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ORIGINAL ARTICLE

Multiple waves of colonization by monarch flycatchers (*Myiagra*, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation

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ABSTRACT

Aim Islands and archipelagos have played an important role in the development of ecological and evolutionary theories. Using a newly compiled molecular phylogeny we infer the biogeographical history of a monarch flycatcher genus, *Myiagra*, which is distributed across the Indo-Pacific. We subsequently integrate biogeographical and ecomorphological data to examine the role of dispersal and trait evolution in the build-up of avian assemblages.

Location Australia, the Moluccas, New Guinea and Pacific islands.

Methods We generated a taxonomically densely sampled mitochondrial DNA dataset that included almost all species and subspecies of the reciprocally monophyletic genera *Myiagra* and *Arses*. We then used maximum likelihoood and Bayesian inference to infer their phylogenetic relationships. To reconstruct their biogeographical history, we first dated the tree topology and then used Lagrange to infer ancestral geographical areas. Finally, we combined ancestral area reconstructions with information on ecomorphological traits to infer mechanisms underlying community assembly.

Results We provide the first comprehensive molecular phylogenetic reconstruction for *Myiagra* and *Arses* monarch flycatchers. Our phylogenetic reconstruction reveals a relatively recent diversification from the Miocene associated with several major dispersal events. Ancestral area reconstruction reveals several independent colonizations of the Moluccas, Melanesia, Fiji and the Micronesian islands. Ancestral state reconstruction of ecological traits suggests that the diversity of traits in co-occurring species of monarch flycatchers results from independent colonization events and ecological niche conservatism rather than *in situ* diversification.

Main conclusions Three waves of colonization, non-overlapping in time, led to independent speciation events in the Bismarcks, Fiji and the Moluccas, in addition to *in situ* speciation events on remote islands of Micronesia, the Solomons, Vanuatu and Samoa. Few of these colonizations have led to the co-occurrence of congenerics or species with similar ecomorphological profiles on the same island. Thus, we suggest that priority effects might prevent new colonizers from establishing themselves if they share high levels of ecological similarity with resident species. We conclude that historical dispersal to and colonization of new islands, combined with ecologically deterministic priority effects, drove the assembly of insular monarch flycatcher communities across the Indo-Pacific.

Keywords
Colonization, community assembly, Indo-Pacific, island biogeography, island evolution, Monarchidae, *Myiagra*, priority effects, speciation, trait evolution.

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INTRODUCTION

Insular communities have played an important role in the development of ecological and evolutionary theories (Darwin, 1859; MacArthur & Wilson, 1963). In particular, as a result of their colonization abilities and insular diversity, avian assemblages represent a good model group for testing ecological and evolutionary hypotheses (Mayr & Diamond, 2001; Rosindell & Phillimore, 2011). Many groups of birds are highly dispersive, allowing them to colonize the most remote islands and archipelagos (Moyle *et al.*, 2009; Jønsson *et al.*, 2011a). In the Pacific archipelagos, many groups have radiated extensively subsequent to their initial colonization, but the mode of speciation driving these radiations is often unclear. Thus, avian adaptive radiations on Pacific islands have been immortalized through studies of rare cases of radiations such as Darwin finches (Grant & Grant, 2008) and Hawaiian honeycreepers (Pratt, 2005). In general, radiations in island systems are scarce (Ricklefs & Bermingham, 2007), with speciation hypothesized to be largely the consequence of geographical isolation (Mayr, 1942). Non-adaptive radiations (Rundell & Price, 2009) typically occur in highly dispersive supertramp lineages (Cibois *et al.*, 2011).

Several factors may slow down diversification in insular systems. In addition to geographical isolation, competitive exclusion of subsequent colonists by the first resident species (Diamond, 1975) may prevent diversification via a priority effect (e.g. Fukami *et al.*, 2007; aka, preemptive colonization, incumbency effect). This might prevent diversification by limiting range expansion, which is considered to be a highly important part of the speciation process in birds (Pigot *et al.*, 2010). Testing various scenarios of timing of colonization and morphological differenciation is crucial for gaining a deeper understanding of the processes regulating diversification and the assembly of insular communities (Waters, 2011).

The core Corvoidea originated in the Oligocene within an island setting in the proto-Papuan area (Jønsson *et al.*, 2011b). A number of studies of the core corvoid families have revealed complex colonization histories, reflecting their great capacity to disperse and adapt within insular regions. The family Monarchidae provides a good example of this, and has undergone several range expansions, including colonization of remote islands, followed by subsequent back-colonization of Australia (Filardi & Moyle, 2005). Members of the Monarchidae are widely distributed from Africa to Australia and the Pacific. The high species diversity of this family consists of numerous island allospecies as the group expanded across mainland as well as island areas (Filardi & Moyle, 2005; Fabre *et al.*, 2012). In monarchs, examples of range expansions followed by speciation are known from the monarch genus *Monarcha* (Filardi & Smith, 2005) and from *Terpsiphone* (Fabre *et al.*, 2012), and examples of remote island colonization are known from the Hawaiian *Chasiempsis* (VanderWerf *et al.*, 2009) and the eastern Polynesian *Pomarea* (Cibois *et al.*, 2004). *Myiagra* is particularly relevant for understanding island colonization and diversification, as species in this genus occupy most forest habitats in the Australasian area, and have colonized several archipelagos around the Australo-Papua regions, as well as remote oceanic islands (Fig. 1). *Myiagra* flycatchers occupy a variety of forest habitats, ranging from humid forest, montane forest, mangrove and woodland to disturbed lowland forest on both continents and islands (Coates *et al.*, 2006). Most species are sedentary with some seasonal migratory movements (*M. inquieta*, *M. rubecula*). They occur sympatrically in Australia, New Guinea (Fig. 1) and some islands (Biak, the Bismarcks, Fiji, the Moluccas). Ten to 14 endemic island species are recognized in the literature based on distribution and plumage characters (Coates *et al.*, 2006), but owing to a lack of molecular data the systematics of some species and subspecies remain unclear and are in need of revision.

Here we aim to resolve the systematic relationships and colonization history among the *Myiagra* monarch flycatchers by using mitochondrial DNA data and dense taxon sampling. Using a highly resolved molecular phylogeny and ancestral area reconstruction, we infer the colonization history and examine patterns of speciation to address the following questions: (1) How many lineages are present on archipelagos across the Indo-Pacific? (2) How many dispersal events are required to explain diversity patterns in different archipelagos, and in the Australo-Papua area? Using patterns of ecomorphological evolution among *Myiagra* from remote Indo-Pacific islands we also address the question: (3) what role have historical patterns of colonization played in community assembly?

MATERIALS AND METHODS

Taxon sampling

To study phylogenetic relationships among the reciprocally monophyletic genera *Arses* and *Myiagra*, samples were obtained from 63 specimens (see Appendix S1 in Supporting Information) representing the 23 extant species in addition to one extinct species (*Myiagra freycineti*) as classified by Clements (2007). Only 150 bp fragment of the *ND2* region was successfully amplified for *M. oceanica* from Chuuk Island and therefore we did not include it in the final analysis. However, we briefly discuss its systematic relationships. We sampled 31 out of the 48 currently defined subspecies (7/8 *Arses* and 24/40 *Myiagra*). To root the trees and assess the monophyly of both genera, samples were also obtained for a number of outgroup taxa including representatives from: (1) the sister clades, the Australasian Monarchidae and the Old World Monarchidae; and (2) five representatives of distantly related core Corvoidea families.

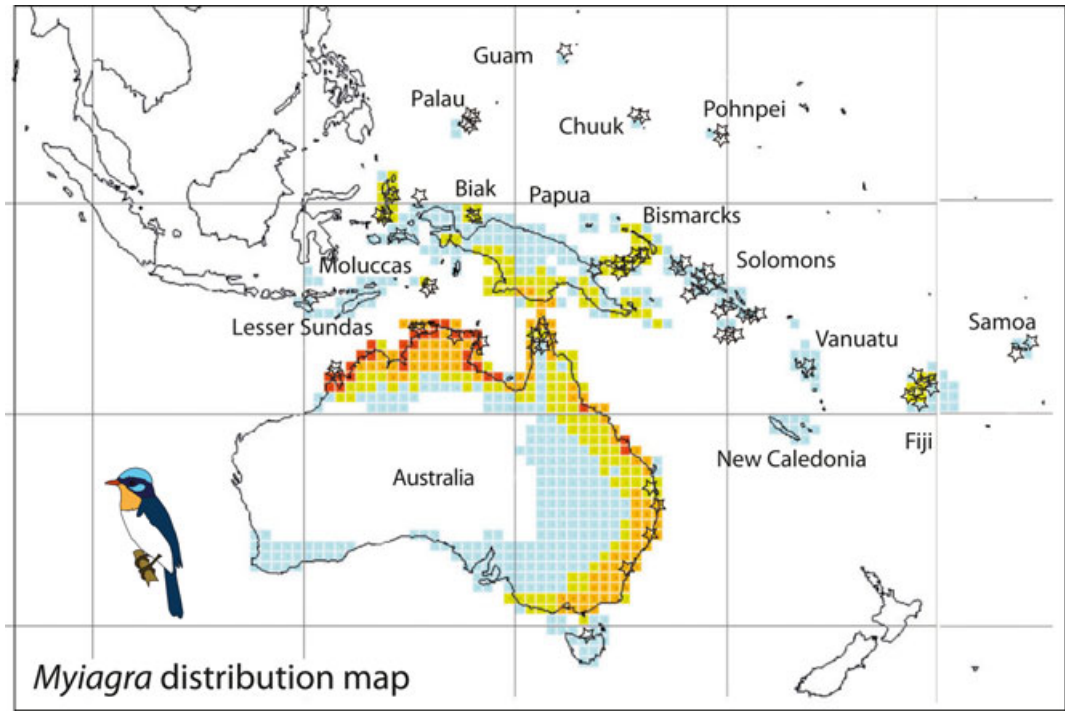

Figure 1 Present variation in species richness of the genus *Myiagra*. Our *Myiagra* samples are indicated by the stars on the map. Distribution data were extracted from a comprehensive global distributional database developed at the Centre for Macroecology, Evolution and Climate and validated by many experts (see Rahbek & Graves, 2001). The database provides 1° × 1° resolution maps (110 km × 110 km at the equator) of breeding distributions of all birds. Maximum species richness in a grid cell for *Myiagra* (warmest colour) is four species. Data were compiled in the WorldMap software (© Paul Williams, The Natural History Museum).

DNA amplification, sequences and alignment

Fresh tissue and blood samples as well as foot pad samples from study skins were obtained from several museums (Appendix S1). DNA extraction was carried out using the QIAamp DNA mini kit (Qiagen, Crawley, UK). For extraction amplification and sequencing procedures we followed those described in Irestedt *et al.* (2006). However, 20 μL of DTT (dithiothreitol) was added in the lysis phase during the extractions to break disulfide bonds in proteins which facilitates the lysis of tissue from old museum specimens. Two mitochondrial genes were amplified and sequenced: NADH dehydrogenase subunit 2 (*ND2*) and NADH dehydrogenase subunit 3 (*ND3*). For fresh samples, the primer pair Lmet (Hackett, 1996) and H6312 (Cicero & Johnson, 2001) was used when sequencing *ND2*, while primer pair L10755 and H11151 (Chesser, 1999) was used for *ND3*. The study skin samples were amplified in short fragments (around 250 base pairs) to increase the ratio of successful amplifications. We used hot-start PCR with an annealing temperature below the melting temperature of any of the primers for the first cycles. A thermocycling programme for a given primer combination started with an initial denaturation at 95 °C for 5 min, followed by a 40 cycle phase of 95 °C for 40 s, 54–63 °C for 40 s and subsequently 72 °C for 60 s. PCR products were purified from 1% agarose gel using Amicon Ultrafree-DNA columns (Millipore, Billerica, MA, USA) and both strands were sequenced using a Big Dye Terminator cycle sequencing kit. Sequenced strands were run on an ABI 3100 automated sequencer (Applied Biosystems, Crawley, UK).

Previously published *ND2* sequences were downloaded from GenBank and added to our dataset (Appendix S1). Sequences were aligned with the MUST package ED editor (Philippe, 1993). From these individual gene alignments, we built one supermatrix with 104 taxa and 1390 sites.

All sequences were checked for the presence of indels and stop codons that may be indicative of pseudogenes. We found no stop codons or indels in the coding gene sequences that would suggest the presence of pseudogenes. We also built alignments for each individual fragment and constructed phylogenetic trees to be able to detect potentially spurious sequences. We did not find any phylogenetic incongruence or spurious branch length patterns among and between individual fragments in our dataset.

Phylogenetic analyses

Phylogenetic tree topologies were generated for each gene independently and for the concatenated dataset using maximum likelihood (ML) and Bayesian methods of phylogenetic reconstruction. MODELTEST 3.07 (Posada & Crandall, 1998) was used to determine the best fitting model of DNA sequence evolution using the Akaike information criterion (AIC). The GTR+I+Γ model selected was for both *ND3* and

ND2 as well as for the concatenated dataset (with codon partition). Maximum likelihood analyses were implemented in RAxML 7.0.4 (Stamatakis, 2006). For all datasets, we used the GTR+MIX option of RAxML, which assumes the faster GTR+CAT model for topological tree searches, and the GTR+Γ model when computing the likelihood value of each topology. The RAxML analyses implemented the default parameters and comprised 10,000 tree pseudoreplicates. Node stability on partitioned supermatrices was estimated using 10,000 nonparametric bootstrap replicates.

Bayesian analyses were performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). All parameters except topology were unlinked across partitions and two independent runs (with one cold and three heated chains) were computed simultaneously, with trees sampled every 1000th generation. The MrBayes analysis was run for 50 million generations and in all cases stationarity had been reached by the end. Majority rule consensus trees were subsequently constructed, with a burn-in of 5 million generations.

Molecular dating

We used beast 1.7.5 (Drummond & Rambaut, 2007) to estimate divergence times, by applying the best fitting model as estimated by Modeltest 3.07 to each of the partitions. We implemented the Tajima's relative rate test using the pegas package (Paradis, 2010) in R (R Development Core Team, 2012) to test whether our dataset was clock-like. Because a molecular clock hypothesis could not be rejected, we applied a strict molecular clock to our matrix partitioning both by genes and codons. Because no fossil data are available for this group, we used a rate of sequence divergence of 1.79% and the standard deviation (SD) was based on the value required to produce 5% and 95% quantiles encompassing rates used to calculate the mean. This rate is based on a bird mitogenomes study (Pereira & Baker, 2006). To corroborate our molecular rate approach, we followed VanderWerf *et al.* (2009), who used the split between *Chasiempis sandwichensis* from Hawai (Kauai oldest island age *c.* 5.1 Ma; Carson & Clague, 1995) and its Southeast Pacific monarch relatives (*Pomarea* clades) as a geological calibration point. To obtain a calibration point based on the split between these species, we applied a normal distribution prior starting at 5.1 Ma (emergence of Kauai Island) and an SD of 0.1 Myr. We assumed a Yule speciation process for the tree prior and used default prior distributions for all other parameters. We ran Markov chain Monte Carlo (MCMC) chains for 250 million generations with a 25% burn-in period and parameters logged every 1000th generation.

Biogeographical analyses

We defined six geographical areas for the Lagrange analysis based on bird distribution maps (Rahbek *et al.*, 2012) and geological and biogeographical evidence (Hall, 2002): Australia, New Guinea (including the Bismarcks and the Admirality Islands, which, given their immediate proximity to New Guinea, have been easily colonizable in recent time), Wallacea (the area east of Borneo and Bali and west of New Guinea), Melanesia, Micronesia and Polynesia.

We used Lagrange to reconstruct ancestral geographical areas (Ree *et al.*, 2005). In this analysis, ancestral areas are optimized onto internal nodes enabling maximum likelihood estimation of the ancestral states (range inheritance scenarios) by modelling transitions between discrete states (biogeographical ranges) along phylogenetic branches as a function of time. As no extant subspecies occupies more than two regions, the analysis was carried out by constraining the maximum number of areas encompassed by the ancestral distributions to two using the maxareas option in Lagrange. We also tested the impact of outgroup presence and absence on the result of this analysis.

Ancestral state estimation and morphological analysis

We obtained data on habitat, foraging and movement from Coates *et al.* (2006) and Higgins *et al.* (2006) (Appendix S2). To evaluate plumage evolution we coded seven plumage colour characters defined in previous taxonomic studies supplemented by additional data obtained from study skins at the Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC), Museum für Naturkunde in Berlin, Germany (ZMB), University Museum of Zoology of Cambridge, UK (UMZC) and the Swedish Museum of Natural History in Stockholm, Sweden (NRM). The following characters were coded (with plumage characters derived from male specimens): (1) insular or continental distribution; (2) the foraging height of birds as follows: lower, mid and upper levels, all levels, mid+lower and mid+upper levels, as described in Coates *et al.* (2006). These six categories rely on the proportion of time a species spends foraging in three particular vegetation strata and the percentage of time overlap at each stratum; (3) crown colour (black, rufous, grey, black-and-blue, black-and-rufous, black-and-white); (4) throat colour (black, rufous, grey, white); (5) wing covert colour (black, rufous, blue, grey, black-and-white); (6) tail colour (black, rufous, blue); (7) breast colour (black, rufous, grey, white); (8) vent colour (black, rufous, white), and (9) belly colour (black, rufous and white).

We inferred ancestral state reconstructions at each node within our phylogeny using a maximum likelihood approach as implemented in Mesquite 2.74 (Maddison & Maddison, 2010) with the Mk1 rate model (Lewis, 2001). Polymorphic characters were coded as mixed characters because Mesquite is unable to process polymorphic data. This ancestral reconstruction approach was used to test whether ecomorphological character states changed before or after colonization of the Bismarcks, Fiji and the North Moluccas where *Myiagra* species co-occur (see Results and Discussion). By comparing nodes A, B, C, E and I before and after the inferred island colonizations (see Results), we computed the number of

character changes before or after colonization of an island for each of these nodes, which we refer to as prior to colonization (PrC) and post-colonization (PoC), respectively. Evolution of the character state after the lineage has colonized an island is considered PoC. All character states that originated outside the remote island, were quoted as PrC. In the case of ambiguous character states, we chose the state returning with the highest likelihood. For example, in Fiji, *M. azureocapilla* and *M. vanikorensis* have a crown colour state through a PoC (black-and-blue) and a PrC (black), respectively, because the state in *M. azureocapilla* differs from that in the subtending node whilst the state in *M. vanikorensis* is the same as that of the subtending node (Appendix S3).

Comparing genetic and morphological divergences

Genetic pairwise distances based on the mitochondrial protein-coding *ND2* gene were computed for species pairs of *Myiagra* and *Arses* using the Kimura two-parameter model as implemented in MEGA 5.05 (Tamura *et al.*, 2011). To examine the history of morphological variation, we measured 17 out of 19 species of *Myiagra* from museum collections (1–10 individuals from each species, 75 individuals altogether). The measurements examined (wing length, tail length, tarsus length, middle toe, bill length, bill width and bill depth measured at the base) are believed to represent adaptations to various habitats and foraging strategies (Miles *et al.*, 1987). All values were log-transformed, and a principal components analysis of the variance–covariance matrix (prcomp command in R version 2.15.0) was used to reduce dimensionality of our dataset and to account for correlations among characters due to overall body size. Following Ricklefs & Bermingham (2007), we computed the pairwise distance (D_{ij}) between two species (i and j) using Euclidean distance from n morphological measurements where x_{ik} and x_{jk} are the k measurement values for taxa i and j, respectively.

RESULTS

The final matrix contained 110 individuals (including outgroups and GenBank ingroup sequences) and 1390 nucleotides (all new sequences are deposited in GenBank; Appendix S1). For 63 samples we obtained partial *ND2* (1036 bp) and *ND3* (395 bp) sequences. For five individuals, shorter *ND2* sequences were obtained and we failed to sequence *ND3* for 15 individuals. Both Bayesian and maximum likelihood analyses inferred very similar topologies (Fig. 2). Differences between the trees largely involve very short branches and unsupported nodes (with bootstrap values < 70 or posterior probabilities < 0.95).

Both *Arses* [bootstrap = 99, posterior probability (PP) = 1] and *Myiagra* (bootstrap = 100, PP = 1) are recovered as monophyletic (Fig. 2), and are inferred to be sister clades (bootstrap = 70, PP = 1). Within *Arses*, *A. telescopthalmus* is paraphyletic due to the inclusion of *A. lorealis* and *A. kaupi*. Our phylogeny reveals a paraphyletic assemblage of (1) *A. telescopthalmus* from western and north-western New Guinea, including Aru (*A. t. aruensis*), and (2) an eastern New Guinea/North Australian clade grouping together *A. kaupi*, *A. lorealis* and *A. telescopthalmus* from south-eastern New Guinea (Fig. 2).

Within *Myiagra*, the phylogenetic hypothesis generally supports traditional classifications except for *M. inquieta*, which has *M. nana* nested within it. The genus (Clade A, Fig. 2) is divided into two main lineages: (1) one clade (B) consists of *M. hebetior* from the Bismarcks, which is sister to the Australo-Papua/Moluccan *M. alecto*; and (2) the other main clade (C) is more diverse and consists of all other species of *Myiagra*. One of the two earliest branching lineages of Clade C is distributed in Fiji (*M. azureocapilla*). Within Clade D three lineages are recovered: (1) a well-supported (bootstrap = 100, PP = 1) Australian/New Guinean/Moluccan lineage of *M. ruficollis* sister to a clade in which *M. inquieta* is paraphyletic with respect to *M. nana*; (2) the *M. erythrops* lineage (bootstrap = 100, PP = 1) from the Palau islands; and (3) a very diverse clade containing several Pacific island lineages (*M. albiventris*, *M. caledonica*, *M. cervinicauda*, *M. ferrocyanea*, *M. freycineti*, *M. pluto* and *M. vanikorensis*), one Wallacean lineage (*M. galeata*) and three Australo-Papua lineages (*M. atra*, *M. cyanoleuca* and *M. rubecula*). Two major Pacific clades are recovered: Clade I (bootstrap = 99, PP = 1) and Clade H (bootstrap = 72, PP = 1). Clade I is largely restricted to the Melanesian and Polynesian archipelagos (south-eastern Solomons, Vanuatu, Fiji and Samoa) including *M. albiventris*, *M. cervinicauda*, *M. vanikorensis* and *M. caledonica*. Within this clade, *M. caledonica* is divided into one south-eastern Solomon clade (*M. c. occidentalis* of Rennell) that is sister to *M. c. marinae* from Vanuatu (bootstrap = 96, PP = 1). Clade H is restricted to Micronesia (*M. pluto* from Pohnpei) and the Solomon islands (*M. ferrocyanea*). The Chuuk Island flycatcher (*M. oceanica*), for which only a partial sequence of 150 bp was obtained, was revealed to have a close relationship with the Pohnpei flycatcher (*M. pluto*) based on ML and Bayesian analyses that included this sequence (results not shown).

Biogeographical analyses and molecular dating

An absolute time-scale for the diversification of *Myiagra* and *Arses* derived from the BEAST analysis is shown in Table 1. Global and relaxed molecular clock models using a rate of 1.79% sequence divergence Myr^{-1} yielded congruent results. The origin of *Arses* and *Myiagra* dates back to the Miocene (approximately 7.53–9.43 Ma).

The LAGRANGE analyses were robust to the inclusion/exclusion of outgroups (compare Table 2 and Appendix S3a). The origin of both *Arses* and *Myiagra* appears to have been in the Papuan region (Table 2, Clade A, Fig. 3) and three major waves of dispersal and colonization are subsequently inferred by our phylogenetic and LAGRANGE results. An early diversification (3.19–4.80 Ma; Table 1) involves the

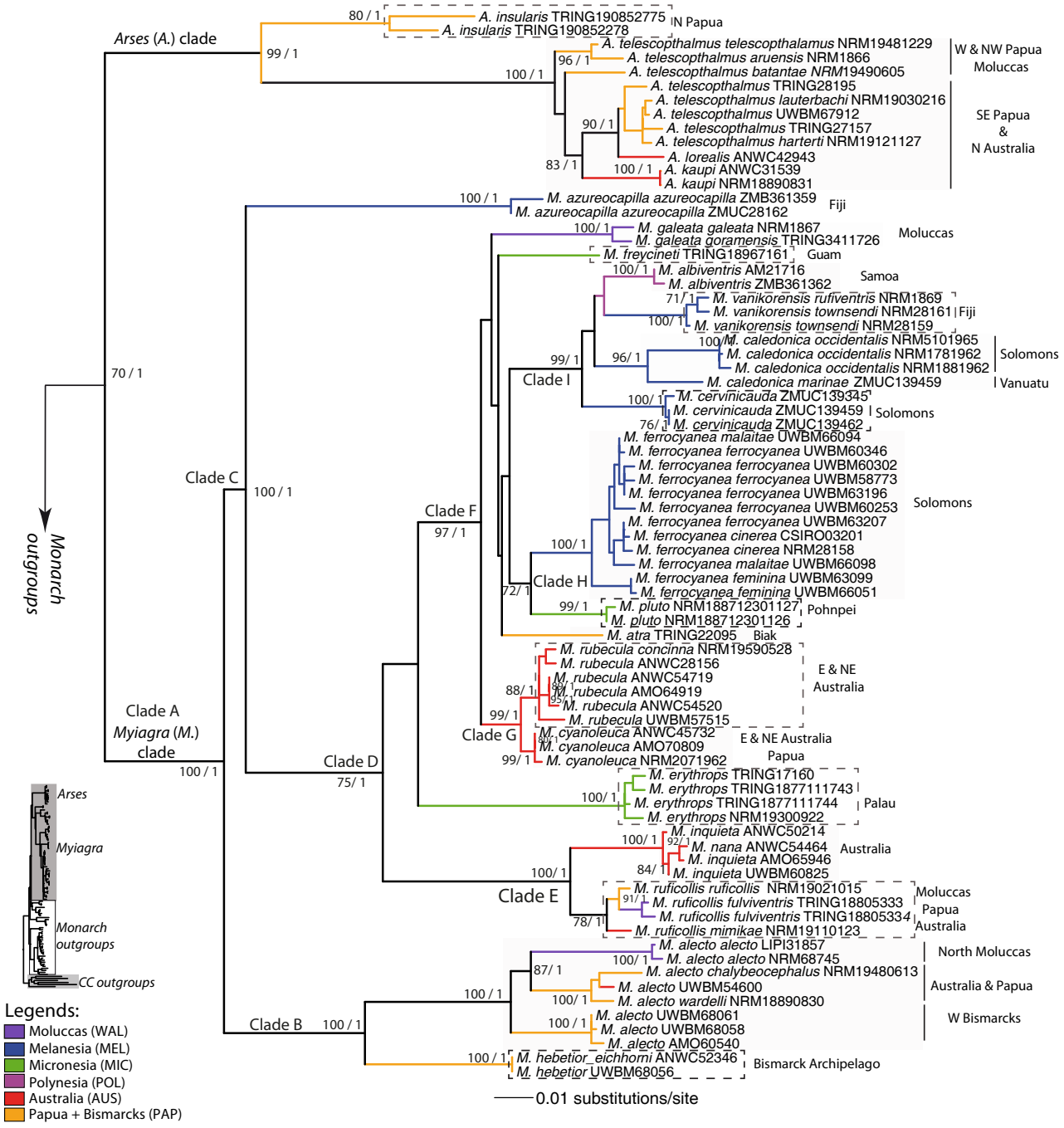

Figure 2 Maximum likelihood topology of *Myiagra* and *Arses* produced from the combined analysis. Labelled clades are discussed in the text. Numbers at nodes represent maximum likelihood (ML) bootstrap support values > 70% and Bayesian posterior probabilities > 0.95. Voucher numbers are indicated for each specimen used for this study. Outgroups were pruned from the full ML topology (see reduced phylogeny on the left side). The monarch ingroup (clade *Arses* and *Myiagra*) is highlighted using the simplified full ML topology containing the outgroups on the left side of the figure. CC outgroups = core Corvoidea outgroups (see Materials and Methods).

M. hebetior and *M. alecto* groups, with an inferred origin in the Papuan areas (Clade B). The *M. alecto* group underwent an expansion in Australia, New Guinea, the Bismarcks and the Moluccas (Fig. 3, Table 2). A late Miocene colonization of Fiji (*M. azureocapilla*) from Australia is also inferred from our analysis (Clade C). A second island diversification involves the Australian *M. ruficollis* and the *M. nana* and *M. inquieta* complex (Clade E); and the colonization event of *M. erythrops* in the Palau archipelago (Micronesia) (Fig. 3, Tables 1 & 2). Within Clade F (Fig. 3) there was a major range expansion and diversification during the Pliocene (2.35–3.24 Ma). We identified three lineages, which orginated

Table 1 Divergence times of Australasian *Myiagra* and *Arses* in million years ago (Ma) with 95% highest posterior densities (HPD) obtained using molecular strict and relaxed clock rates and island constraints. Letters correspond to clades in Fig. 2.

	Divergence times (Ma) [95% HPD]		
	ND2 mt rate 1.79%		Island calibration
Clade	Strict	Uncorrelated log	Strict
Arses/Myiagra	8.48 [7.53–9.43]	8.60 [7.06–10.22]	12.67 [10.51–14.81]
Arses	5.44 [4.35–7.00]	5.28 [3.52–7.12]	7.07 [4.76–9.52]
A	6.86 [6.01–7.74]	7.03 [5.64–8.51]	10.39 [8.46–12.28]
B	3.97 [3.19–4.80]	4.31 [2.93–5.83]	5.25 [3.26–7.32]
C	6.06 [5.15–6.98]	6.12 [4.82–7.52]	9.49 [7.69–11.24]
D	4.09 [3.79–4.69]	4.27 [3.35–5.33]	7.02 [5.59–8.56]
E	1.36 [0.98–1.78]	1.48 [0.84–2.16]	2.44 [1.45–3.45]
F	2.79 [2.35–3.24]	3.08 [2.39–3.85]	3.68 [2.91–4.47]
G	0.71 [0.44–0.99]	0.84 [0.39–1.35]	0.80 [0.47–1.27]
H	1.66 [1.24–2.10]	1.92 [1.25–2.65]	2.73 [1.44–3.07]
I	1.95 [1.55–2.37]	1.91 [1.36–2.52]	2.46 [1.79–3.17]

in the Melanesian/Micronesian areas: (1) an Australian lineage represented by *M. rubecula* and *M. cyanoleuca* (Clade G); (2) an eastern Polynesian and Melanesian clade (Fiji, Samoa, Vanuatu, south Solomons and probably New Caledonia; Clade I); and (3) multiple unresolved lineages involving colonization of the island of Biak, the remote Micronesian archipelago of Caroline and Ponhpei (*M. oceanica* and *M. pluto*) and the Moluccas (*M. galeata*) (Fig. 3, Table 2).

Habitat and plumage state reconstruction for coexisting lineages

Ancestral character states (Appendix S3b) were computed to test whether plumage and ecological character diverged before or after a colonization event. Based on our ancestral estimation and information from the literature, we highlight characters that may have an influence on the coexistence of closely related island species (Appendices S2 & S3b). Using these results, we investigated whether character changes occurred before or after island colonizations. Furthermore, we investigated these character changes along nodes and branches before and after a colonization event in each archipelago where *Myiagra* taxa co-occur (Table 3, Appendix S3). On the Bismarck archipelago, males of *M. alecto* and *M. hebetior* display little plumage differentiation (both being dark). *Myiagra hebetior* has a smaller body length than *M. alecto* (15–17 mm vs. 17–19 mm; Coates *et al.*, 2006), and is also found at higher elevations when they co-occur. Additionally, both taxa display different foraging heights (Appendix S3b). There is a marked male plumage difference between the completely black *M. alecto* and both *M. hebetior* and *M. cyanoleuca*, which display a white belly and vent. *Myiagra alecto* and *M. hebetior*, respectively, display 2 post-colonization character changes (PoC) and 7 prior to colonization character changes (PrC) (2 PoC/7 PrC) and 3 PoC/6 PrC compared

Table 2 Lagrange ancestral area estimation for Australasian *Myiagra* and *Arses* based on the strict-molecular clock chronogram. Ln*L* = log-likelihood of the Lagrange reconstruction, *d* = estimated dispersal rate; *e* = estimated extinction rate. Areas: Australia (AUS), Melanesia (MEL), Micronesia (MIC), Papua (PAP), Polynesia (POL), and Wallacea (WAL). The states returning the highest log-likelihood are indicated in bold.

	Ancestral biogeographical estimation			
	With outgroup		Without outgroup	
Clade	Ln*L* = 79.405 *d* = 0.05 *e* = 0.01		Ln*L* = 97.6714 *d* = 0.08 *e* = 0.12	
Arses/Myiagra	**PAP**	**0.5**	**PAP**	**0.23**
	AUS	0.22	PAP_POL	0.22
	AUS_PAP	0.16	AUS_PAP	0.2
			PAP_MIC	0.18
			Others	0.11
A	**PAP**	**0.22**	**AUS_PAP**	**0.28**
	AUS_PAP	0.2	PAP	0.23
	PAP_POL	0.16	PAP_MIC	0.14
	PAP_MIC	0.13	PAP_POL	0.13
	AUS	0.13	PAP_MEL	0.07
	PAP_MEL	0.08	PAP_WAL	0.04
B	**PAP**	**0.79**	**PAP**	**0.83**
	AUS_PAP	0.14		
C	**AUS**	**0.21**	**AUS**	**0.2**
	POL	0.12	MIC	0.16
	MIC	0.09	POL	0.1
	PAP	0.09	MIC_POL	0.09
	AUS_POL	0.08	PAP_MIC	0.07
	Others	0.3		0.24
D	**AUS_MIC**	**0.21**	**AUS_MIC**	**0.19**
	MIC	0.14	MIC_POL	0.17
	AUS	0.11	MIC	0.15
	MIC_POL	0.11	MIC_MEL	0.11
	Others	0.29	Others	0.26
E	**AUS**	**0.54**	**AUS**	**0.51**
	AUS_WAL	0.33	AUS_WAL	0.35
	AUS_PAP	0.08		
F	**MIC_MEL**	0.42	**MIC_MEL**	**0.42**
	MIC_POL	0.18	MIC_POL	0.23
	AUS_MEL	0.15	AUS_MEL	0.09
G	**AUS**	**0.88**	**AUS**	**0.87**
H	**MIC_MEL**	**0.65**	**MIC_MEL**	**0.66**
	MIC	0.19	MIC	0.2
	MEL	0.11	MEL	0.1
I	**MEL**	**0.5**	**MEL_POL**	**0.52**
	MEL_POL	0.47	MEL	0.45

to no PrC in *M. ruficollis* (Table 3). On Fiji, we find differences between *M. vanikorensis* and *M. azureocapilla* in the following characters: plumage (crown, throat, wing coverts, tail and breast), foraging strategies (upper stratum vs. middle lower stratum) and body length (13 mm vs. 16 mm, respectively). The earliest colonizer, *M. azureocapilla,* displays 6 PoC/3 PrC compared to the recent colonizer *M. vanikorensis*, which shows no PoC. Differences between *M. alecto* and *M. galeata* on Halmahera involve all seven plumage characters, body length (18 mm vs. 14 mm) and foraging

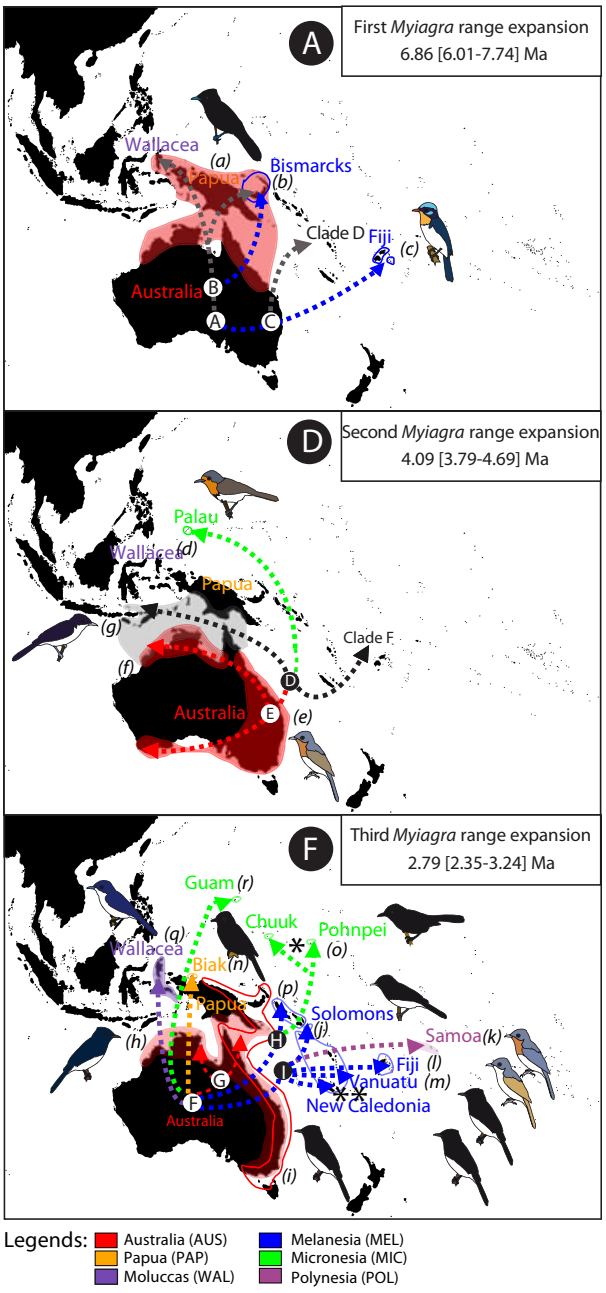

Figure 3 Map indicating the dispersal and colonization routes of members of the *Myiagra* in the Indo-Pacific archipelagos. The nodes A (top), D (middle) and F (bottom) illustrate the three dispersal waves non-overlapping in time that led to independent speciation events on different archipelagos. These dispersal and colonization routes were inferred from the chronogram and the LAGRANGE biogeographical analyses (see Tables 1 & 2). Coloured dotted lines indicate dispersal into the Indo-Pacific (see legends) and each terminal arrow indicates one colonization event of one species (see Appendix S3a for species letter labels). Asterisks (*) indicate putative dispersal routes for two missing taxa (*M. oceanica* and *M. caledonica caledonica* & *M. c. viridinitens*). Divergence times of nodes A, D and F are indicated in million years ago (Ma) with 95% highest posterior densities (HPD) specified in the brackets.

Table 3 Ecomorphological character states that changed prior to colonization or post-colonization of the Bismarcks, Fiji and the North Moluccas where *Myiagra* species co-occur. By comparing the clades A, B, C, E, and I before and after the inferred island colonizations (see Results), we computed the number of character changes prior to colonization (PrC) and post- colonization (PoC) for each of these nodes. Labels and ages of the nodes of interest are also indicated. All the ancestral reconstruction and character states are displayed in Appendix S3b.

Remote island lineages	Clade	Colonization date (Ma)	Number of	
			PrC	PoC
WALLACEA: North Moluccas				
M. alecto	B	3.19–4.80	7	2
M. galeata	F	2.35–3.24	4	5
MELANESIA: Bismarks				
M. alecto	B	3.19–4.80	7	2
M. hebetior	B	3.19–4.80	6	3
M. ruficollis	E	0.98–1.78	0	9
MELANESIA: Fiji				
M. azureocapilla	C	5.15–6.98	3	6
M. vanikorensis	I	1.55–2.37	9	0

strategies. In the North Moluccas, *M. alecto* is the first colonizer and displays 2PoC/7PrC in contrast to 5 PoC in *M. galeata*, which arrived more recently.

Co-occurring *Myiagra* species display overall higher molecular ($mean_{moldist}$ = 0.11; ANOVA, $F_{1,238}$, $P < 0.01$) and morphological distances ($mean_{mordist}$ = 4.96; ANOVA, $F_{1,238}$, $P = 0.64$) than allopatric taxa ($mean_{moldist}$ = 0.08; $mean_{mordist}$ = 4.77).

DISCUSSION

Biogeographical origin of *Myiagra* and *Arses* lineages

The ancestral area analysis (Table 2, Fig. 3) suggests that Australo-Papua was the most likely area of origin for *Arses* and *Myiagra*. This area appears to have been central for the entire monarch radiation; the endemic Australo-Papuan *Arses* clade and three independent nested lineages of *Myiagra* all occur within this region (nodes B, E, G). This is also supported by the distribution of basal taxa within the phylogeny (Fig. 2), several of which have distributions extending in Australo-Papua. Furthermore, the sister clades *Grallina* and *Monarcha* are also hypothesized to have originated in this region (Filardi & Moyle, 2005). An Australo-Papuan origin for *Myiagra* and *Arses* is also concordant with several other studies on core corvoid island lineages (Jønsson *et al.*, 2010a,b). However, our biogeographical model of colonization and tree topology also indicate a role for Melanesia and the Moluccas in terms of recent dispersals from the Australo-Papuan species pool (nodes A, B, C, D). Population structuring between the Australo-Papuan landmasses and nearby archipelagos such as Melanesia and the Moluccas, seems to

have played an important role in the evolutionary history of these continental *Myiagra* lineages (*M. alecto*, *M. cyanoleuca*, *M. ruficollis*). Within the Australo-Papuan area, three *Myiagra* lineages persisted through the Plio-Pleistocene before subsequent colonization and speciation on most of the peripheral Indo-Pacific islands (Table 1).

Colonization of close and remote archipelagos

Our results strongly support independent (non-overlapping in time) colonizations of remote archipelagos (Table 1). Our results also suggest more spatially structured colonizations, from the continent to the nearest island groups, and onwards to more remote islands. Unlike in the *Monarcha* group (Filardi & Moyle, 2005), there is no case of back-colonization to Australia.

Recent (Pliocene) dispersal from the Australo-Papuan mainland to the nearest archipelagos includes colonization of the Bismarcks (*M. alecto*, *M. cyanoleuca* and *M. hebetior*) and Wallacea (*M. alecto*, *M. galeata* and *M. ruficollis*). These colonizations involved lineages of mangrove specialists (*M. alecto* and *M. ruficollis*). Because several of the remote island species occur in both forest and mangrove areas, it seems that adaptation to mangrove could have spurred initial diversification and colonization of remote land areas (Nyári & Joseph, 2012). There were also two or three colonizations of the Bismarcks (*M. alecto*, *M. hebetior* and *M. cyanoleuca*). One possible interpretation of this is that the Bismarck taxa represent two colonizations by the ancestor of *M. alecto*/*M. hebetior* and subsequently by that of *M. cyanoleuca*. Alternatively, early dispersal by an Australasian ancestor of *M. hebetior* to the Bismarcks was followed by another colonization of the Bismarcks in the Pliocene by *M. alecto* and *M. cyanoleuca*. Our phylogenetic results suggest that the Bismarck taxa have undergone a different colonization history compared to taxa of other Melanesian archipelagos, as suggested by Mayr & Diamond (2001), because the colonization of the more remote Melanesian archipelagos of New Caledonia, the Solomons and Vanuatu by *Myiagra* has been more complex. Our results indicate that lineages on these archipelagos originated from an Australo-Papuan ancestor and involved independent colonizations of the Solomons (*M. caledonica*, *M. cervinicauda* and *M. ferrocyanea*), Vanuatu (*M. vanikorensis*) and probably New Caledonia (*M. caledonica*). In the Solomons two independent lineages have colonized different islands (*M. ferrocyanae* in the western Solomons, *M. cervinicauda* on Makira and *M. caledonica* on Rennell and potentially New Caledonia). Our phylogeny supports a recent geographical range expansion of *Myiagra* throughout the Solomons, New Caledonia, Vanuatu and western Polynesia. A similar biogeographical pattern within this region is found in other monarch clades (*Neolalage*, *Mayrornis*, *Clytorhynchus* clade; Filardi & Moyle, 2005) and also in *Alopecoenas* ground-doves (Jønsson *et al.*, 2011a). The age of *Myiagra* is in accordance with the timing suggested by Filardi & Moyle (2005) (> 1.5 Myr), indicating that perhaps sea-level changes and land-bridge formations during the Plio-Pleistocene might have favoured stepping stone dispersal within this region (Voris, 2000). This dynamic geographical history may in part have created the observed complex patterns of allopatric distributions and dispersal routes (Lohman *et al.*, 2011).

The ancient Fiji archipelago was colonized during the Pliocene by two independent lineages: *M. azureocapilla* and *M. vanikorensis*. Like the Bismarcks, Fiji is a large archipelago with greater area and resources that could support a higher number of 'sympatric' taxa (Mayr & Diamond, 2001) relative to small remote islands (MacArthur & Wilson, 1963). Considering other related lineages (Filardi & Moyle, 2005), two genera (*Clytorhynchus*, *Mayrornis*) colonized Fiji independently, leading to an intra-archipelago monarch radiation. The radiation of Pacific monarch flycatchers is in many ways similar to radiation patterns of Fijian lizards (Townsend *et al.*, 2011) and arthropods (Bickel, 2009).

The Micronesian archipelagos were colonized three times independently and these colonizations did not follow the stepping-stone pattern seen across the Micronesian islands. The three lineages of Micronesia (*M. erythrops*; *M. pluto* and *M. oceanica*; *M. freycineti*) do not appear to share common ancestry, except perhaps for the birds from the Chuuk (*M. oceanica*) and Ponhpei (*M. pluto*) archipelagos (Fig. 3). These remote archipelagos were colonized during the late Miocene by *M. erythrops* (Palau), during the Plio-Pleistocene by *M. pluto* and *M. oceanica* (Pohnpei and Chuuk) and recently by the extinct *M. freycineti* (Guam). A sister relationship between *M. pluto* and *M. ferrocyanea* from the Solomons suggests an expansion from Melanesia to Micronesia during the Plio-Pleistocene. Colonization of Palau and Guam seems to be related to an Australo-Papuan ancestor but recent extinctions in the Pacific may obscure historical distributions. Although multiple colonizations occurred in Fiji, the Moluccas and the Bismarcks, species from different *Myiagra* lineages are not known to co-occur on the other remote islands.

Assembly of *Myiagra* flycatcher communities on Pacific islands

Several evolutionary and ecological processes have been suggested to influence the assembly of communities on islands. Diamond (1975) argued that competitive exclusion would cause particular pairs of species never to co-occur on the same island, a phenomenon he referred to as 'checkerboard' species distributions. However, subsequent re-analyses of data on the distributions of birds in the Bismarcks and the Solomon Islands suggested that stochastic (Connor & Simberloff, 1979) and, more recently, historical (Collins *et al.*, 2011) processes determine the composition of species assemblages (but see Sanderson *et al.*, 2011).

Several independent dispersal events from the Australo-Papuan source pool to remote archipelagos of the Indo-Pacific played an important role in the assembly of insular

Myiagra, supporting some degree of stochasticity. The low co-occurrence of congenerics on any given island suggests that historical priority effects might also be important. Overlap in the geographical distributions of insular *Myiagra* species results from several independent colonizations from Australo-Papua to Fiji, the Bismarcks and the Moluccas (Fig. 3). Consequently, the geographical distributions of species in the genus *Myiagra* overlap in four areas: Australia (six species: *M. alecto, M. cyanoleuca, M. inquieta, M. nana, M. rubecula* and *M. ruficollis*), on Halmahera in the Moluccas (two species: *M. alecto, M. galeata*), on New Britain (*M. alecto*, *M. ruficollis* and *M. hebetior*), Umboi (*M. alecto* and *M. cyanoleuca*) and New Ireland, Lavangai and Mussau in the Bismarks (*M. alecto* and *M. hebetior*) and on Viti Levu, Vanua Levu and Taveuni in the Fiji archipelago (*M. azureocapilla* and *M. vanikorensis*). Few colonization events, however, have led to co-occurring species of monarch flycatchers on the same island, in agreement with other studies focusing on closely related taxa within the Monarchidae (Filardi & Moyle, 2005; Fabre *et al.*, 2012). Thus it might be that species of *Myiagra* cannot co-occur on the same island because they are closely related or ecologically similar, as hypothesized by Diamond (1975). However, we cannot exclude the possibility that low co-occurrence of closely related species results from (1) single-colonization of the island, or (2) swamping of sister populations on other islands through hybridization (e.g. Mayr & Diamond, 2001, on *Myzomela*).

There are some instances of sympatry within *Myiagra*, but such cases tend to be restricted to species which differ in some aspects of their evolutionary history and/or autecology. Our ancestral reconstruction of trait evolution and geographical areas suggest that (1) morphological and molecular distances (see results for $\text{mean}_{\text{moldist}}$ and $\text{mean}_{\text{mordist}}$), (2) foraging strategy, and (3) plumage features (Table 3, Appendix S3) diverge more among sympatric than allopatric taxa in *Myiagra*. Moreover, our results suggest that the ecological trait structure of sympatric *Myiagra* species arises from multiple dispersal events among species of *Myiagra*, which acquired divergent ecological traits elsewhere. These traits remained evolutionarily conserved following the colonization of islands and archipelagos (i.e. ecologically conservative dispersal; Stephens & Wiens, 2004) as demonstrated via the recent range expansion of Clade F (Figs 2 & 3). In this clade, most lineages display a white belly and a darker dorsal plumage acquired recently through their Australo-Papuan diversification. These plumage characters were inferred to be different from the plumage of older colonists on islands on which they co-occur. This pattern is evident for colonizations of the North Moluccas, the Bismarcks and Fiji, for which the first *Myiagra* colonizers display more derived features (PoC) than do subsequent colonizers. Based on these results, we suggest that plumage divergence and habitat adaptation may have diverged prior to colonization for late colonizers. That is, late colonizers or secondary colonizers arrive with traits they acquired elsewhere, whereas first colonizers will display more derived traits that evolved *in situ*. We note that our results might also depend on the time since first colonization, such that the oldest species rapidly diverged into vacant niches, with the result that the younger ones are ecologically constrained (Price, 2010). In sum, it appears that the composition of insular communities of *Myiagra* results from stochastic dispersal from the source pool and ecologically deterministic colonization of islands and archipelagos.

CONCLUSIONS

Our study demonstrates that diversification of *Myiagra* in the Indo-Pacific is the result of three waves of colonization, non-overlapping in time. Our results reveal an additional example of the important role of recent range expansions and dynamic colonizations of new habitat and geographical areas in driving speciation (cf. Clade F). Three colonizations have led to the co-occurrence of *Myiagra* species with similar ecomorphological profiles on the same island. The higher diversity of *Myiagra* spp. on the remote archipelago of Fiji relative to that of the less isolated Solomons and Vanuatu, however, supports both MacArthur & Wilson (1967) equilibrium theory and Rosindell & Phillimore's (2011) unified model of island biogeography, wherein a high level of isolation increases speciation rate and ultimately, species diversity. Whereas the presence of old and isolated lineages of *Myiagra* on remote islands (cf. *M. azureocapilla*, *M. erythrops* and probably *M. oceanica*) suggests high persistence through time, gaps in the distribution of some of these older *Myiagra* lineages suggest that widespread extinctions might have created disjunctions in the geographical distributions of species. Dispersal and extinction are likely to play an important role in the distribution and structure of monarch flycatcher assemblages, but ecological interactions among species might also explain some of the biogeographical patterns we observe.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Taxonomic sampling, voucher numbers, molecular methodology and loci used in this study.

Appendix S2 *Myiagra* ecomorphological data extracted and coded from Coates *et al.* (2006) and Higgins *et al.* (2006).

Appendix S3 Chronograms and ancestral state reconstructions based on the maximum likelihood tree.

BIOSKETCH

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Author contributions: P.-H.F. conceived the ideas, designed the methods, analysed the data and wrote the paper; M.M., M.I. and P.-H.F. carried out the molecular work; P.-H.F. analysed the data; P.-H.F. designed the project and drafted the manuscript; M.I., J.-P.L., J.F. and K.A.J. contributed to the interpretations of data and writing.

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