG002770	HG002464	HG002602	HG002714	HG003029
M. pteleifolia	*de Wilde 6812* (L)	Thailand	B	HG971233	HG971403	HG971556	HG971103	HG971697
M. pteleifolia	*de Wilde 6786* (L)	Thailand	B	HG002836 + HG002912	HG002465	HG002603	HG002715	HG003030
M. pteleifolia	*Wen 11376* (US)	China	B	HG971234	HG971404	HG971557	HG971104	HG971698
M. pteleifolia	*Zhou 1046* (KUN)	China	B	HG971235	HG971405	HG971558	HG971105	HG971699
M. pteleifolia	*GSBS 31117* (GH)	China, Yunnan	B	*MG668993	*MG595162	*MG668950	*MG668963	*MG668974
M. pteleifolia	*Van den Bult 1186* (M)	Thailand	B	*MG668981	–	*MG668951	–	*MG668975
M. puberula	*Wagner 6895* (US)	USA, Hawaii, Kaua‘i	G	EU493229	EU493172	HG002604	EU493191	HG003031
M. puberula	*Wood 14144* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002837 + HG002913	HG002466	HG002605	HG002716	–
M. puberula	*Wood 7438* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002838 + HG002914	HG002467	HG002606	HG002717	–
M. puberula	*Wood 7448* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002839 + HG002915	HG002468	HG002607	HG002718	HG003032
M. puberula	*Wood 8252* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002771	HG002469	HG002608	HG002719	HG003033
M. puberula	*Wood 8255* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002840 + HG002916	HG002470	HG002609	HG002720	–
M. quadrangularis	*Wood 0859* (PTBG)	USA, Hawaii, Kaua‘i	G	EU493227	EU493170	HG002610	EU493189	–
M. quadrilocularis	*404833* (MAK)	Japan, Chichijima Island	E	AB766361	AB766360	–	AB766363	–
M. quadrilocularis	*Katoh B128* (MAK)	Japan, Chichijima Island	E	AB766357	AB766356	–	AB766359	–
M. radiata	*Wagner 5966* (US)	USA, Hawaii, Hawai‘i	G	HG002841 + HG002917	HG002472	HG002612	HG002722	HG003035
M. radiata	*Wood 12335* (PTBG)	USA, Hawaii, Hawai‘i	G	HG002842 + HG002918	HG002473	HG002613	HG002723	HG003036
M. radiata	*Wood 12345* (PTBG)	USA, Hawaii, Hawai‘i	G	HG002843 + HG002919	HG002474	HG002614	HG002724	HG003037
M. reflexa	*Wood 7419* (PTBG)	USA, Hawaii, Maui	G	HG002772	HG002475	HG002615	HG002725	HG003038
M. reflexa	*Wood 7408* (PTBG)	USA, Hawaii, Maui	G	HG002773	HG002476	HG002616	HG002726	HG003039
M. remyi	*Perlman 17674* (PTBG)	USA, Hawaii, Hawai‘i	G	HG002858 + HG002937	HG002505	HG002645	HG002749	HG003060
M. retusa	*Whistler 6676* (US)	Polynesia, Tonga	F	HG002774	HG002477	HG002617	HG002727	HG003040
M. revoluta	*Meyer 888*	Marquesas islands	F	EU493231	EU493174	HG002618	EU493193	–

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. rhytidocarpa	*Gideon 20131* (L)	Papua New Guinea	D	*MG668994	*MG595163	*MG668952	*MG668964	*MG668976
M. richii	*Whistler 3664* (B)	Samoa	F	*MG668995	*MG595164	*MG668953	*MG668965	*MG668977
M. rostrata	*Wood 14210* (PTBG)	USA, Hawaii, Kaua'i	G	HG002859 + HG002938	HG002506	HG002646	HG002750	HG003061
M. rostrata	*Wood 8223* (PTBG)	USA, Hawaii, Kaua'i	G	EU493238	EU493181	HG002647	EU493200	HG003062
M. rotundifolia	*Wagner 6901* (US)	USA, Hawaii, O'ahu	G	HG002844 + HG002920	HG002478	HG002619	HG002728	HG003041
M. rotundifolia	*Wood 4133* (PTBG)	USA, Hawaii, O'ahu	G	HG002775	HG002479	HG002620	HG002729	HG003042
M. rubra	*Takeuchi 20069* (L)	Papua New Guinea	D	HG971280 + HG971298	HG971406	HG971559	HG971106	–
M. rubra	*James 612* (LAE, BISH, GOET)	Papua New Guinea	D	HG971236	HG971407	HG971560	HG971107	HG971700
M. rubra	*Appelhans 425* (LAE, US)	Papua New Guinea	D	HG971237	HG971408	HG971561	HG971108	HG971701
M. rubra	*Appelhans 397* (US)	cultivated SING (Nr. 0010298*L)	D	HG971238	HG971409	HG971562	HG971109	HG971702
***M. rubra* (aff.)**	*Takeuchi 19249* (L)	Papua New Guinea	D	*MG668979	*MG595155	*MG668942	–	–
M. sambiranensis	*Antilahimena 4763* (MO)	Madagascar	A	HG971281 + HG971299	HG971410	HG971563	HG971110	HG971703
M. schraderi	*Johns 9022* (L)	Papua New Guinea	D	HG971239	HG971411	HG971564	–	–
M. schraderi	*Appelhans 421* (US)	Papua New Guinea	D	HG971240	HG971412	HG971565	HG971111	HG971704
M. schraderi	*Appelhans 444* (LAE, US)	Papua New Guinea	D	HG971241	HG971413	HG971566	HG971112	HG971705
M. schraderi	*Appelhans 445* (LAE, US)	Papua New Guinea	D	HG971242	HG971414	HG971567	HG971113	HG971706
M. semecarpifolia	*Wagner 6588* (US)	China, Taiwan	B	HG971243	HG971415	HG971568	HG971114	HG971707
M. semecarpifolia	*Sugawara 2012080812* (MAK)	China, Taiwan	B	AB766281	AB766280	–	AB766283	–
M. sessilis	*Oppenheimer 60138* (US)	USA, Hawaii, Maui	G	HG002845 + HG002921	HG002480	HG002621	HG002730	–
M. sessilis	*Oppenheimer 80004* (US)	USA, Hawaii, Maui	G	HG002776	HG002481	HG002622	HG002731	–
M. sessilis	*Perlman 15706* (PTBG)	USA, Hawaii, Maui	G	HG002777	HG002482	HG002623	–	–
M. sessilis	*Wagner 6913* (US)	USA, Hawaii, O'ahu	G	HG002778	HG002483	HG002624	HG002732	HG003043
M. sessilis	*Wood 14769* (PTBG)	USA, Hawaii, Maui	G	HG002846 + HG002922	HG002484	HG002625	HG002733	HG003044
M. sessilis	*Wood 6207* (PTBG)	USA, Hawaii, Maui	G	HG002779	HG002485	HG002626	HG002734	HG003045
M. simplex	*Gardner 3188* (L)	New Zealand	D	HG002847 + HG002923	HG002486	HG002627	HG002735	HG003046
M. simplex	*Pelser 3121* (GOET)	New Zealand	D	*MG668996	*MG595165	*MG668954	*MG668966	*MG668978
M. sororia	*Beaman 9611* (US)	Borneo	B, C	HG971244	HG971416	HG971569	HG971115	HG971708
M. sororia	*Appelhans 384* (US)	Borneo	B, C	HG971245	HG971417	HG971570	HG971116	HG971709
M. spathulata	*Wagner 6893* (US)	USA, Hawaii, Kaua'i	G	EU493239	EU493182	HG002648	EU493201	HG003063

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
M. spathulata	*Wood 12723* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002785	HG002507	HG002649	HG002751	HG003064
M. spathulata	*Wood 14213* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002860 + HG002939	HG002508	HG002650	HG002752	HG003065
M. spathulata	*Wood 8264* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002861 + HG002940	HG002509	HG002651	HG002753	HG003066
M. spec.	*Wood 7719* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002848 + HG002924	HG002487	HG002628	HG002736	HG003047
M. spec.	*Wood 8266* (PTBG)	USA, Hawaii, Kaua‘i	G	HG002849 + HG002925	HG002488	HG002629	HG002737	HG003048
M. spec.	*Pitopang 1049* (GOET)	Indonesia, Sulawesi	–	*MG668980	*MG595169	*MG668955	–	–
M. spec.	*Munzinger 785* (MO)	New Caledonia	D	HG971282	HG971420	HG971573	HG971119	–
M. spec.	*NT 11847* (L)	Indonesia, Papua	–	HG971248	HG971421	HG971574	HG971120	HG971712
M. spec.	*Rakotovao 2873* (MO)	Madagascar	–	HG971249	HG971422	HG971575	HG971121	HG971713
M. spec.	*Ravelonarivo 1703* (MO)	Madagascar	–	HG971250	HG971423	HG971576	HG971122	HG971714
M. spec.	*Ravelonarivo 1781* (MO)	Madagascar	–	HG971251	HG971424	HG971577	HG971123	HG971715
M. spec.	*Munzinger 1111* (P)	New Caledonia	–	HG971300	HG971425	HG971578	HG971124	HG971716
M. spec.	*Munzinger 927* (P)	New Caledonia	D	HG971252	HG971426	HG971579	HG971125	HG971717
M. spec.	*Appelhans 429* (LAE, US)	Papua New Guinea	–	HG971253	HG971427	HG971580	–	–
M. spec.	*Appelhans 446* (LAE, US)	Papua New Guinea	–	HG971254	HG971428	HG971581	HG971126	HG971718
M. stellulata	*Appelhans 427* (LAE, US)	Papua New Guinea	D	HG971255	HG971429	HG971582	HG971127	HG971719
M. subunifoliolata	*Beaman 8948* (L)	Borneo	C	HG971256	HG971430	HG971583	HG971128	HG971720
M. subunifoliolata	*Appelhans 383* (US)	Borneo	C	HG971257	HG971431	HG971584	HG971129	HG971721
M. ternata	*Appelhans 487* (GOET)	cultivated Botanical Garden Goettingen	D	HG971258	HG971432	HG971585	HG971130	HG971722
M. trachycarpa	*Appelhans 430* (LAE, US)	Papua New Guinea	D	HG971259	HG971433	HG971586	–	HG971723
M. trachycarpa	*Appelhans 431* (LAE, US)	Papua New Guinea	D	HG971260	HG971434	HG971587	HG971131	HG971724
M. trichantha	*Fosberg 47679* (NY)	Caroline Islands	E	HG971261	HG971435	HG971588	–	–
M. triphylla	*Appelhans 394* (GOET)	cultivated Hortus Botanicus Leiden	C, D	HG002780	HG002489	HG002630	HG002738	HG003049
M. triphylla	*Utteridge 252* (L)	Indonesia, Papua	C, D	HG971262	HG971436	HG971589	–	–
M. vatiana	*Whistler 4170* (US)	Samoa	F	HG002850 + HG002926	HG002490	HG002631	HG002739	–
M. vieillardii	*McPherson 18066* (MO)	New Caledonia	D	HG002781	HG002491	HG002632	HG002740	HG003050
M. viticina	*Chantarasuwan 2011-01* (US)	Thailand	B	HG971263	HG971437	HG971590	HG971132	HG971725
M. viticina	*Esser 11-47* (M)	Thailand	B	HG971264	HG971438	HG971591	HG971133	HG971726
M. vitiflora	*Forster 29363* (L)	Australia	D	HG002851 + HG002927	HG002492	HG002633	HG002741	HG003051

Continued

Table 1 Continued

Taxon	Voucher information		Area code	*trnL-trnF*	ITS	ETS	*psbA-trnH*	*NIAi3*
	Collector & number (Herbarium)	Origin						
***M. vitiflora* (cf)**	*Appelhans 433* (LAE, US)	Papua New Guinea	D	HG971265	HG971439	HG971592	HG971134	–
M. volcanica	*Oppenheimer 100029* (US)	USA, Hawaii, Maui	G	HG002782	HG002493	HG002634	HG002742	HG003052
M. volcanica	*Wood 13735* (PTBG)	USA, Hawaii, Maui	G	HG002852 + HG002928	HG002494	HG002635	HG002743	HG003053
M. volcanica	*Wood 4650* (PTBG)	USA, Hawaii, Hawai'i	G	HG002853 + HG002929	HG002495	HG002636	–	–
M. volcanica	*Wood 6797* (PTBG)	USA, Hawaii, Maui	G	HG002854 + HG002930	HG002496	HG002637	–	–
M. waialealae	*Wood 8148* (PTBG)	USA, Hawaii, Kaua'i	G	HG002855 + HG002931	HG002497	HG002638	HG002744	HG003054
M. waialealae	*Wood 8185* (PTBG)	USA, Hawaii, Kaua'i	G	HG002783	HG002498	HG002639	HG002745	HG003055
M. waialealae	*Wood 8233* (PTBG)	USA, Hawaii, Kaua'i	G	HG002856 + HG002932	HG002499	HG002640	–	HG003056
M. wawraeana	*Wood 7463* (PTBG)	USA, Hawaii, Kaua'i	G	HG002933	HG002500	HG002641	HG002746	HG003057
M. wawraeana	*Wood 8147* (PTBG)	USA, Hawaii, Kaua'i	G	HG002857 + HG002934	HG002501	HG002642	HG002747	HG003058
M. wawraeana	*Wood 7464* (PTBG)	USA, Hawaii, Kaua'i	G	HG002784	HG002502	HG002643	HG002748	HG003059
M. xanthoxyloides	*Takeuchi 15373* (L)	Papua New Guinea	D	HG971301	HG971440	HG971593	HG971135	–
Ma. spec.	*John 145743* (L)	Malaysia, Sabah	B, C	HG971289	HG971329	HG971483	–	–
Me. glandulosa	*Forster 25045* (L)	Australia, Queensland	D	HG971172	HG971330	HG971484	HG971045	–
My. macrocarpa	*Van Balgooy 6955* (L)	New Caledonia	D	*MG668983	*MG595166	–	*MG668956	–
My. myrtoidea	*McPherson 18026* (MO)	New Caledonia	D	HG971283	HG971441	–	HG971136	–
My. spec.	*Lowry II 6464* (L)	New Caledonia	D	*MG668982	*MG595167	–	*MG668957	–
Pe. parviflorum	*Pullen 7313* (US)	Papua New Guinea	D	HG971267	HG971443	HG971595	HG971138	–
Pic. glandulosa	*McKee 3189* (US)	New Caledonia	D	HG971268	HG971444	HG971597	HG971140	HG971727
Pic. glandulosa	*McPherson 18598* (MO)	New Caledonia	D	HG971269	HG971445	HG971598	HG971141	HG971728
Pic. ignambiensis	*McPherson 19132* (MO)	New Caledonia	D	HG971284 + HG971302	HG971446	HG971599	HG971142	HG971729
Pit. haplophyllus	*Ford 4821* (L)	Australia, Queensland	D	HG971270	HG971447	HG971600	HG971143	HG971730
S. follicularis	*Munzinger 668* (MO)	New Caledonia	D, F	HG971303	HG971448	HG971601	HG971144	HG971731
T. tetrandrum	*Beaman 8917* (L)	Borneo	C, D	HG971271	HG971449	HG971602	HG971145	HG971732
T. tetrandrum	*Utteridge 544* (L)	Papua New Guinea	C, D	*MG668984	*MG595152	*MG668939	–	–
T. tetrandrum	*Utteridge 436* (L)	Indonesia, Papua	C, D	LN849198	LN849159	LN849250	LN849176	LN849219
T. tetrandrum	*Brambach 1472* (GOET)	Indonesia, Sulawesi	C, D	*MG668985	*MG595153	*MG668940	–	*MG668967

Herbarium acronyms are according to Index Herbariorum (http://sweetgum.nybg.org/science/ih/). Specimens used for the AAR and the diversification analyses are marked in bold. Abbreviations of genus names are: *A.* = *Acronychia*, *Bo.* = *Boronella*, *Br.* = *Brombya*, *C.* = *Comptonella*, *D.* = *Dutaillyea*, *E.* = *Euodia*, *Ma.* = *Maclurodendron*, *Me.* = *Medicosma*, *M.* = *Melicope*, *My.* = *Myrtopsis*, *Pe.* = *Perryodendron*, *Pic.* = *Picrella*, *Pit.* = *Pitaviaster*, *S.* = *Sarcomelicope*, *T.* = *Tetractomia*. For the definition of the area code see Fig. 1. Sequences generated for this study are marked with *.

Table 2 Models of sequence evolution for all single marker alignments (full dataset and reduced dataset for Ancestral Area Reconstruction in BioGeoBEARS and Diversification Analyses in BAMM) estimated using the Akaike Information Criterion (AIC) algorithm in jModeltest 2.1.7 (Darriba et al., 2012)

	trnL-trnF	ITS	ETS	*psbA-trnH*	*NIAi3*
Full dataset					
Best AIC model	TVM + I + G	GTR + I + G	TIM2 + G	TVM + G	TPM3uf + G
Best AIC model available for MrBayes	GTR + I + G	GTR + I + G	GTR + G	GTR + G	GTR + G
Best AIC model available for BEAST	GTR + I + G	GTR + I + G	GTR + G	GTR + G	GTR + G
BioGeoBEARS & BAMM dataset					
Best AIC model	TVM + G	TIM2ef + I + G	TIM2 + G	TVM + G	TIM3 + I + G
Best AIC model available for MrBayes	GTR + G	GTR + I + G	GTR + G	GTR + G	GTR + I + G
Best AIC model available for BEAST	GTR + G	GTR + I + G	GTR + G	GTR + G	GTR + I + G

The table shows the models with the highest likelihood scores and the highest available models available in MrBayes 3.2.5 and BEAST v.1.8.4.

1981) represent *Tetradium* Lour. species, a genus only distantly related to *Melicope* (Poon et al., 2007).

Since no reliable fossils were available, a secondary calibration was used to constrain the root age. Appelhans et al. (2012) used a dataset including all major lineages of Rutaceae as well as all families of Sapindales for a molecular dating analysis, employing four fossil calibration points. We used the estimated split between *Melicope* and the Australian *Correa* Andrews - *Philotheca* Rudge clade from Appelhans et al. (2012) to constrain the root age in the present study. *Myrtopsis*, the outgroup taxon in our study belongs to this clade (Bayly et al., 2013). The prior for the root age was assigned a normal distribution and was truncated to an upper limit of 48.99 Ma (millions of years ago) and a lower limit of 35.61 Ma, reflecting the 95% credibility interval for this split as inferred by Appelhans et al. (2012).

The models of sequence evolution were set as in Table 2. Two independent BEAST runs consisted of 50 million generations each with tree sampling every 1000th generation. A UPGMA starting tree was used, a lognormal relaxed clock was applied and the tree prior was set to the birth-death process. The resulting tree files contained 50 000 trees, and we used LogCombiner v.1.8.4 (Drummond et al., 2012) to resample states at lower frequency and thereby shrinking the resulting tree files to 10 000 trees. Of these, ten percent were discarded as burn-in using LogCombiner, and a maximum clade credibility (MCC) tree was calculated in TreeAnnotator v.1.8.4 (Drummond et al., 2012) after checking if effective sample sizes (ESS) were above 200 for all parameters in Tracer 1.6.0 (Rambaut et al., 2014).

2.4 Ancestral area reconstruction

The BioGeoBEARS package (Matzke, 2013) implemented in R 3.1 was used for AAR.

Seven areas of endemism were delimited based on clusters of distributions of member species of the clade. These areas are similar to those based on wider assessments of floras of the regions by Takhtajan (1986).

These areas are: (A) Madagascar and the Mascarene Islands; (B) Mainland S & E Asia, including Hainan, Taiwan and the Ryukyu Islands, excluding the Malay peninsula; (C) Malesia; (D) Australasia (New Guinea to Vanuatu, Australia, New Caledonia, New Zealand, Lord Howe Island, Kermadec Islands); (E) Micronesia, Ogasawara and Bonin Islands; (F) Fiji to Marquesas, Society, and Austral Islands; and (G) Hawaiian Islands (Fig. 1).

For the AAR, each specimen was assigned to the distribution area of the species, except for the genera *Maclurodendron*, *Medicosma*, *Sarcomelicope* and *Tetractomia* and the *Melicope sororia* T.G.Hartley clade. These taxa each contain between five to 22 species, but only one species each was included in our analyses. We assigned the distribution area of the whole taxon to the sampled specimen in order not to neglect any geographical information. All other genera were represented with species throughout their geographic range. The outgroup taxa *Boronia* (section *Boronella*) and *Myrtopsis* are representatives of large and mainly Australian clades (Kubitzki et al., 2011; Bayly et al., 2013).

BioGeoBEARS implements the two most frequently used biogeographic models: the Dispersal-Vicariance (DIVA; Ronquist, 1997) model and the Dispersal-Extinction-Cladogenesis (DEC) model (Ree & Smith, 2008). In addition, the BAYAREA model is available in BioGeoBEARS, which resembles the Bayesian Binary Model in RASP (Yu et al., 2015). These three models can be modified by adding a factor "J" for founder-event speciation or jump dispersal (Matzke, 2013, 2014) and we compared the six models "DIVALIKE", "DIVALIKE+J", "DEC", "DEC+J", "BAYAREA" and "BAYAREA+J".

2.5 Diversification analyses

Diversification analyses were carried out using BAMM (Bayesian Analysis of Macroevolutionary Mixtures; Rabosky et al., 2014). To account for incomplete taxon sampling with non-random distribution of missing taxa throughout the phylogeny, all missing taxa were assigned to one of the major clades based on morphological evidence (Hartley, 1974, 1983, 1984, 2001, 2013; Hartley & Mabberley, 2003). For this, the dated phylogenetic tree based on the dataset that contains only one sample per species was subdivided into 17 major clades (Table 3). The numbers of species per clade are largely different because several clades allowed assigning missing taxa with high confidence (e.g., "CD" clade), whereas the uncertainty to place missing taxa in other clades was higher, resulting in a broader definition of a group (e.g., "Le" clade). For each clade, the percentage of sampled species was calculated and used as input for BAMM (Table 3). As a control to evaluate the effects of clade sizes, we did a BAMM analysis in which the dataset was split up in only nine clades of similar

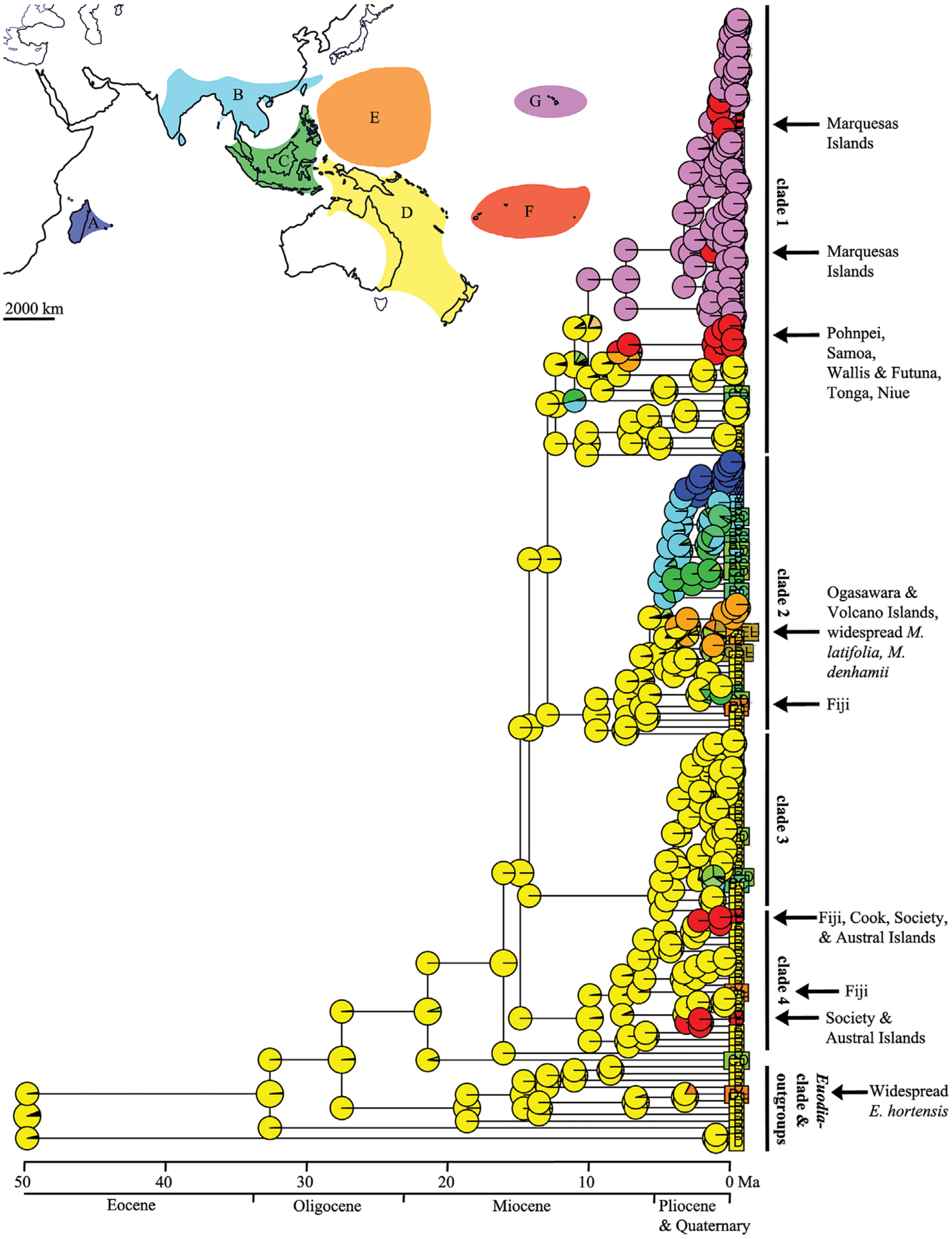

Fig. 1. Definition of areas and results of the Ancestral Area Reconstruction using BioGeoBEARS. The dispersal events into the Pacific are highlighted on the right. See 2.4 for the definitions of areas A to G. Source of the map: www.d-maps.com.

size (clades CD, M2, NC, Sa and VP merged into one clade; clades Ha, M1, Pe, Pl and So merged into one clade).

All BAMM analyses consisted of four Markov chain Monte Carlo (MCMC) chains, which were run for 10 million generations, with all other settings left at their defaults. The visualization of the results was done using the R-package 'BAMMtools' (Rabosky et al., 2014).

3 Results

3.1 Phylogeny & molecular dating

The phylogenetic reconstructions are congruent with Appelhans et al. (2014a, 2014b) and Holzmeyer et al. (2015) and are not described or discussed in detail here. The *Acronychia-Melicope* clade shows the same four main clades as described by Appelhans et al. (2014a), and also the sister relationships of *Acronychia-Melicope* with *Medicosma*, and of *Acronychia-Melicope-Medicosma* with *Tetractomia* are supported (Figs. 2, S1).

The results of the BEAST analyses were congruent with the MrBayes analysis. BEAST analyses based on the full dataset and the smaller dataset, which included one specimen per species were nearly identical except for the root age. The root age of the full dataset was estimated to 35.6 Ma, while that of the smaller dataset was 49.1 Ma and the credible intervals did not overlap. However, all age estimates concerning the ingroup showed differences of less than 1 Myr in the two

Table 3 Definitions of clades specified in the BAMM analysis and the numbers and percentages of included and missing taxa. For the exact placement of the clades in the phylogenetic trees, see Fig. 4

Clade name	Description of included taxa	Total number of taxa (included + missing)	Number of missing taxa	Percentage of missing taxa	Percentage of included taxa
Ac	*Acronychia* & *Maclurodendron*	55	31	0.56	0.44
CD	*Comptonella, Dutaillea, Dutailliopsis*	11	6	0.55	0.45
Eu	*Euodia* incl. *M. vitiflora, Pitaviaster, Brombya*	11	4	0.36	0.64
Ha	Hawaiian & Marquesas *Melicope* section *Pelea*	55	15	0.27	0.73
Le	*Melicope* section *Lepta*	102	64	0.63	0.37
M1	*Melicope* section *Melicope* part 1	28	20	0.71	0.29
M2	*Melicope* section *Melicope* 2 (incl. type species)	6	1	0.17	0.83
Me	*Medicosma*	22	21	0.95	0.05
NC	New Caledonian *Melicope* section *Pelea*	5	2	0.40	0.60
Pd	*Perryodendron*	1	0	0.00	1.00
Pe	Non-Hawaiian/Marquesas, non-New-Caledonian *Melicope* section *Pelea*	25	14	0.56	0.44
Pl	*Platydesma*	4	0	0.00	1.00
Sa	*Sarcomelicope*	9	8	0.89	0.11
So	*Melicope sororia* and relatives	5	4	0.80	0.20
Te	*Tetractomia*	6	5	0.83	0.17
VP	*Melicope* section *Vitiflorae* pro parte plus *Picrella*	10	5	0.50	0.50
Total ingroup	*Acronychia-Euodia-Melicope* clade	355	200	0.56	0.44
Outgroups	*Boronella* & *Myrtopsis*				

datasets and only the age estimates of the full dataset are described here. The oldest fossils that might belong to the *Acronychia-Euodia-Melicope* group were not included in our analyses because of their unclear affinities, but their ages are congruent with our molecular dating results that suggest an origin of the main lineages in the Late Oligocene to Mid Miocene. This is congruent with other molecular dating analyses in the order Sapindales (Manafzadeh et al., 2014; Koenen et al., 2015; Muellner-Riehl et al., 2016).

The BEAST analyses (Fig. 2) supported the tree topology of the Bayesian phylogenetic reconstruction (Fig. S1). The *Euodia* clade dated back to Mid or Early Miocene with a crown age of 17.3 Ma (credibility interval: 12.1–24.6 Ma). The crown age marked the split between *Perryodendron* from the remainder of the *Euodia* clade. *Euodia* (including *Pitaviaster*, *Brombya* and *Melicope vitiflora*) was also estimated to be of Miocene origin (mean: 14.1 Ma; credibility interval: 9.6–19.5 Ma).

The BEAST analysis supported *Melicope* and *Acronychia* as close relatives and sister to *Medicosma*, and this clade was then sister to *Tetractomia*. The *Acronychia-Medicosma-Melicope-Tetractomia* clade started to diversify in the Late Oligocene or Early Miocene (20.7 Ma; 15.0–26.9 Ma) and the *Acronychia-Medicosma-Melicope* clade diversified later (15.9 Ma; 11.3–21.3 Ma). *Acronychia* was nested within *Melicope* in the BEAST MCC tree, but statistical support was lacking (0.86 pp) and the clade dated from the Early to Late Miocene (14.8 Ma; 10.6–19.8 Ma).

There were four main clades in the *Acronychia-Melicope* group (=clades 1 to 4 in Figs. 1, 2). Clade 1: *Melicope* section *Pelea* (A.Gray) Hook.f. p.p., the former genus *Platydesma*, as well as two clades of *Melicope* section *Melicope* p.p., was estimated to have originated in the Late or Mid Miocene (12.3 Ma; 8.5–16.9 Ma). Clade 2: section *Lepta* (Lour.) T.G. Hartley, was slightly younger (9.6 Ma; 6.2–14.1 Ma). Clade 3: *Acronychia* and *Maclurodendron*, dated to the Late Miocene or Early Pliocene (4.9 Ma; 3.1–8.1 Ma). Within the *Acronychia-Maclurodendron* clade, all early-branching clades were Australian taxa, while all New Guinean and Malesian species belonged to one clade that was estimated to the Pliocene to Early Pleistocene (2.5 Ma; 1.5–4.1 Ma). Clade 4: *Melicope* sections *Melicope* p.p. and *Vitiflorae* T.G.Hartley p.p., *Sarcomelicope* and several New Caledonian genera, had a similar age as the species-rich clades 1 and 2 (9.9 Ma; 6.1–15.1 Ma).

The ages of several geographic clades were of particular interest. The Malagasy and Mascarene species were monophyletic within clade 2 with an origin in the Pliocene or Early Pleistocene (2.8 Ma; 1.7–4.4 Ma). Within this clade, the specimens from La Réunion and Mauritius formed a clade, which was dated to the Pleistocene (0.8 Ma; 0.3–1.7 Ma). Clade 4 contained a high proportion of taxa from New Caledonia. All New Caledonian subclades are dated to the Mid Miocene to Early Pliocene.

The Hawaiian clade that also contained all species from the Marquesas Islands had a stem age from the Mid or Late

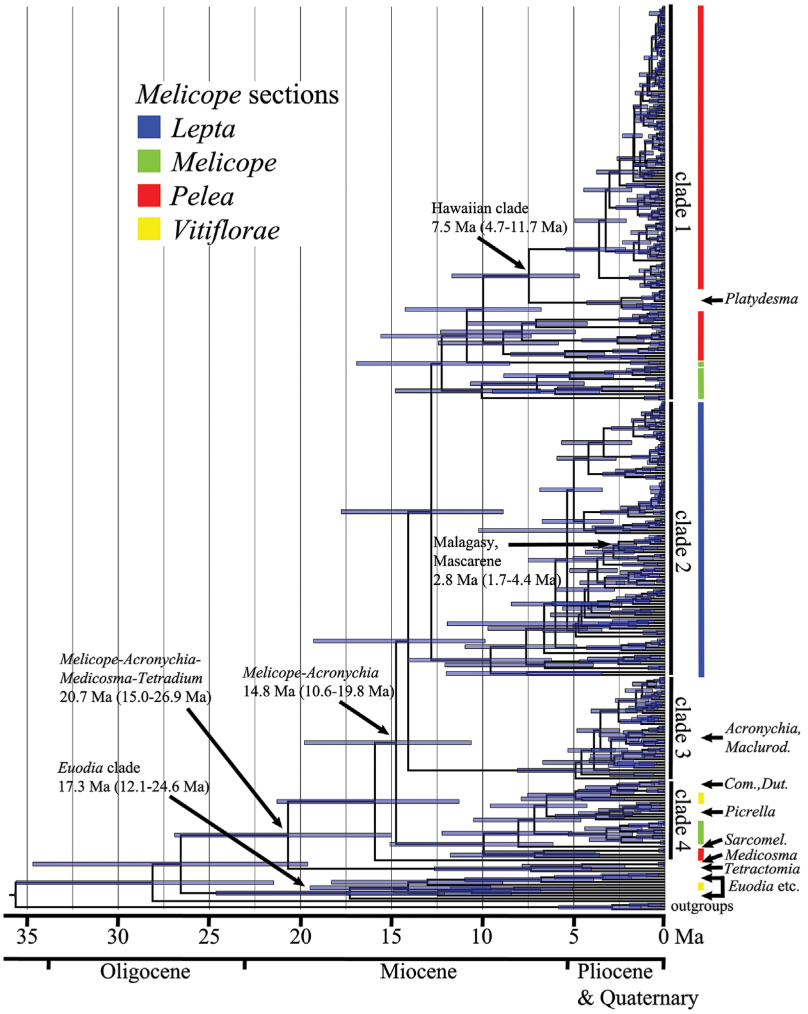

Fig. 2. Molecular dating of the *Acronychia-Euodia-Melicope* clade using BEAST. The maximum clade credibility consensus tree is shown with the credibility intervals of the age estimations displayed as bars. Important nodes are highlighted and their mean age estimates and credibility interval (in brackets) are shown. Colored bars indicate the four sections of *Melicope*, and the positions of other genera are marked with arrows. Abbreviations of genus names are: *Com.* = *Comptonella, Dut.* = *Dutaillyea, Maclurod.* = *Maclurodendron, Sarcomel.* = *Sarcomelicope.*

Miocene (10.0 Ma; 6.8–14.3 Ma), while the diversification began in the Late Miocene or Early Pliocene (7.5 Ma; 4.7–11.7 Ma). Compared to the Hawaiian clade, all other Pacific clades are relatively young with estimated origins in the Pleistocene.

3.2 Ancestral area reconstruction

The comparison of the six available methods revealed that the DEC+J model suited our dataset the best. Adding jump dispersal (J) increased the likelihood of the AAR in all cases (DEC, DIVALIKE, BAYAREA) (Table 4).

The AAR clearly identified Australasia (area D) as the geographic origin of both the *Acronychia-Melicope* clade and the *Euodia* clade (Fig. 1). Within the *Euodia* clade, only the widespread species *E. hortensis* J.R.Forst. & G.Forst. colonized areas outside Australasia, and it is also found in the South Pacific area F.

The *Acronychia-Melicope* clade showed a more complex biogeographic pattern. In clade 1 (Fig. 1), the Hawaiian lineage was sister to the remainder of section *Pelea*, and our results suggested an origin of the Hawaiian lineage from an Australasian ancestor (colonization number 1 in Fig. 3). A second lineage from clade 1, containing species from Pohnpei, Samoa, Wallis & Futuna, Tonga and Niue (number 2 in Fig. 3) dispersed eastward. Clade 2 (Fig. 1) did not disperse far into the Pacific Ocean and only three species colonized Fiji, Tonga and Samoa (numbers 7 to 9 in Fig. 3). Members of clade 2 also colonized the North Pacific. The widespread *Melicope denhamii* (Seem.) T.G.Hartley reaches its northern limit in the Philippines and is also found on Palau and Pohnpei (numbers 3 and 6 in Fig. 3). A second lineage colonized Palau and the Ogasawara and Volcano Islands, respectively (numbers 4 and 5 in Fig. 3). A larger lineage colonized Malesia (area C) and mainland southern Asia (area B) as far west as southern India and Sri Lanka. This lineage gave rise to the Malagasy and Mascarene species (area A). Clade 3 (Fig. 1) was of Australasian origin and most of the species are endemic to

Table 4 Comparison of the six models for Ancestral Area Reconstruction

Model	LnL
DEC	−214.7720
DEC + J	−204.5273
DIVALIKE	−223.0560
DIVALIKE + J	−211.6971
BAYAREA	−248.3574
BAYAREA + J	−208.7406

New Guinea and Australia. Only two lineages extend from Australasia. These are: *A. trifoliolata* Zoll. & Moritzi, which reaches its westernmost distribution in Java, and the *A. pedunculata* Miq. and *Maclurodendron* clade, which occurs from New Guinea to India and Sri Lanka. Clade 4 contains mostly species from New Caledonia and this clade dispersed into the South Pacific at least twice (numbers 10 and 11 in Fig. 3). Both dispersal events led to the colonization of the Society and Austral Islands.

3.3 Diversification analyses

The diversification analyses were visualized as a heatmap plotted on the time-calibrated phylogenetic tree and as a lineage-through-time plot (Fig. 4). The heatmap (Fig. 4A) showed clades in colors according to their relative diversification rates and blue colors indicated low rates, while red colors identified high rates. The lowest relative diversification rates can be observed for the *Euodia* clade (clades Eu and Pd in Fig. 4). Also *Tetradium* (Te) and *Medicosma* (Me), the successive sister groups to the *Acronychia-Melicope* clade, exhibit low relative diversification rates. Medium relative diversification rates characterize the mainly New Caledonian clade (CD, M2, NC, Sa, VP). Medium to higher relative diversification rates are found in the three sister clades (M1, So, Pe) to the Hawaiian taxa and in section *Lepta* (Le). The highest relative diversification rates were found in two young clades: the *Acronychia-Maclurodendron* clade (Ac) and especially the Hawaiian clade (Ha).

On average, the lineage-through-time plot (Fig. 4B) showed a relatively constant diversification. This was interrupted by two phases with increased relative diversification rates (marked with orange bars in Fig. 4). The first phase lasted from about 18 to 14 Ma and marked the timeframe in which the major lineages of the *Acronychia-Euodia-Melicope* clade originated. The second phase started at about 3.5 to 4 Ma and lasted until now. The major part of the diversification within the *Acronychia-Maclurodendron* clade (Ac) and the Hawaiian clade (Ha) fell within this phase.

The second BAMM analysis, in which the dataset was subdivided into nine instead of 16 clades, delivered identical results.

4 Discussion

4.1 Origin and the ages of the *Acronychia-Euodia-Melicope* group

Our ancestral area reconstruction clearly suggests an Australasian origin of the *Acronychia-Euodia-Melicope* group. Broader phylogenetic studies of Rutaceae showed that *Acronychia* and *Melicope* are part of a larger clade of mainly Australasian genera (Groppo et al., 2008; Appelhans et al., 2012; Bayly et al., 2013) and the three successive sister clades to the

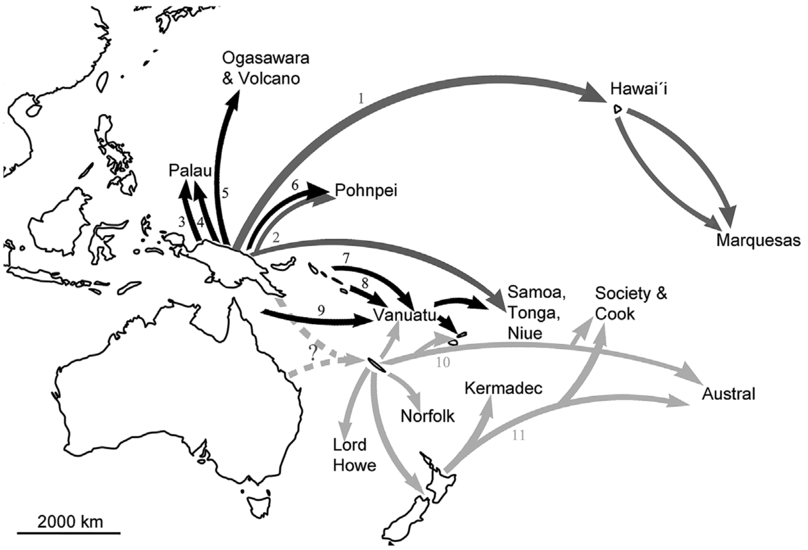

Fig. 3. Dispersal patterns of *Melicope* in the Pacific inferred from the Ancestral Area Reconstruction. Arrows in dark gray refer to lineages from clade 1, black arrows indicate lineages from clade 2, and light gray arrows are for lineages from clade 4 (see Figs. 1, 2, S1). An alternative pathway for the colonizations of Palau, Pohnpei, Ogasawara and Volcano Islands (black arrows) would be from the Philippines instead of New Guinea. The numbers (1-11) refer to those mentioned in the results section (3.2). The question mark and the dashed line indicate that it is unclear whether the colonization to New Caledonia is from an Australian or New Guinean ancestor. Source of the map: www.d-maps.com.

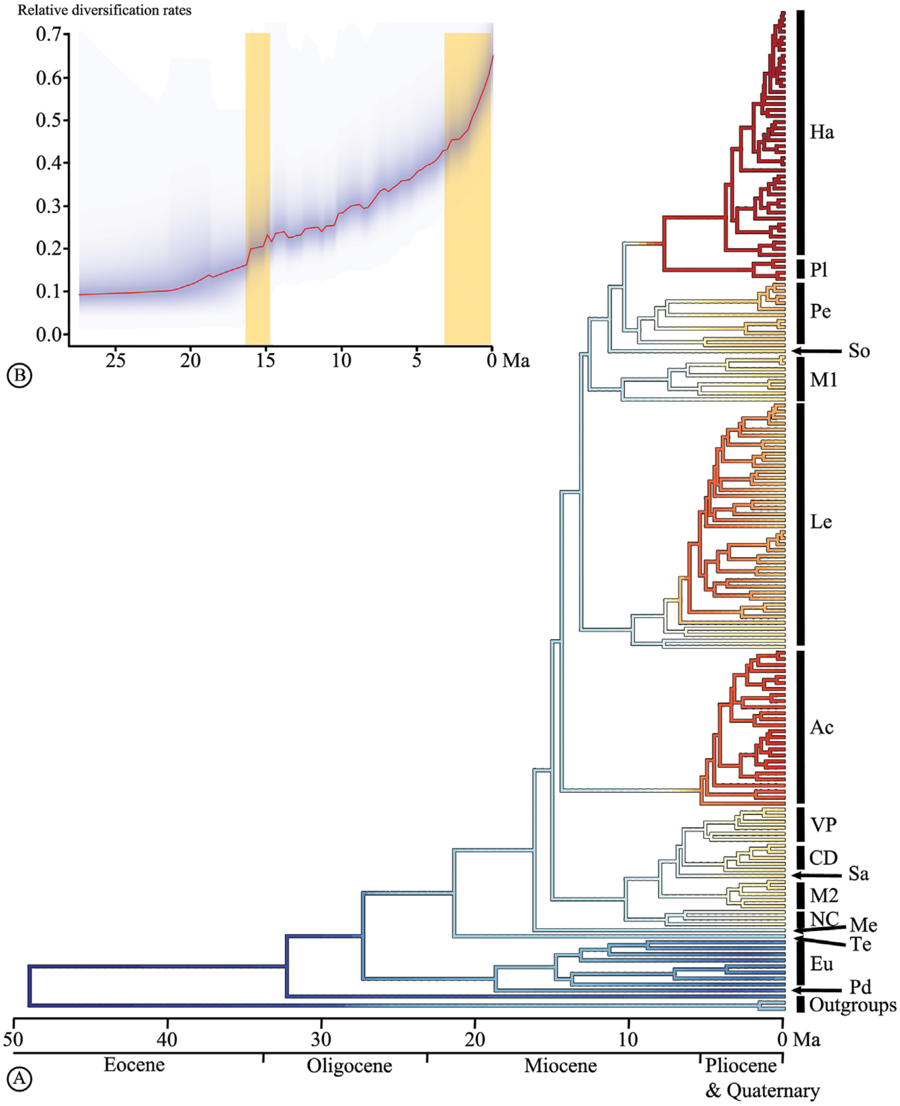

Fig. 4. Results of the diversification analyses. The lineage-through-time plot is displayed with time in millions of years on the x-axis and relative diversification rates on the y-axis. Two epochs with major shifts in diversification rates are highlighted in orange (**B**). The branches in the phylogenetic tree are colored by their relative diversification rates, and red/orange colors represent high diversification rates whereas blue colors indicate low diversification rates. See Table 3 for definitions of the clade names (**A**).

Acronychia-Euodia-Melicope group are Australasian and mostly endemic to Australia (Bayly et al., 2013). The reconstruction of Australasia as the geographic origin of the *Acronychia-Euodia-Melicope* group is therefore not surprising.

While species of the *Euodia* clade and clades 3 and 4 (Fig. 1) are mainly restricted to Australasia, several lineages of clades 1 and 2 moved out of Australasia. In clade 1, three lineages moved out of Australasia. One lineage migrated into Malesia in the Late or Mid Miocene (10.9 Ma; 7.3–15.6 Ma; Fig. 2). This lineage consists of *M. sororia* and putatively five morphologically similar species that have not been sampled. This group colonized an area from Borneo to Hainan (China) and southern India (Hartley, 2001). The other two migrations relate to Pacific lineages, which will be discussed in the next section. The westward migration from Australasia in clade 2 (Fig. 1) is more complex, however, the number and timing of these migrations cannot be determined with confidence because of low statistical support of several subclades and the present low sampling of species from Sumatra and the Philippines. Clade 2 contains at least two well-supported subclades mainly from Malesia and mainland SE Asia. Their divergences from the Australasian lineages are dated to the Late Miocene to Pliocene (6.0 Ma; 4.1–8.4 Ma; and 4.9 Ma; 3.5–6.7 Ma; Fig. 2). The slightly younger subclade also contains the Malagasy and Mascarene species of *Melicope*. The closest relatives of these species are *M. glomerata* (Craib) T.G.Hartley and *M. vicitina* (Wall. ex Kurz) T.G.Hartley from mainland SE Asia and the split of the Malagasy and Mascarene lineage from these two species was dated to the Pliocene (3.4 Ma; 2.0–5.0 Ma; Fig. 2). This disjunction is one of the many examples of biogeographic connections of tropical Asia and Madagascar (Schatz, 1996).

4.2 Dispersal routes in the Pacific

Our analyses suggest numerous independent dispersal events across the Pacific archipelagos in the *Acronychia-Euodia-Melicope* group (Figs. 1, 3).

The Solomon Islands, Vanuatu and New Caledonia played a crucial role in the diversification of the *Acronychia-Euodia-Melicope* group in the South Pacific. Within *Euodia* only one species (*E. hortensis*) colonized areas east of Vanuatu. Pacific Islanders utilize this species for its strong fragrance and for medicinal proposes. Its occurrence east of Fiji might not be natural, as it is found there only in cultivation and disturbed areas (Smith, 1985; Hartley, 2001). The *Acronychia-Melicope* clade contains many New Caledonian endemics (Fig. 1, clade 4) and New Caledonia was the origin of several dispersal events deeper into the Pacific Ocean. One dispersal event to New Zealand resulted in three species, of which one is also found on the Kermadec Islands. This New Zealand lineage also colonized Tahiti (2 spp.) and the remote Austral Islands (1 sp.). A second lineage of New Caledonian ancestry colonized Fiji, and the Cook, Society and Austral Islands; and Tahiti and the Austral Islands have thus been colonized twice independently. Within the New Caledonian lineage (clade 4), two independent colonization events for Lord Howe Island are inferred. The first colonization corresponds to the widespread species *Sarcomelicope simplicifolia* (Endl.) T.G.Hartley, which also occurs from eastern Australia to Fiji (Hartley, 1982). The second colonization refers to the Lord Howe endemic *M. polybotrya* (C.Moore & F.Muell.) T.G. Hartley (Hartley, 2001). One additional colonization event to Lord Howe Island occurred in clade 2 (*M. contermina* C. Moore & Muell.) and is probably derived from an Australian ancestor. Australia is the most important source area for the Lord Howe Island flora, so is New Caledonia's role as a major source area (Papadopulos et al., 2011). *Melicope* (including *Sarcomelicope*) is the only known plant genus with three independent colonizations into Lord Howe Island.

With ten species, Samoa has the second highest number of *Acronychia-Euodia-Melicope* species in the Pacific. In addition to the widespread species *E. hortensis* and *M. latifolia* (DC.) T.G.Hartley, the remaining species from Samoa belong to section *Pelea* (clade 1, Fig. 1) and five out of eight species have been sampled here. These five species form a clade, and are therefore probably the result of a single colonization event. *Melicope sulcata* T.G.Hartley, one of the Samoan species that could not be sampled here, is morphologically different from other Samoan species (Hartley, 2001) and might be the result of an independent colonization event. The Samoan clade is sister to *M. ponapensis* Lauterb. from Pohnpei (Caroline Islands), which is supported by morphology (Hartley, 2001). The closest relatives of this clade are from New Guinea (Fig. S1), which is likely the ancestral area of this group. The Caroline Islands (Pohnpei and Kosrae) were colonized a second time by the widespread *M. denhamii* (clade 2, Fig. 1). This species also colonized Palau and in turn, Palau was colonized by a second lineage. This lineage consists of two endemic species, which are related to the widespread *M. latifolia* in clade 2 (Appelhans et al., 2014a; Fig. 1). The Japanese Ogasawara and Volcano Islands represent the northernmost colonization of *Melicope* in the Pacific. The three endemic species are most likely the result of a single colonization event either from New Guinea or the Philippines (Figs. 1, 3).

By far the most species-rich lineage within *Melicope* is the Hawaiian radiation with 55 endemic species (Wood et al., 2017). The seven species from the Marquesas Islands are part of the Hawaiian lineage (Fig. 1), but belong to two different subclades, supporting two colonization events to the Marquesas Islands.

Most colonization events in the Pacific region east of the andesite line are dated to the Pleistocene (Fig. 2) and all archipelagos, on which *Melicope* species occur, were already present in the Pleistocene (Clouard & Bonneville, 2005; Neall & Trewick, 2008). The Hawaiian Islands represent the only archipelago, for which our molecular dating results conflict with the age of islands. The stem age of Hawaiian *Melicope* is dated to the Mid or Late Miocene, while the oldest of the current main islands are about 5 Myr old (Price & Clague, 2002; Neall & Trewick, 2008). The Hawaiian Islands are part of the Hawaiian-Emperor seamount chain and other islands of the chain were present in the Mid to Late Miocene. The initial colonization of the Hawaiian Islands might have occurred on the Gardner Pinnacles, French Frigate Shoals, Necker or Nihoa, which are now low islands with depauperate vegetation (Amerson, 1975; Price & Clague, 2002). Since only small and distantly spaced islands were present at the Hawaiian-Emperor seamount chain when Kaua'i formed, Price & Clague (2002) hypothesized a 'bottleneck' for colonization between 8 and 5 Ma. This bottleneck is supported by molecular dating analyses: most Hawaiian lineages have crown ages of 5 Ma or less (Keeley & Funk, 2011). Nevertheless, some Hawaiian lineages, most notably the *Drosophila* Fallén (Russo et al., 1995) and Lobeliad (Givnish et al., 2009) lineages, have estimated ages older than the current main islands, like in *Melicope*. Thus at least some lineages were able to get through the bottleneck. The age estimates for *Melicope* further suggest that the split between the two major Hawaiian clades (*Melicope* section *Pelea* and the former genus *Platydesma*) occurred on one of the leeward islands.

The largely New Caledonian clade (clade 4; Figs. 1, 2) has an estimated crown age in the Mid to Late Miocene. This estimation is in agreement with the hypothesis that New Caledonia was re-colonized via oceanic dispersals after being submerged from the Late Cretaceous to about 37 Ma (Pillon, 2012).

4.3 Differences in diversification rates

The crown ages of the *Euodia* clade and the *Acronychia-Melicope* clade are estimated to be of a nearly identical age (Mid to Early Miocene; 17.3 Ma; 12.1–24.6 Ma vs. 14.8 Ma; 10.6–19.3 Ma). The *Euodia* clade contains about 12 species, while the *Acronychia-Melicope* clade consists of more than 315 species (Kubitzki et al., 2011). With the close relationship among *Zieria*, *Neobyrnesia* and the *Euodia* clade, and that of *Boronia* section *Cyanothamnus* with the *Acronychia-Melicope* clade (Duretto M, unpublished data) considered, this ratio would be about 72 versus more than 338 species (Kubitzki et al., 2011). This large difference in species richness is reflected in the distribution of the two groups. While the *Acronychia-Melicope* clade is widely distributed from Madagascar to the Hawaiian Islands (Fig. 1), the *Euodia* clade is only from the Moluccas in the west to Samoa and Niue in the east (Hartley, 1997, 2001) and its occurrence east of Fiji might not be natural (Smith, 1985). Most species of the *Euodia* clade grow in ever-wet tropical rainforest up to 1200 m, and only two reach higher altitudes of up to 2250 m (Hartley, 1997, 2001, 2013). Most species of the *Acronychia-Melicope* clade are from tropical regions. However, some lineages colonized subtropical areas in Australia and New Zealand (Hartley, 2001). While most species occur in rainforests, several species have adapted to other vegetation types including monsoon forests, savannahs, *Eucalyptus* L'Hér. woodlands, subalpine shrublands, alpine grasslands and bogs (Wagner et al., 1990; Hartley, 2001). The *Acronychia-Melicope* clade also reaches much higher altitudes compared to the *Euodia* clade, with many species found above 3000 m in New Guinea, and *M. brassii* to 4275 m (Hartley, 2001). Adaptations to a wider ecological range might partly explain the higher species richness in the *Acronychia-Medicosma-Melicope* clade.

Species of the *Euodia* clade and the *Acronychia-Melicope* clade are similar in many morphological characters including habit, leaf morphology, indumentum, and flower morphology (Hartley, 2001; Kubitzki et al., 2011). The main differences between the two clades are in fruit types, presentation of seeds and seed coat anatomy. Several genera of the *Acronychia-Melicope* clade have drupaceous fruits, while most (including *Melicope*) have dehiscent fruits in which the ripe seeds remain attached upon dehiscence and are thereby displayed to potential seed dispersers. In contrast, species of the *Euodia* clade (except the drupaceous *Pitaviaster haplophyllus* (F.Muell.) T.G.Hartley) have follicular fruits in which seeds are elastically discharged with the endocarp when the fruit opens (Hartley, 2001, 2013). The seeds of the *Euodia* clade have a thin and brittle testa without the shiny pellicle (Hartley, 2001; Kubitzki et al., 2011). Seeds of the *Acronychia-Melicope* clade have a thick sclerotesta, a spongy nutritious sarcotesta, and a shiny black pellicle; features that have been interpreted as adaptations for bird dispersals, with the spongy sarcotesta as the nutrient layer, the shiny pellicle as visual attractant, and the sclerotesta to protect the embryo from digestion (Hartley, 2001). The visibility of the seeds in the open fruits is further enhanced by a colorful and fleshy exocarp in some *Melicope* species (Hartley, 2001). Field observations confirm that birds act as seed dispersers for *Acronychia* and *Melicope* (Frith et al., 1976; Floyd, 1989; Innis, 1989; Hartley, 2001; Medeiros, 2004). On the Hawaiian Islands, where 71% of the native bird species have become extinct (Aslan et al., 2013), *Melicope* seeds are dispersed by two invasive bird species (Medeiros, 2004; Foster & Robinson, 2007). Bird-dispersal has been postulated for many taxa, especially for the colonization of the Hawaiian Islands and other isolated oceanic islands (Carlquist, 1967; Sakai et al., 1995; Foster & Robinson, 2007; Keeley & Funk, 2011; Aslan et al., 2013; Roy et al., 2013).

While several morphological traits seem obvious adaptations to bird dispersal, it is impossible to exclude additional dispersal vectors of primarily bird-dispersed species (Wenny et al., 2016). Since LDD events are generally rare and unusual, the standard dispersal vector(s) might not account for LDD. Instead, either an unusual behavior of the standard vector (e.g., a vagrant in the case of ornithochory) or a different vector might have caused a LDD event (Higgins et al., 2003; Nathan et al., 2008). It is premature to accept adaptations to bird dispersal as the sole factor to explain the differences in distribution and species richness between the *Acronychia-Melicope* and *Euodia* groups. Nevertheless, bird-dispersal might have played a crucial role especially in island systems such as the Malesian region and/or within the Hawaiian Islands.

Acknowledgements

We thank the numerous individuals (F. Brambach, B. Chantarasuwan, H.-J. Esser, T. Hartley, S. James, D. Lorence, H. Oppenheimer, P. Pelser, S. Perlman, S. Razafimandimbison, M. Rossetto, Y. Sirichamorn, G. Weiblen, W. de Wilde, B. de Wilde-Duyfjes, K. Wood, and Z. Zhou) and institutions (Herbaria A, C, CANB, L, LAE, MO, NY, P, PTBG, QRS, SNP; Australian National Botanic Garden, Hortus Botanicus Leiden, National Tropical Botanical Garden, Southern Cross University) for providing samples for this study, J. Krüger (GOET) for lab assistance, and A.J. Harris for assistance with MrBayes via the use of the Oklahoma State University High Performance Computing Center Resources.

References

Amerson AB. 1975. Species richness on the nondisturbed northwestern Hawaiian Islands. *Ecology* 56: 435–444.

Appelhans MS, Keßler PJA, Smets E, Razafimandimbison SG, Janssens SB. 2012. Age and historical biogeography of the pantropically distributed Spathelioideae (Rutaceae, Sapindales). *Journal of Biogeography* 39: 1235–1250.

Appelhans MS, Wen J, Wagner WL. 2014a. A molecular phylogeny of *Acronychia*, *Euodia*, *Melicope* and relatives (Rutaceae) reveals polyphyletic genera and key innovations for species richness. *Molecular Phylogenetics and Evolution* 79: 54–68.

Appelhans MS, Wen J, Wood KR, Allan GJ, Zimmer EA, Wagner WL. 2014b. Molecular phylogenetic analysis of Hawaiian Rutaceae (*Melicope*, *Platydesma* and *Zanthoxylum*) and their different colonisation patterns. *Botanical Journal of the Linnean Society* 174: 425–448.

Appelhans MS, Wood KR, Wagner WL. 2017. Reduction of the Hawaiian genus *Platydesma* into *Melicope* section *Pelea* (Rutaceae) and notes on the monophyly of the section. *PhytoKeys* 91: 125–137.

Aslan CE, Zavaleta ES, Tershy B, Croll D, Robichaux RH. 2013. Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. *Conservation Biology* 28: 478–488.

Baldwin BG, Wagner WL. 2010. Hawaiian angiosperm radiations of North American origin. *Annals of Botany* 105: 849–879.

Bayly MJ, Holmes GD, Forster PI, Cantrill DJ, Ladiges PY. 2013. Major clades of Australasian Rutoideae (Rutaceae) based on *rbcL* and *atpB* sequences. *PLoS ONE* 8: e72493.

Blackburn DT, Sluiter IRK. 1994. The Oligo-Miocene coal floras of southeastern Australia. In: Hill RS ed. *History of the Australian vegetation: Cretaceous to recent*. Cambridge: University Press. 328–367.

Burney DA, James HF, Burney LP, Olson SL, Kikuchi W, Wagner WL, Burney M, McCloskey D, Kikuchi D, Grady FV, Gage II R, Nishek R.

2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs* 71: 615–641.

Carlquist S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club* 94: 129–162.

Clouard V, Bonneville A. 2005. Ages of seamounts, islands and plateaus on the Pacific plate. *Geological Society of America Special Papers* 388: 71–90.

Conran JG, Lee WG, Lee DE, Bannister JM, Kaulfuss U. 2014. Reproductive niche conservatism in the isolated New Zealand flora over 23 million years. *Biology Letters* 10: 20140647.

Cowie RH, Holland BS. 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography* 33: 193–198.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Donlan CJ, Nelson PA. 2003. Observations of invertebrate colonized flotsam in the eastern tropical Pacific, with a discussion of rafting. *Bulletin of Marine Science* 72: 231–240.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.

Floyd AG. 1989. *Rainforest trees of mainland South-Eastern Australia*. Melbourne, Sydney: Inkata Press.

Foster JT, Robinson SK. 2007. Introduced birds and the fate of Hawaiian rainforests. *Conservation Biology* 21: 1248–1257.

Frith HJ, Crome FHJ, Wolfe TO. 1976. Food of fruit-pigeons in New Guinea. *Emu* 76: 49–58.

Givnish TJ, Millam KC, Mast AR, Paterson TB, Theim TJ, Hipp AL, Henss JM, Smith JF, Wood KR, Sytsma KJ. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* 276: 407–416.

Groppo M, Pirani JR, Salatino MLF, Blanco SR, Kallunki JA. 2008. Phylogeny of Rutaceae based on two noncoding regions from cpDNA. *American Journal of Botany* 95: 985–1005.

Harbaugh DT, Wagner WL, Allan GJ, Zimmer EA. 2009. The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: An example from the plant genus *Melicope* (Rutaceae). *Journal of Biogeography* 36: 230–241.

Hartley TG. 1974. A revision of the genus *Acronychia* (Rutaceae). *Journal of the Arnold Arboretum* 55: 469–567.

Hartley TG. 1982. A revision of the genus *Sarcomelicope* (Rutaceae). *Australian Journal of Botany* 30: 359–372.

Hartley TG. 1983. A revision of the genus *Comptonella* (Rutaceae). *Bulletin du Muséum National d'Histoire Naturelle Paris, Section B, Adansonia* 5: 391–413.

Hartley TG. 1984. A revision of the genus *Dutaillyea* (Rutaceae). *Bulletin du Muséum National d'Histoire Naturelle Paris, 4e serie, 6, Section B, Adansonia* 1: 29–35.

Hartley TG. 1997. Five new rain forest genera of Australasian Rutaceae. *Adansonia* 19: 189–212.

Hartley TG. 2001. On the taxonomy and biogeography of *Euodia* and *Melicope* (Rutaceae). *Allertonia* 8: 1–341.

Hartley TG. 2013. Rutaceae. In: Wilson A ed. *Flora of Australia: Meliaceae, Rutaceae, Zygophyllaceae, vol.* 26. Canberra/Melbourne: ABRS/CSIRO. 43–510.

Hartley TG, Mabberley DJ. 2003. The identity of *Picrella* Baill. (Rutaceae) with a revision of the genus. *Adansonia* 25: 251–259.

Higgins SI, Nathan R, Cain ML. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84: 1945–1956.

Holzmeyer L, Duretto M, Crayn D, Hörandl E, Heslewood M, Jayanthan J, Appelhans MS. 2015. Phylogeny of *Acronychia* (Rutaceae) and first insights into its historical biogeography and the evolution of fruit characters. *PLoS ONE* 10: e0136296.

Innis GJ. 1989. Feeding ecology of Fruit Pigeons in subtropical rainforests of South-Eastern Queensland. *Australian Wildlife Research* 16: 365–394.

Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: New patterns revealed by molecular phylogenetic studies. In: Bramwell D, Caujapé-Castells J eds. *The biology of island floras*. Cambridge: University Press. 57–88.

Kershaw AP, Bretherton SC, van der Kaars S. 2007. A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 23–45.

Koenen EJM, Clarkson JJ, Pennington TD, Chatrou LW. 2015. Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. *New Phytologist* 207: 327–339.

Kubitzki K, Kallunki JA, Duretto M, Wilson PG. 2011. Rutaceae. In: Kubitzki K ed. *The families and genera of vascular plants, vol. 10*. Berlin: Springer Verlag. 276–356.

Le Roux JJ, Strasberg D, Rouget M, Morden CW, Koordom M, Richardson DM. 2014. Relatedness defies biogeography: The tale of two island endemics (*Acacia heterophylla and A. koa*). *New Phytologist* 204: 230–242.

Manafzadeh S, Salvo G, Conti E. 2014. A tale of migrations from east to west: The Irano-Turanian floristic region as a source of Mediterranean xerophytes. *Journal of Biogeography* 41: 366–379.

Matzke NJ. 2013. BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis in R Scripts, CRAN: The Comprehensive R Archive Network, Vienna, Austria [online]. Available from http://cran.r-project.org/package=BioGeoBEARS [accessed December 8, 2016].

Matzke NJ. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63: 951–970.

Medeiros AC. 2004. *Phenology, reproductive potential, seed dispersal and predation, and seedling establishment of three invasive plant species in a Hawaiian rain forest*. Ph.D. Thesis. Mānoa: University of Hawai'i.

Muellner-Riehl AN, Weeks A, Clayton JW, Buerki S, Nauheimer L, Chiang YC, Cody S, Pell SK. 2016. Molecular phylogenetics and molecular clock dating of Sapindales based on plastid *rbcL*, *atpB* and *trnL-trnF* DNA sequences. *Taxon* 65: 1019–1036.

Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution* 23: 638–647.

Neall VE, Trewick SA. 2008. The age and origin of the Pacific islands: A geological overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 3293–3308.

Papadopulos AST, Baker WJ, Crayn D, Butlin RK, Kynast RG, Hutton I, Savolainen V. 2011. Speciation with gene flow on Lord Howe Island. *Proceedings of the National Academy of Sciences USA* 108: 13188–13193.

Pillon Y. 2012. Time and tempo of diversification in the flora of New Caledonia. *Botanical Journal of the Linnean Society* 170: 288–298.

Poon WS, Shaw PC, Simmons MP, But PPH. 2007. Congruence of molecular, morphological, and biochemical profiles in Rutaceae: A cladistic analysis of the subfamilies Rutoideae and Toddalioideae. *Systematic Botany* 32: 837–846.

Price JP, Clague DA. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society B: Biological Sciences* 269: 2429–2435.

Rabosky DL, Grundler M, Anderson C, Title P, Shi JJ, Brown JW, Huang H, Larson JG. 2014. BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution* 5: 701–707.

Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Tracer v1.6 [online]. Available from http://tree.bio.ed.ac.uk/software/tracer/.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4–14.

Ronquist F. 1997. Dispersal–vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology* 46: 195–203.

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Roy T, Chang TH, Lan T, Lindqvist C. 2013. Phylogeny and biogeography of New World Stachydeae (Lamiaceae) with emphasis on the origin and diversification of Hawaiian and South American taxa. *Molecular Phylogenetics and Evolution* 69: 218–238.

Russo CAM, Takezaki N, Nei M. 1995. Molecular phylogeny and divergence times of Drosophilid species. *Molecular Biology and Evolution* 12: 391–404.

Sakai AK, Wagner WL, Ferguson DM, Herbst DR. 1995. Origins of dioecy in the flowering plants of the Hawaiian Islands. *Ecology* 76: 2517–2529.

Schatz GE. 1996. Malagasy/Indo-Australo-Malesian phytogeographic connections. In: Lourenco WR ed. *Biogéographie de Madagascar*. Paris: Orstom Editions. 73–83.

Sharma PP, Wheeler WC. 2013. Revenant clades in historical biogeography: The geology of New Zealand predisposes endemic clades to root age shifts. *Journal of Biogeography* 40: 1609–1618.

Smith AC. 1985. *Flora Vitiensis Nova*, Vol. 3. Honolulu: SB Printers Inc.

Takhtajan A. 1986. *Floristic regions of the world*. Berkeley: University of California Press.

Tiffney BH. 1980. Fruits and seeds of the Brandon Lignite, V. Rutaceae. *Journal of the Arnold Arboretum* 61: 1–40.

Tiffney BH. 1981. *Euodia* costata, new combination (Rutaceae) from the Eocene of southern England. *Paläontologische Zeitschrift* 55: 185–190.

Wagner WL, Herbst DR, Sohmer SH. 1990. *Manual of the flowering plants of Hawai'i*. Volume 2. Honolulu: University of Hawai'i Press, Bishop Museum Press.

Wenny DG, Sekercioglu CH, Cordeiro NJ, Rogers HS, Kelly D. 2016. Seed dispersal by fruit-eating birds. In: Sekercioglu CH, Wenny DG, Whelan CJ eds. *Why birds matter – Avian ecological function and ecosystem services*. Chicago: University of Chicago Press. 107–146.

Wood KR, Appelhans MS, Wagner WL. 2017. *Melicope stonei*, section *Pelea* (Rutaceae), a new species from Kaua'i, Hawaiian Islands: With notes on its distribution, ecology, conservation status, and phylogenetic placement. *Phytokeys* 83: 119–132.

Yu Y, Harris AJ, Blair C, He X. 2015. RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87: 46–99.

Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12299/suppinfo:

Fig. S1. Phylogenetic reconstruction of the *Acronychia-Euodia-Melicope* clade using Bayesian inference. The 50% majority-rule consensus tree of the MrBayes analysis is shown with posterior probability (pp) values above the branches.