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SYNTHESIS

The historical biogeography of coral reef fishes: global patterns of origination and dispersal

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ABSTRACT

Aim To use recently published phylogenies of three major reef fish families to explore global patterns of species origin and dispersal over the past 65 million years. The key questions are: when and where did reef fishes arise, and how has this shaped current biodiversity patterns?

Location Biogeographic reconstructions were performed on globally distributed reef fish lineages. Patterns of lineage origination and dispersal were explored in five major biogeographic regions: the East Pacific, the Atlantic, the Indian Ocean, the Indo-Australian Archipelago hotspot, and the Central Pacific.

Methods A dispersal, extinction and cladogenesis (DEC) model implemented in LAGRANGE was used to infer the most likely biogeographic scenarios at nodes on chronograms of three diverse reef fish families (Labridae, Pomacentridae, Chaetodontidae). For the terminal branches ANOVA was used to compare patterns of origination on a regional and global scale. Patterns of origination and dispersal were examined within discrete time periods for the five biogeographic regions.

Results Temporal examination of hypothetical ancestral lineages reveal a pattern of increasing isolation of the East Pacific and Atlantic regions from the Eocene, and the changing role of the Indo-Australian Archipelago from a location of accumulating ranges in the Palaeo/Eocene, a centre of origination in the Miocene, to extensive expansion of lineages into adjacent regions from the Pliocene to Recent.

Main conclusions While the East Pacific and Atlantic have a history of isolation, the Indo-Australian Archipelago has a history of connectivity. It has sequentially and then simultaneously acted as a centre of accumulation (Palaeocene/Eocene onwards), survival (Eocene/Oligocene onwards), origin (Miocene onwards), and export (Pliocene/Recent) for reef fishes. The model suggests that it was the proliferation and expansion of lineages in the Indo-Australian Archipelago (the Coral Triangle) during the Miocene that underpinned the current biodiversity in the Indian and Pacific Oceans.

Keywords

Biodiversity hotspot, centre of origin, coral reef, Coral Triangle, DEC model, dispersal, evolution, Indo-Australian Archipelago, Lagrange, survival.

INTRODUCTION

Understanding the historical forces shaping biodiversity is an important aspect of marine biogeography. More than 5000 species of fishes are associated with coral reefs globally (Bellwood *et al.*, 2010). A maximum diversity is reached on reefs within the central Indo-Australian Archipelago (IAA), the largest marine biodiversity hotspot. This 'bull's eye' pattern has both latitudinal and longitudinal gradients in diversity. The latitudinal gradients in species diversity away from the

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IAA hotspot have been recognized for some time (Ekman, 1935; Rosen, 1981), and reflect the temperate–tropical gradients seen in terrestrial systems. However, the longitudinal decline in marine species diversity has inspired much debate in the literature (Palumbi, 1997; Briggs, 1999; Hoeksema, 2007). Central to the debate over the last 30 years have been three cornerstone 'centre of' hypotheses describing the origin and maintenance of faunal diversity within the IAA hotspot: whether it is a centre of origin, overlap, and/or accumulation. As in terrestrial biogeography, rates of origination have been used as the primary basis for evaluating these various hypotheses. These hypotheses examine processes maintaining biodiversity in the IAA hotspot and are framed within the context of the Indo-Pacific region. Yet, the Indo-Pacific does not exist in isolation. There has been little attempt to explore global patterns of origination and dispersal between regions to directly compare the major marine biogeographic provinces. Particularly, how do rates of origination within the IAA compare with those of adjacent regions in the Indo-Pacific (Indian Ocean, Central Pacific) and other more distant regions (Atlantic, East Pacific)? There are challenges to addressing these questions. The lack of physical barriers in the marine environment and connectivity through larval dispersal has blurred the biogeographic origins of marine species (Bellwood & Meyer, 2009a). Even on shallow time-scales it is often unclear whether speciation has occurred in allopatry through vicariance, or in sympatry (Barraclough & Vogler, 2000; Losos & Glor, 2003; Rocha *et al.*, 2005; Quenouille *et al.*, 2011). However, large-scale patterns are becoming increasing open to quantitative evaluation (e.g. Hughes *et al.*, 2002; Floeter *et al.*, 2008; Rocha & Bowen, 2008; Williams & Duda, 2008). Nevertheless, a detailed appraisal of global patterns in origination and dispersal among the major biogeographic regions for coral reef fishes remains to be seen.

Since their initial formulation by Potts (1985) in the context of reef building corals, the three 'centre of' hypotheses have been repeatedly modified and expanded (reviewed by Bellwood *et al.*, 2012) in an attempt to explain the extensive overlapping and widespread ranges seen in multiple coral reef taxa (Hughes *et al.*, 2002; Connolly *et al.*, 2003). Furthermore, a fourth 'centre of survival' (Heck & McCoy, 1978; Barber & Bellwood, 2005) has been added which seeks to explain why most of the taxa remain in the IAA regardless of the location of origin of the taxa. This hypothesis allows multiple sources of biodiversity, widespread ranges and post-speciation range expansion. Recent study has shown that coral reefs may provide the mechanism for this survival in the IAA, allowing both higher rates of diversification and reduced vulnerability to extinction for associated lineages (Cowman & Bellwood, 2011). Several phylogeographic studies of reef fish evolution centred in the IAA have invoked one or more of the 'centre of' hypotheses to explain current biogeographic patterns (Bernardi *et al.*, 2002; McCafferty *et al.*, 2002; Timm *et al.*, 2008). However, there has been no family-level study for reef fishes exploring congruence in global patterns of biogeographic origination, dispersal and geographic range inheritance in a temporal framework. Central questions regarding rates and locations of origination, direction and amplitude of dispersal over time, and the extent of range inheritance along lineages need to be answered before we can begin to understand the drivers of coral reef biodiversity. To answer these questions a global perspective is needed, for multiple groups, across all of the major marine biogeographic realms.

The circum-tropical belt can be divided into three major realms: the Indo-Pacific, Atlantic, and East Pacific. These realms are distinguished by a taxonomic makeup resulting from a long history of vicariance associated with both hard and soft barrier formation dating as far back as the Eocene (Bellwood & Wainwright, 2002; Floeter *et al.*, 2008). The formation of three separate barriers has acted to divide these regions: (1) the East Pacific Barrier (EPB), an open expansion of ocean which separates the Indo-Pacific from the East Pacific; (2) the Terminal Tethian event (TTE), which largely cuts off dispersal between the Indo-Pacific and the Atlantic (but see Bowen *et al.*, 2006); and (3) the Isthmus of Panama (IOP), which separates the Atlantic from the East Pacific (reviewed by Lessios, 2008). Within the Indo-Pacific, the lack of hard barriers (land bridges) has allowed many taxa to maintain widespread geographic ranges spanning from the east coast of Africa to islands in the central Pacific, or in some cases to the Pacific coast of the Americas (Hughes *et al.*, 2002; Reece *et al.*, 2011). However, the combination of tectonic activity and several semi-permeable hydrological barriers (Barber *et al.*, 2000, 2002; Santini & Winterbottom, 2002) has resulted in a complex distribution of taxa including both provincial endemics and widespread species that characterize the Indian Ocean, the IAA hotspot, and the Central Pacific island arcs (Bellwood & Wainwright, 2002; Jones *et al.*, 2002; Connolly *et al.*, 2003; Hoeksema, 2007). These conditions make it extremely difficult to identify origination and directionality of dispersal between regions. For both endemic taxa and those that are widespread across the entire Indo-Pacific (Indian Ocean, IAA, Central Pacific) we need to answer several questions: (1) In what region did a lineage first arise? (2) To what extent has within-region and between-region origination contributed to patterns of diversity? (3) How has dispersal affected their distribution? In a temporal framework, the answers to these questions will illuminate both the evolutionary history of the IAA hotspot, and its relationship with adjacent and distant geographic regions.

Within the IAA, it may be difficult to detect the overall contribution of vicariant speciation through isolation due to the transient nature of barriers and rapid dispersal potential of marine fishes (Quenouille *et al.*, 2011). However, on a larger taxonomic and geographic scale, vicariance between biogeographic regions may be clearly observed in deeper lineages (Losos & Glor, 2003). Likewise, at a regional scale it may be beneficial to quantify the extent of lineage origination within a biogeographic region (regional origination) versus between regions. In considering dispersal between regions, it is important to quantify the frequency with which dispersal is followed by vicariance and whether it reflects the palaeogeographic record.

To address these issues, we examine inferred patterns of origination and dispersal in the reef fish families Labridae, Pomacentridae and Chaetodontidae under a dispersal, extinction and cladogenesis (DEC) model. All three families are amongst the most diverse and abundant families distributed on coral reefs globally (Bellwood & Wainwright, 2002). They also inhabit other tropical reef habitats as well as more temperate latitudes within the five biogeographic regions. Chronograms for these families have recently been reconstructed that include the highest taxon sampling to date (45% labrids, 46% pomacentrids, 75% chaetodontids), with relatively even representation in all regions and habitats (Cowman & Bellwood, 2011; see Table S1, Appendix S1 in the Supporting Information). These chronologies show remarkable congruence in the tempo of diversification (Cowman & Bellwood, 2011), with previous work highlighting temporal concordance in trophic innovation (Cowman *et al.*, 2009; Bellwood *et al.*, 2010). The three families contain endemic species in most major regions, as well as widespread species (Moura & Sazima, 2000; Jones *et al.*, 2002; Kuiter, 2002; Floeter *et al.*, 2008; Craig *et al.*, 2010). Previous studies have explored biogeographic patterns of various taxa within each family (Floeter *et al.*, 2001, 2008; McCafferty *et al.*, 2002; Barber & Bellwood, 2005; Rocha *et al.*, 2005; Westneat & Alfaro, 2005; Beldade *et al.*, 2009; Hodge *et al.*, 2012). However, there has been no biogeographic reconstruction of ancestral ages at the family level. These three families, therefore, present ideal candidates for ancestral range reconstruction and the exploration of patterns of origination on coral reefs. Using recently developed software for biogeographic reconstruction (Ree & Smith, 2008) hypothetical inheritance scenarios along the molecular lineages can be inferred from extant ranges. This can provide us with a framework in which we can assess patterns of origination within each region, and dispersal between them.

The aim of this study, therefore, is to examine patterns of origination and dispersal in the biogeographic histories of the Labridae, Pomacentridae and Chaetodontidae. In a global context this will provide an opportunity to evaluate possible sources of current biodiversity, directionality of dispersal, and the relationship between the major biogeographic realms over the past 65 Myr. The specific questions to be answered are:

1. Do the three focal families of coral reef fishes display congruent patterns of origination on a global scale?

2. How have post-speciation dispersal and range inheritance contributed to current patterns of biodiversity of coral reef fishes?

3. Has the role of the IAA hotspot changed through time?

MATERIALS AND METHODS

Chronologies and geographic range data

Recently constructed chronograms for the families Labridae (wrasses), Pomacentridae (damselfishes) and Chaetodontidae (butterflyfishes) were used in the ancestral range reconstruction analysis. These chronograms were obtained using Bayesian inference and fossil data (see Cowman & Bellwood, 2011). The chronograms focused on relative ages within the three families. Given the uncertainty in stem lineage ages some older origins may be possible for some taxa, especially the Chaetodontidae (Santini *et al.*, 2009). The geographic ranges of all nominal species in each family were assessed using published sources (Randall *et al.*, 1990; Allen, 1991; Allen *et al.*, 1998; Kuiter, 2002; Randall, 2005) and FishBase (Froese & Pauly, 2011). Geographic ranges were allocated into five separate regions: (1) Indian Ocean, (2) IAA, (3) Central Pacific, (4) East Pacific, and (5) Atlantic (Table S1, Appendix S1; areas incorporated in each region provided in Table S2, Appendix S1). Presence within a geographic region required a record of one location within the region; there was no limit to the number or order of regions occupied. Temperate lineages are included in each region for each of the three families to maintain taxonomic completeness of clades where possible. For taxa sampled in the chronograms, the presence or absence of a species in each region was coded as a character state to be used in the ancestral range reconstruction (Table S3, Appendix S1). Although not complete, all major lineages and tribes contain high and relatively even taxon sampling across all regions (Table S1, Appendix S1).

Ancestral range reconstruction

Reconstruction of ancestral ranges based on the time-calibrated phylogenies was implemented in the program Lagrange 2.01 (likelihood analysis of geographic range evolution; Ree & Smith, 2008). Lagrange implements a maximum likelihood approach based on a stochastic model of geographic range evolution involving dispersal, extinction and cladogenesis (DEC model). The DEC model implemented by the Lagrange program has been used in several recent studies of various taxa: plants (Smith, 2009), snakes (Kelly *et al.*, 2009), insects (Ramírez *et al.*, 2010), and gastropods (Göbbeler & Klussmann-Kolb, 2010). In marine fishes, it has been used to investigate biogeographic patterns in the smelt *Hypomesus* (Ilves & Taylor, 2007). Buerki *et al.* (2011) show, using palaeogeographic evidence, that it can lead to more accurate reconstructions than previous approaches, provided care is taken with defining the initial model.

In the DEC model, anagenetic (internode) range evolution is governed by a Q matrix of instantaneous transition rates that infer dispersal (range expansion) between geographic regions, or local extinction (range contraction) within a region along phylogenetic branches that can be calibrated to time (Ree & Smith, 2008). The model also allows global rates of dispersal and local extinction to be estimated by maximum likelihood (Ree & Smith, 2008). Dispersal was restricted to only occur between adjacent regions.

Cladogenetic (node speciation) change is modelled under three alternative inheritance scenarios (Ree *et al.*, 2005): (1)

vicariance, where a widespread ancestor diverges across a regional boundary with descendants present in adjacent regions (Fig. S1a, Appendix S2); (2) within-region origination, where the ancestor and both descendants are present in the same region (Fig. S1b, Appendix S2); and (3) peripheral cladogenesis, where an ancestral lineage maintains a range across more than one of the defined regions, while one descendant originates within one of the regions (Fig. S1c, Appendix S2). The third range inheritance scenario allows a widespread ancestral range to be inherited by a single descendant lineage. It is this scenario that will be most useful in modelling range evolution within these fish families, which is not implemented in traditional range reconstruction software such as DIVA (Ronquist, 1997). For each node, range inheritance scenarios are ranked according to the fractional likelihood they received by the analysis. Where other likely scenarios exist for range inheritance, LAGRANGE ranks these scenarios within two log-likelihood units of the optimal scenario.

LAGRANGE also allows constraints to be placed on the DEC model to reflect past geological events (e.g. formation of barriers) and fossil information. Each family was exposed to three separated models: M0, an unconstrained model allowing equal probability of dispersal between adjacent areas at any time; M1, a constrained model reflecting formation of biogeographic barriers; and M2, a constrained model with an added fossil constraint at the root of each tree reflecting the fossil record for each family (Fig. S2, Appendix S2). The constrained model, M1, reduced the probability of dispersal from the Central Pacific to the East Pacific to 0.05 for the entire duration of the chronogram (i.e. from root to tip) reflecting the East Pacific Barrier. The probability of dispersal from the Indian Ocean to the Atlantic Ocean was reduced to 0.05 from 18 Ma onwards, reflecting the closure of the Tethys seaway (Steininger & Rögl, 1979), but allowing the possibility of dispersal around the Horn of Africa (Bowen *et al.*, 2006). Dispersal from the Atlantic to the East Pacific was not allowed from 3.1 Ma to present, reflecting the closure of the Isthmus of Panama (Lessios, 2008).

The fossil constrained model, M2, forced the range of the root node to include the Atlantic (Tethys) region, based on fossils from Monte Bolca (Bellwood, 1996; Fig. S2, Appendix S2). The three models were compared using log-likelihood scores, and range inheritance scenarios were compared across the tree. The best model was used to map origination, dispersal and extinction events on to the family chronograms.

Exploring patterns

Patterns of origination and dispersal among the Labridae, Pomacentridae and Chaetodontidae were assessed based on the DEC model with the best likelihood score. By mapping the range inheritance scenarios reconstructed by the DEC model, the estimated timing and location of origination was recorded for each of the lineages on each of the chronologies. Inferred dispersal events were recorded along each branch. The timing for each dispersal event was taken as the midway point along the branch on which it occurred. This procedure was employed for the tips of the trees (i.e. the extant taxa) and across the entire chronology (i.e. hypothetical ancestral molecular lineages).

Patterns of origination were compared as a proportion of 'sampled regional diversity' (extant lineages sampled in the trees present in each region) and as a proportion of 'sampled family diversity' (extant lineages sampled in the trees) for each family. This was to identify regions where origination of lineages through regional cladogenesis has been a major contribution to diversity of the region, and to identify which regions have been a major contributor to the diversity of each family. To investigate if taxon sampling has had an effect on the patterns observed we also compare regional origination as a proportion of 'total regional diversity' (all nominal species in the region for each family) and 'total family diversity' (all nominal species in the family) for each family. All proportional values were arcsin transformed prior to analyses.

In order to investigate the pattern of origination and dispersal throughout the evolutionary history of the three families, the number of lineages present in each region at four time intervals were calculated from the ancestral reconstruction: the Eocene/Oligocene boundary (33 Ma), the Oligocene/Miocene boundary (25 Ma), the Miocene/Pliocene boundary (5 Ma), and the present (0). This gives an estimate of hypothetical relative 'palaeodiversity' from the molecular history (N.B. this is only relative and makes no allowances for subsequent extinction). The palaeodiversity in each region is the result of lineage origination within the region, and lineage dispersal into the region during the previous epoch. In cases where vicariance has occurred after dispersal, the sum of origination and dispersal into the region will be greater than the total palaeodiversity. Where a lineage has inherited a range, origination and dispersal will be less than palaeodiversity. Proportions of origination, dispersal, and inheritance were estimated in each family for each epoch (Palaeocene/Eocene, Oligocene, Miocene, Pliocene/Recent).

RESULTS

Range reconstruction

The constrained models, M1 (barrier constrained) and M2 (fossil constrained), were favoured over the unconstrained model M0, with significantly better log-likelihood scores (over 30 log-likelihood units) for all three families (Table S4, Appendix S1). In all cases M1 had a better likelihood score than M2; however, this was negligible for the Labridae (0.3 units) and Chaetodontidae (1 unit). For the Pomacentridae, the addition of the fossil calibration gave a lower log-likelihood score by 2.7 units. Optimal reconstructed scenarios showed consistently higher likelihood under M1. Global rates of dispersal were slightly higher under constrained models while extinction rates were similar under all three models (Table S4, Appendix 1). Node reconstructions of model M1 are therefore used to explore patterns of origination and dispersal. Node reconstructions were overlaid onto family chronograms (Figs S3–S5, Appendix S2).

Origination and dispersal of extant taxa

For sampled regional diversity of each family, the relative contribution of origination, dispersal and range inheritance to regional biodiversity was calculated from the Lagrange M1 reconstruction (Table 1). For all three families, the East Pacific, Atlantic and IAA show high rates of within-region origination (75–100%; Table 1). Dispersal into these regions is low (1–6%). The Atlantic region appears to be isolated except for two putative dispersal events into the region around the Cape of Good Hope: *Halichoeres maculipinna*; *Anampses caeruleopunctatus* (Fig. S3, Appendix S2). Both the Indian Ocean and Central Pacific are characterized by low origination (20–40% Indian Ocean; 10–16% Central Pacific), but high dispersal of lineages into the region, from the IAA (Fig. 1a, Table 1). Dispersal from the IAA into the Indian Ocean and the Central Pacific appears to be of a similar magnitude (Fig. 1a). The Central Pacific, while having comparable species richness to the Indian Ocean (Fig. 1a), has lower origination (7–16%). For all three families ancestral inheritance in the Central Pacific appears to be higher than within-region origination (Table 1).

In order to investigate whether patterns of origination (both as a proportion of sampled regional diversity and sampled family diversity) varied among regions and families, a two-way ANOVA was used, with regions and families treated as fixed effects. There was no significant family effect on regional origination as a proportion of sampled regional diversity ($F_{2,8} = 0.29$, $P = 0.76$) i.e. patterns of origination within each region were consistent among families. However, there was a significant region effect on origination as a proportion of sampled diversity in each region ($F_{4,8} = 32.7$, $P < 0.0001$), i.e. there were significant regional differences in the contribution of within-region origination to sampled regional diversity. Tukey–Kramer post-hoc comparisons showed that lineage originations in the IAA, Atlantic, and East Pacific were significantly higher than in the Indian Ocean and Central Pacific (Fig. 1b).

Regional origination as a proportion of sampled family diversity likewise showed no significant family effect ($F_{2,8} = 0.001$, $P = 0.99$). There was, again a significant region effect on regional origination as a proportion of sampled family diversity ($F_{2,8} = 56.7$, $P < 0.0001$). Tukey–Kramer post-hoc comparisons identified the IAA as having a significantly higher proportion of origination contributing to the sampled diversity of each of the three families, compared with the other four regions (Fig. 1c).

Regional origination as a proportion of total regional diversity and total family diversity showed similar results. There was no significant family effect found for regional origination as a proportion of total regional diversity ($F_{2,8} = 3.2$, $P = 0.09$) or total family diversity ($F_{2,8} = 2.4$, $P = 0.15$) i.e. patterns of regional origination both as a proportion of total regional diversity and total family diversity did not differ significantly among families. As with sampled diversity, there was a significant region effect on the proportion of regional origination of both total regional diversity ($F_{2,8} = 10.22$, $P < 0.005$), and total family diversity ($F_{2,8} = 20.3$, $P < 0.001$), i.e. the contribution of regional origination to both the total biodiversity of a region, and the total biodiversity of each family, differed significantly between regions. Tukey–Kramer post-hoc comparisons identified the same groups as reported for sampled regional diversity (EP, Atl, IAA versus In, CP) and for sampled family diversity (IAA versus all other regions)

Origination and dispersal through time

The ancestral reconstruction implemented in Lagrange allowed patterns of anagenetic and cladogenetic change to be investigated in different epochs. As with the extant tips of the trees, this allowed the contribution of origination and dispersal to the palaeodiversity (of molecular lineages) in each biogeographic region to be estimated for the Labridae (Fig. 2a–d), Pomacentridae (Fig. 2e–h), and the Chae-

Table 1 Relative contribution of origination (Origin), dispersal (Disp.) and inheritance (Inh.) per capita regional biodiversity of the Labridae, Pomacentridae, and Chaetodontidae in five major biogeographic regions. Origination is the proportion of species that arose within that region; Dispersal is the proportion of species within each region that dispersed to that region and maintain it as part of its range; Inheritance is the proportion of species that inherited that region as a part of an ancestral lineage range that arose in another region.

	Labridae			Pomacentridae			Chaetodontidae		
Region	Origin	Disp.	Inh.	Origin	Disp.	Inh.	Origin	Disp.	Inh.
EP	0.76	0.06	0.18	0.90	0.00	0.10	0.67	0.00	0.33
Atl.	0.99	0.01	0.00	1.00	0.00	0.00	1.00	0.00	0.00
In	0.21	0.64	0.15	0.41	0.49	0.10	0.40	0.47	0.14
IAA	0.96	0.03	0.01	0.88	0.11	0.01	0.95	0.05	0.00
CP	0.10	0.78	0.12	0.07	0.72	0.21	0.16	0.53	0.30

EP, East Pacific; Atl, Atlantic; In, Indian; IAA, Indo-Australian Archipelago; CP, Central Pacific.

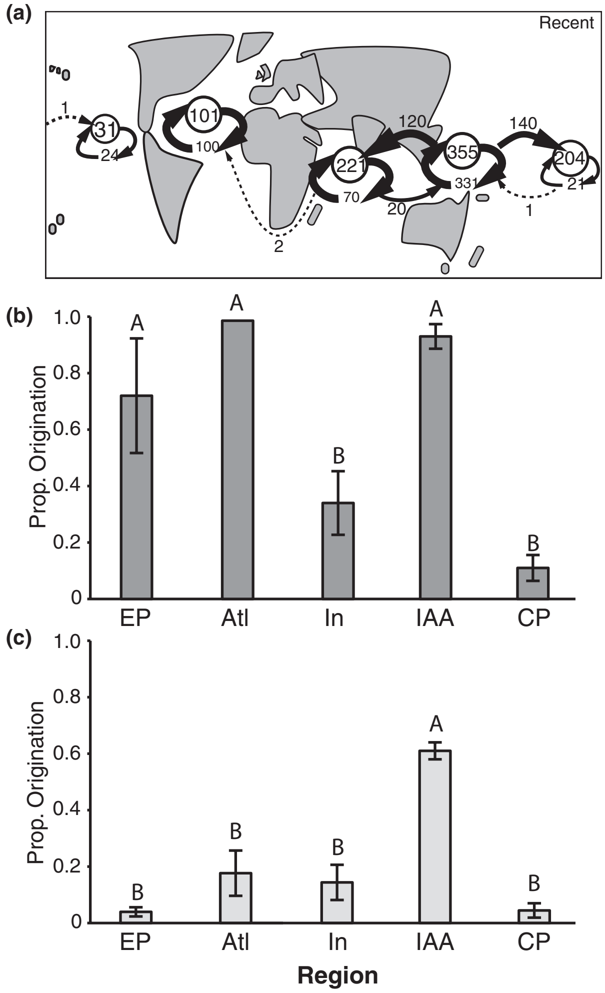

Figure 1 (a) Schematic drawing of the globe displaying regional patterns of combined diversity, origination and dispersal of extant labrids, pomacentrids and chaetodontids (the tips of the trees) in each region. EP = East Pacific, Atl = Atlantic, In = Indian, IAA = Indo-Australian Archipelago, CP = Central Pacific. Numbers in circles show extant diversity of sampled fishes in each region. Numbers below circles indicate within-region originations. Numbers next to arrows between adjacent regions indicate inferred dispersal events. Line thickness of arrows reflects the number of lineage originations in each region, and number of dispersal events between regions based on the reconstruction. For example, of the 355 lineages in the IAA, 331 arose within the region; 21 dispersed in and 260 out (see Appendix S2 for family reconstructions). (b) Proportion (± SE) of lineage originations in each region (regional origination/sampled regional richness; $n = 3$ families). (c) Proportion of lineage origination (± SE) in each region (regional origination/sampled family diversity; $n = 3$ families). A and B above bars mark non-significant groups in Tukey's post-hoc comparisons ($P < 0.001$).

todontidae (Fig. 3). Within the Palaeo/Eocene, Oligocene, Miocene, and Pliocene/Recent epochs the reconstructions yielded congruent patterns among the three families. These epochs will be considered separately below.

Palaeo/Eocene (65–33 Ma)

Both the Labridae and Pomacentridae have highest palaeodiversity in the IAA with relatively low dispersal of lineages from the area (Fig. 2a,e). The Chaetodontidae have yet to diverge at this stage, but the reconstruction places the origin of the family in the IAA (Fig. 3a; Fig. S5, Appendix S2). Dispersal is potentially possible between all five regions but the number of lineages that potentially dispersed between regions is low. The East Pacific, Atlantic and IAA regions contain lineages that have origins within the region, and lineages that have dispersed from adjacent regions. However, within the Indo-Pacific, the Indian Ocean and Central Pacific contain only lineages that have dispersed in to the regions. The panmixia inferred from the reconstruction suggests that lineages of the hypsigenyines and scarines may have maintained widespread ranges. By 33 Ma we have highest lineage diversity in the IAA, of which the majority remain restricted there (Fig. 2a,e). The most recent common ancestor (MRCA) of widespread lineages overlap with lineages restricted to the Atlantic (Labrini), and the IAA (Cheilini, Julidini, Odacini, *Bodianus, Choerodon;* Figs S3 & S4, Appendix S2). For the Pomacentridae, the root is placed within the IAA, but by the end of the Eocene three major lineages representing precursors to the Stegastinae, Chrominae and Abudefdufinae are widespread, overlapping with the basal lineages of the Pomacentrinae that are restricted to the IAA (Fig. S4, Appendix S2). Overall, there are several widespread lineages that have resulted from initial connectivity between regions from the beginning of the Palaeocene, and dispersal throughout the Eocene. However, the accumulation of widespread lineages with those restricted to the IAA marked the region as an early centre for palaeodiversity of molecular lineages (Fig. 2a,e).

Oligocene (33–23 Ma)

The Oligocene sees an increase in diversity within the IAA, but again dispersal out of the region is limited (Figs 2b,f & 3b). Cladogenesis appears to be suppressed in all regions except the in the IAA. For both the Labridae and the Pomacentridae, further diversification of lineages restricted to the IAA more than doubles the inferred palaeodiversity from the previous epoch (Fig. 2b,f). By comparison, the adjacent regions in the Indo-Pacific (Indian Ocean, Central Pacific) show little or no within-region origination. Similarly, the East Pacific and Atlantic show limited support for diversification of lineages during this epoch. The Atlantic region becomes increasingly isolated from the Indo-Pacific during this period. There is no connection maintained either side of the Atlantic region through lineage inheritance, or through dispersal of labrid lineages (Fig. 2b). For the duration of the Oligocene, the Atlantic is severed from the Indo-Pacific, with the exception of a single dispersal event of a damselfish lineage (*Chromis*) from the Atlantic to the Indian Ocean, and a

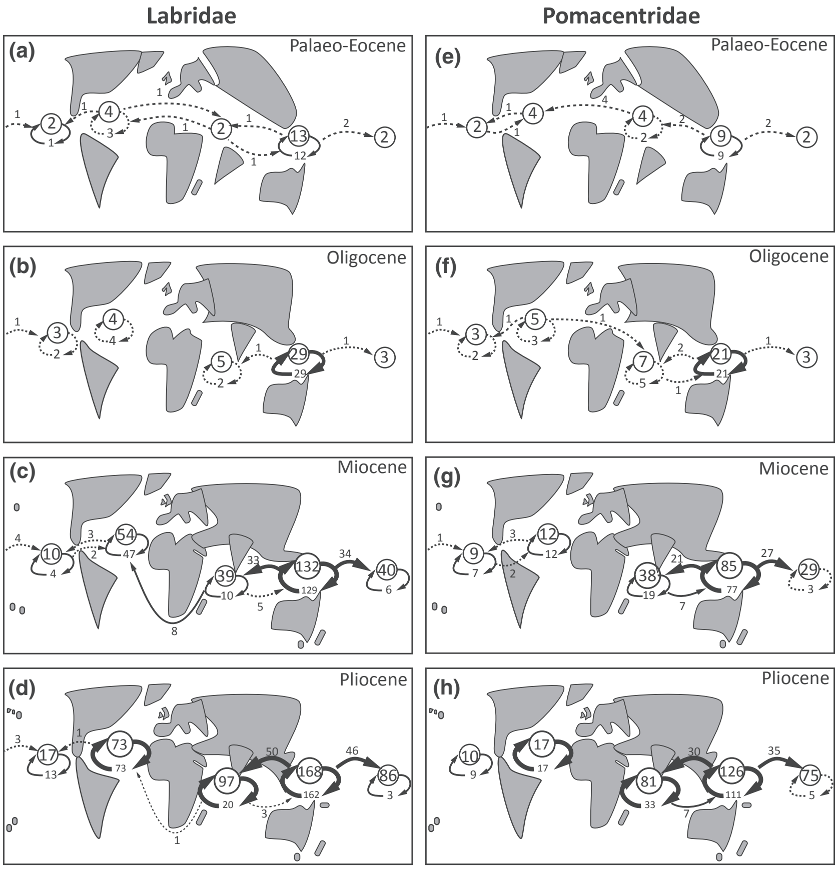

Figure 2 Schematic drawing of global palaeomaps for four time periods: Palaeo/Eocene (65–33 Ma); Oligocene (33–23 Ma); Miocene (23–5 Ma); Pliocene/Recent (5–0 Ma). Numbers show total hypothetical palaeodiversity (in circle), origination (below circle), and dispersal events (next to arrow) for each region in each period for the Labridae (a–d) and the Pomacentridae (e–h). Where dispersal in + origination is less than regional richness, the difference is range inheritance from the previous epoch. Where it is greater than regional richness, the difference is origination through vicariance.

continuous range of the *Abudefduf* lineage between these two regions (Fig. 2f; Fig. S4, Appendix S2). Vicariance events split lineages between the Atlantic and the Indian Ocean in the Labridae (*Calotomus/Sparisoma* clade) and the Pomacentridae (Chrominae, Stegastinae) (Fig. 2b,f; Figs S3 & S4, Appendix S2). In contrast, the Chaetodontidae reconstruction shows the initial divergence between the two major lineages; the bannerfish lineage restricted to the IAA, while the crown *Chaetodon* lineage disperses out to the Central Pacific, and through the Indian Ocean into the Atlantic, maintaining this widespread range into the Miocene (Fig. 3b).

Miocene (23–5 Ma)

In all three families, in all five regions, the Miocene is characterized by a leap in the palaeodiversity of molecular lineages (Figs 2c,g & 3c). Within the Atlantic and the IAA, this increase in palaeodiversity is characterized by high rates of within-region origination, which accounts for over 90% of the diversity in each of the two regions. However, the rate of origination and overall diversity in the IAA is far higher than in the Atlantic. This increased diversity is followed by numerous dispersal events from the IAA to the Indian Ocean and the Central Pacific, increasing overall diversity in those two adjacent regions. There is no dispersal between the Indian Ocean and the Atlantic for the Pomacentridae; however, within the Abudefdufinae the Atlantic is retained in its widespread range until the early Pliocene. Both labrids and pomacentrids display a similar pattern of lineage origination and dispersal. Lineage diversity is highest in the IAA and dispersal from the IAA to adjacent regions of the Indian Ocean and the Central Pacific is of a similar magnitude (i.e. *c.* 25% of labrids and 25–30% of pomacentrid lineages arising in the IAA disperse out to either the Indian Ocean or Central Pacific; Fig. 2c,g). This pattern of lineage expansion from the IAA is also seen in the chaetodontid lineages (25–30% to adjacent regions; Fig. 3c). In addition, the reconstruction infers dispersal of chaetodontid lineages from the Indian to the Atlantic (MRCA *Chaetodon* C2 & C3 & C4); across the EPB (*Chaetodon* C4, *Amphichaetodon*, MRCA *Johnrandallia/Heniochus*); and from the East Pacific to the Atlantic (*Chaetodon* C4) (Fig. 3c; Fig. S5, Appendix S2). Dispersal from the Indian Ocean to the Atlantic also occurs along several labrid lineages, both before (*Bodianus, Thalassoma, Coris, Novaculines*) and after (*Bodianus, Scarus*) the TTE (*c.* 12–18 Ma; Fig. 2c,g; Fig. S3, Appendix S2). Labrid lineages restricted to the Atlantic appear to have undergone more cladogenesis than the pomacentrid or chaetodontid lineages there. Several vicariance events occur between Indian and IAA regions in all three families.

Pliocene/Recent (5 Ma)

Exceptionally high origination within the IAA continues in the Pliocene to Recent (Figs 2d,h & 3d) and dispersal from

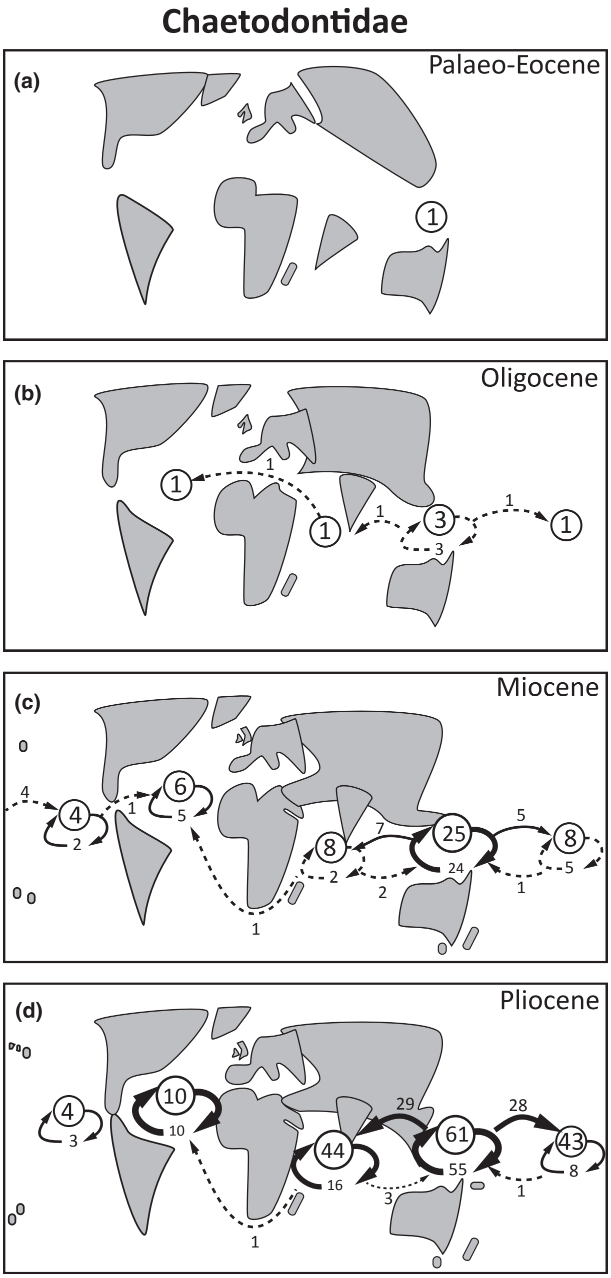

Figure 3 Schematic drawing of global palaeomaps for four time periods: Palaeo/Eocene (65–33 Ma); Oligocene (33–23 Ma); Miocene (23–5 Ma); Pliocene/Recent (5–0 Ma). Numbers show total hypothetical palaeodiversity (in circle), origination (below circle), and dispersal events (next to arrow) for each region in each period for the Chaetodontidae. See Fig. 2 for detailed legend.

the region continues to be the main source of diversity in adjacent regions. Again, the reconstruction infers a similar magnitude of lineage expansion into the Indian Ocean and/or the Central Pacific, from the IAA (27–30% of labrids and pomacentrids, 50% of chaetodontids). Within the Indian Ocean and Central Pacific regions, we now see evidence of range inheritance from the Miocene. This is particularly apparent in the Central Pacific for labrid and pomacentrid lineages, where regional origination and dispersal from the IAA during the Pliocene only accounts for *c.* 50% of the biodiversity present (Fig. 2d,h). The East Pacific and Atlantic become separated by the IOP, and this is reflected by several vicariance events (Figs S3–S5, Appendix S2). No dispersal is apparent out of the Atlantic for any lineage. Lineages dispersing into the Atlantic region from the Indian Ocean quickly get separated by vicariance (Figs S3–S5, Appendix S2), with the exception of the recent movement of *Anampses caeruleopunctatus* [recorded on FishBase (Froese & Pauly, 2011) in the south-east Atlantic]. In the Pomacentridae and Chaetodontidae, no dispersal is evident across the EPB, while the Labridae maintains five separate widespread ranges across the barrier (*Calotomus carolinus, Scarus rubroviolaceus, Scarus ghobban, Novaculichthys taeniourus, Stethojulis bandanensis;* Fig. S3, Appendix S2).

DISCUSSION

The reconstruction provides a clear global overview of the last 65 Myr, with evidence of regional isolation, connection and cladogenesis reflecting the major tectonic and biogeographic events. The East Pacific and Atlantic have been largely independent regions, a pattern that reflects the increasing isolation of these regions in the Tertiary. High extinction within these regions appears to have resulted in a restricted cladogenic history. The Indo-Pacific, in contrast, is characterized by extensive origination and connectivity between adjacent regions. The reconstruction suggests that the hotspot in the IAA is, at least in part, a result of prolonged origination over the past *c.* 30 Myr and that diversity in the Indian Ocean and Central Pacific is largely a result of dispersal from the IAA in the last 5 Myr. Survival of ancestral lineages in the IAA laid the foundation for the subsequent cladogenesis and range expansion that has led to present-day patterns of biodiversity across the entire Indo-Pacific.

Our study is the first to apply the DEC model to the exploration of globally distributed coral reef fish taxa. The results of the reconstruction presented herein show striking parallels with the patterns found in other taxa. Most notable is the congruence with global patterns of dispersal with terrestrial plants, where Australia and the IAA support numerous lineages with extensive evidence of dispersal from the Miocene onwards (Buerki *et al.*, 2011). The use of the DEC model highlights the origins and progression of biodiversity in the marine tropics, with disparate rates of extinction and survival playing key roles in shaping the global distribution of reef associated fishes. The changing role of the IAA hotspot in driving the current biodiversity across the entire Indo-Pacific is illustrated from inferred pattern of palaeodiversity of molecular lineages.

Origination and biodiversity through time and space

Each of the five regions can be grouped reflecting three basic patterns of origination and diversity:

1. Independent and isolated (East Pacific and Atlantic).
2. A macroevolutionary source of diversity (IAA).
3. Diversity recipients, or macroevolutionary sinks (Indian Ocean and Central Pacific).

Each will be examined separately below, reflecting these associations.

East Pacific and Atlantic

The history of the East Pacific and Atlantic biota, before the closing of the IOP, are closely linked. Both regions share a subset of the families present in the Indo-Pacific, although there are a few absent families or subfamilies in the Atlantic and East Pacific that are present in the Indo-Pacific (e.g. Caesionidae, Nasinae, Siganidae) (Bellwood & Wainwright, 2002). The origination of extant lineages within the East Pacific and Atlantic regions are comparable with other areas in terms of percentage regional origination (Fig. 1b). However, there appears to have been less origination as a percentage of all extant lineages in each family (Fig. 1c). This may reflect reduced speciation capacity within the two regions, or increased rate of lineage extinction. Historically, both regions have experienced periods of increased faunal turnover (McCoy & Heck, 1976; Budd, 2000; Bellwood & Wainwright, 2002; O'Dea *et al.*, 2007). Increased extinction may result in fewer extant species despite the region having potentially high origination. The lack of connection to the Indo-Pacific has reduced the potential for lineage replenishment. Our results offer support for the recent works of Rocha *et al.* (2005), Floeter *et al.* (2008) and Joyeux *et al.* (2008), which have suggested that these areas are largely independent and have been isolated from the Indo-Pacific for some time. However, the reconstruction highlights the early development of this isolation in the Oligocene following broader connectivity in the Palaeocene.

During the Palaeocene/Eocene, the East Pacific and Atlantic were linked to the Indo-Pacific by dispersal through the Tethys Sea. Evidence of this can be seen in the fossil record of Monte Bolca in Italy with the majority of the fish families represented in the deposits being present in both the Atlantic and Indo-Pacific (reviewed by Bellwood & Wainwright, 2002). This pantropical connection between the Atlantic and Indo-Pacific is evident from the reconstruction, with several inferred dispersal events between all tropical marine regions for the Labridae and Pomacentridae (Fig. 2a,e). While panmixia is possible during the Eocene, we begin to see incipient provinciality with restricted lineages in each region, while the inferred palaeodiversity of molecular lineages in the Atlantic and East Pacific is lower than in the IAA. This lower palaeodiversity maybe a consequence of high extinction throughout the epoch, or a period of high extinction at the end of the Eocene, which has been hypothesized for both these fishes (Cowman & Bellwood, 2011) and for flowering plants (Antonelli & Sanmartín, 2011).

The isolation of the Atlantic and East Pacific regions from the Indo-Pacific in the Eocene escalates in the Oligocene, with few dispersal events inferred between the Indian Ocean and Atlantic, or the Central Pacific and East Pacific regions. Dispersal between the East Pacific and Atlantic is also reduced. These earlier divisions may reflect earlier, temporary barriers within the Atlantic (Hallam, 1973), and East Pacific (Lessios *et al.*, 1995). However, by the end of the Miocene, the Atlantic and the East Pacific are largely isolated from the Indo-Pacific and from each other.

The Miocene epoch represents the time period with the highest lineage diversification in the East Pacific and Atlantic especially within the Labridae, reflecting patterns previously described in the labrid genus *Halichoeres* (Barber & Bellwood, 2005) and other reef genera (Floeter *et al.*, 2008). Circum-African lineages within the Labridae and Chaetodontidae appear to allow some Indo-Pacific lineage expansion into the Atlantic. This is not possible for pomacentrid lineages (with the exception of *Abudefduf*), perhaps lacking ability to survive in the more temperate climes of the Southwest African coast (cf. Floeter *et al.*, 2008). A temporary reconnection before the final closure of the IOP is implied by several bidirectional dispersal events between the East Pacific and Atlantic in each of the three families (Figs S3–S5, Appendix S2). After the closure of the IOP the regions are completely separated from each other and the Atlantic is largely isolated from the Indo-Pacific. While the influence of the Indo-Pacific biota on the Atlantic fauna has been recorded recently (Robertson *et al.*, 2004; Rocha *et al.*, 2005; Bowen *et al.*, 2006), it has made little overall impact to the extant biodiversity of the Atlantic and East Pacific regions (Fig. 1a; Floeter *et al.*, 2008). Regional origination does continue in the Atlantic and East Pacific during the Pliocene/Recent epoch, but little significant increase in regional richness is observed (with the possible exception of Atlantic wrasses; Barber & Bellwood, 2005).

Indo-Australian archipelago

For the Labridae, Pomacentridae, and Chaetodontidae, the reconstruction suggests that the IAA has been a centre for lineage survival, origination, and range expansion at different stages in the history of the region (Fig. 4). In terms of global diversity for each family, the IAA stands out as a significant source of diversity in terms of both origination within the region and the expansion of lineages into adjacent regions. Based on the reconstruction, the origination of extant lineages within the IAA accounts for *c.* 60% of total global biodiversity for each family (Fig. 2c). This is relatively direct evidence for the IAA as a centre of origin in contrast to inferred origination based on an assumed preponderance of endemic taxa (e.g. Briggs, 2003; Mora *et al.*, 2003; Roberts *et al.*, 2002; but see Bellwood & Meyer, 2009a,b). Patterns of dispersal inferred from the reconstruction also show the connectivity within Indo-Pacific, with the IAA acting as a source of biodiversity for the Indian Ocean and Central Pacific (Table 1; Fig. 4a). However, a temporal perspective highlights the progression of high biodiversity in the IAA from overlapping ranges in the Eocene, survival in the Oligocene, origination in the Miocene, and expansion in the Pliocene and Recent (Fig. 4).

During the Palaeocene/Eocene, the IAA is reconstructed by the model as a centre of palaeodiversity of molecular lineages, with both localized cladogenesis and overlapping widespread ranges (Labridae, Pomacentridae). A similar West Pacific origin for basal julidine lineages has been suggested previously (Westneat & Alfaro, 2005). However, fossil evidence from the middle Eocene (42–39 Ma) highlights the Tethys regions as the centre for palaeodiversity of reef associated taxa (Renema *et al.*, 2008). Indeed, fossils from the Eocene of Monte Bolca mark the earliest record of many extant reef fish forms (Bellwood, 1996), with fewer fossils found in the Indo-Pacific or IAA region. The conflicting biogeographic patterns from the fossil record and the ancestral reconstruction of molecular lineages presented here may reflect the influence of extinction in other regions (Budd, 2000; Bellwood & Wainwright, 2002). The greater palaeodiversity of ancestral molecular lineages in the IAA from the early Oligocene onwards may highlight also the ability of the IAA to support ancestral lineages, i.e. it is a centre of survival of ancestral lineages (Barber & Bellwood, 2005; Cowman & Bellwood, 2011). In this, it appears that the key to variation is in the ability to support taxa. As mentioned by Rabosky (2009), ecology may overshadow temporal patterns of diversity. In this respect the expansion of coral reef area in the IAA may have underpinned the observed pattern. Indeed, total reef area is the primary variable explaining variation in reef fish diversity (Bellwood & Hughes, 2001; Bellwood *et al.*, 2005). Thus, the expansion in the IAA is probably not just age and cladogenesis but the capacity of the area to maintain and support species, even in the Oligocene. By the beginning of the Oligocene, the IAA is already emerging as a centre for diversity, however, this may be the result of higher rates of survival within the region rather than exceptional rates of origination.

The IAA hosts the initial divergences of the Chaetodontidae in the Oligocene and the origination of labrid and pomacentrid lineages continues. There is little dispersal into the Indian Ocean, possibly highlighting adverse conditions there (Hallam, 1984). However, it is in the Miocene that the diversity synonymous with the IAA begins to emerge, coinciding with the expansion of coral-dominated reefs and a mosaic of reef habitats (Renema *et al.*, 2008). Lineages that have previously been highlighted as containing exceptional diversity, have inferred ancestral origins in the IAA during the Miocene and many show strong links to coral reefs (Cowman & Bellwood, 2011). It is in the Miocene that lineages from the IAA now begin to recolonize the Indian Ocean. Origination continues in the Pliocene/Recent epochs primarily in *Chaetodon* lineages. The extensive dispersal from the IAA to the Indian Ocean and Central Pacific regions highlight the role of the IAA as a source of diversity across the entire Indo-Pacific during this period (Fig. 4).

It appears that the survival of ancient lineages in the IAA resulted in more subsequent cladogenesis, which in turn permitted extensive range expansion and the export of lineages

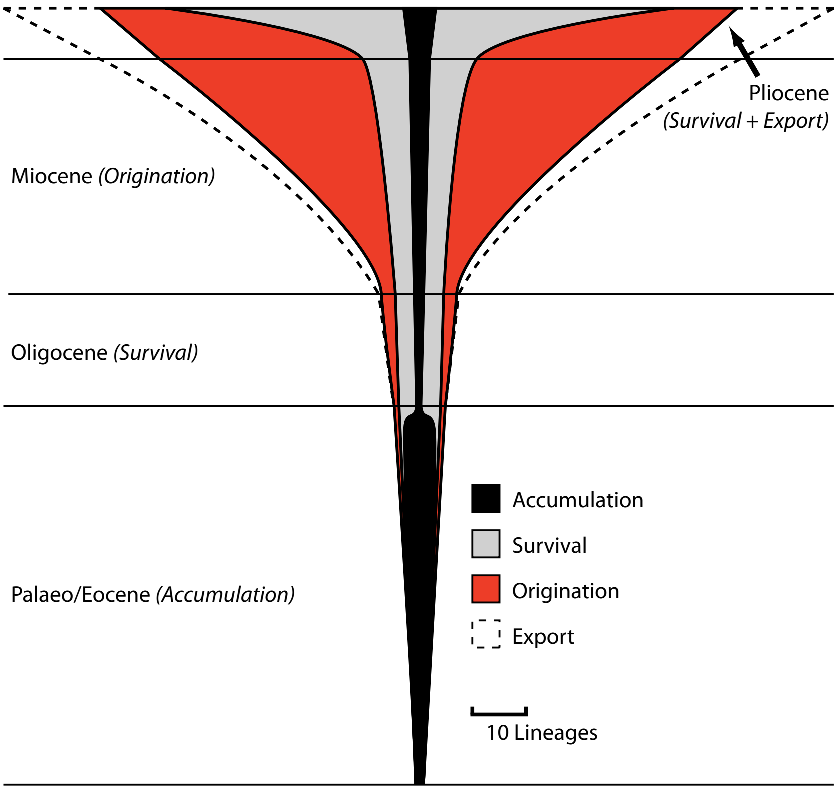

Figure 4 Schematic diagram illustrating the changing role of the Indo-Australian Archipelago (IAA) hotspot in the origins of Indo-Pacific reef fish biodiversity, inferred from the reconstruction. In each epoch, the dominant roles of the IAA hotspot changed from accumulation (Palaeo/Eocene), survival (Oligocene), origination (Miocene) and export (Pliocene) of lineages. Accumulation = lineages acquired from outside the IAA; Survival = lineages retained from the previous epoch (= Accumulation + Origination from previous epoch); Origination = lineages arising in the IAA during that epoch; Export = lineages in the IAA that were exported/expanded to adjacent regions during that epoch. Each process has been dominant at one time, but most act simultaneously through time. The relative width of the four main roles, accumulation (black), origination (red, or dark grey in greyscale), survival (pale grey) and export (open) reflect the relative contribution to palaeodiversity in the labrid reconstruction (a–d).

into adjacent regions. In summary, the IAA has sequentially and then simultaneously acted as a centre of accumulation (Palaeocene/Eocene onwards), survival (Eocene/Oligocene onwards), origin (Miocene onwards), and export/expansion (Pliocene/Recent) for reef fishes in the three families (Fig. 4). In this way, it reflects the general patterns of the 'hopping hotspot' discussed by Renema *et al.* (2008). However, this is the first clear evidence of the IAA being a centre for lineage export/expansion over an extended period of time.

Indian Ocean and Central Pacific

The Indian Ocean and Central Pacific regions are both recipients, or macroevolutionary sinks, for biodiversity from the IAA. Regional origination accounts for little of the diversity in both regions (Table 1). While both regions appear to have relatively low regional origination since the Palaeocene, the influence of expanding IAA lineages has escalated from the Miocene to Recent. The timing of these events is examined below for each region**.**

The current biodiversity of the Indian Ocean is the result of moderate cladogenesis in the region, with the majority of species being of IAA origin that maintain the Indian Ocean as part of a wider Indo-Pacific range (cf. Hughes *et al.*, 2002). It has been a sink for lineages from the IAA since the Miocene. Excluding the Chaetodontidae, the majority of lineages that have arisen in the Indian Ocean are of late Miocene/early Pliocene age. Invasion of Indian Ocean species into the IAA appears to be much less frequent. However, they may make up almost half of the total origination in the Indian Ocean due to the low origination of lineages there. Dispersal from the IAA to the Indian Ocean and to the Central Pacific seems to be of a similar magnitude in both directions. Starting in the early Miocene and continuing into the Pliocene, approximately 25–30% of lineages arising in the IAA disperse to adjacent regions.

The pattern in the Indian Ocean reflects the ancient history of the region with links to declining or receding hotspots (Renema *et al.*, 2008). By the end of the Eocene the Arabian hotspot would have been in place in the western Indian Ocean (Renema *et al.*, 2008). Tectonic rearrangement and global cooling in the Oligocene/Miocene would have had a dramatic effect on the shallow water reefs in this area (Hallam, 1994). With the restriction of the tropics and decline in reef area in the Arabian hotspot, faunal loss would have occurred in the Indian Ocean throughout the Oligocene/early Miocene. Those lineages that maintained an extended range into the IAA would presumably have been able to survive best at this time. This pattern appears to hold for mangrove, foraminifera, and other reef associated organisms (Renema *et al.*, 2008), with the resistance to extinction in the IAA (Cowman & Bellwood, 2011) being based on the unique features of the area (Hoeksema, 2007) and the diversity of reef habitats (Rosen, 1984). This loss is counteracted by invasion from the IAA to maintain palaeodiversity.

In contrast to the Indian Ocean, the island arcs that make up the Central Pacific region have been closely linked to the IAA, with gene flow between the two regions allowing the Central Pacific to easily inherit ancestral widespread ranges (and vice versa; see Craig *et al.*, 2010; Gaither *et al.*, 2011). The EPB has prevented the invasion of East Pacific/Atlantic species (but see Lessios & Robertson, 2006), resulting in most of the diversity seen in the Central Pacific being of IAA origin. The Central Pacific has comparable species richness to the Indian Ocean; however, its low regional origination appears to be a function of a higher occurrence of range inheritance and speciation through peripheral isolation (cf. Planes & Fauvelot, 2002; Hodge *et al.*, 2012). The reconstruction suggests that while there is moderate range expansion of lineages originating in the Indian Ocean to the IAA, expansion appears very limited from the Central Pacific to the IAA (Fig. 1a). Overall, the Central Pacific remains largely a recipient of lineages from the IAA.

Recent dispersal from the Indian Ocean to the IAA has been highlighted in previous work where populations form temporal rather than geographic clades (Horne *et al.*, 2008; Gaither *et al.*, 2011). From the IAA to the Central Pacific region there is evidence of geographic clade structure of both populations (Planes & Fauvelot, 2002; but see Horne *et al.*, 2008) and species (Bernardi *et al.*, 2002). However, these are all relatively young associations. The reconstruction herein identifies prolonged movement from the IAA to the Indian and Pacific Oceans beginning in the Miocene and escalating during the Pliocene to Recent. While the Indian Ocean reflects a history of extinction and faunal recovery from lineages arising in the IAA, the Central Pacific is characterized by widespread ancestrally inherited ranges, with a smaller number of peripheral endemics.

Caveats and considerations

The combined use of dated phylogenetic trees and the DEC model implemented in LAGRANGE has allowed the evolutionary history of the Labridae, Pomacentridae and Chaetodontidae to be explored in a biogeographic context. There are, however, several sources of potential bias. This applies to the phylogenetic trees used for this reconstruction (discussed in Cowman & Bellwood, 2011), and with the ancestral reconstruction itself. Five major caveats need to be considered when interpreting the results:

1. This is a hypothetical reconstruction, based on present-day distributions of taxa and as such, there are limitations to the interpretation of a lineage's geographic origin (Losos & Glor, 2003). Post-speciation expansion is fast, giving allopatric species the ability to become completely sympatric within 4 Myr (Quenouille *et al.*, 2011), (although the reverse may also be true). For older lineages this has the potential to obscure geographic origins, especially on a smaller within-region scale. For the broad, regional patterns described herein the effect will be relatively limited. Discussion was therefore limited to patterns between ocean basins known to have distinct faunal assemblages. Discussions of patterns within regions are restricted to lineage origination with no implications for the mode of speciation.

2. Incomplete taxon sampling of extant lineages will also affect the biogeographic reconstruction. For example, the *Prognathodes* lineage of the Chaetodontidae was reconstructed to be restricted to the Atlantic; however, species not sampled in the phylogenies have been recorded in the Indo-Pacific (*P. guezei*) and the East Pacific (*P. falcifer*) (Kuiter, 2002). Inclusion of these species has the potential to change the geographic origins of the clade (Fig. S5, Appendix S2). This problem may be exacerbated by unsampled cryptic speciation. Recent phylogeographic studies in the Atlantic have identified cryptic species in *Halichoeres* lineages (Rocha *et al.*, 2005). Such studies have been limited in the Indo-Pacific (Rocha & Bowen, 2008) and those that have been undertaken have not found the level of species division seen in the Atlantic. Nevertheless, further studies may alter presently accepted taxonomy and species distributions. In turn, this may affect the mean ages of lineages within regions, and may reveal more recent cladogenic events in the Indo-Pacific.

The relatively even sampling of taxa across regions and among clades within families (Table S1, Appendix S1), and near complete generic sampling (Cowman & Bellwood, 2011), allows for some confidence in the interpretation of patterns of historical biodiversity of lineages. By examining the origination of lineages, rather than species, at the larger scale of the five major biogeographic regions, interpretations for global patterns should be relatively robust. Furthermore, analysis using total species counts rather than just species sampled within clades resulted in no change in the observed patterns. However, a more detailed evaluation of the effect of sampling would be valuable, especially if analyses are to be informative at a finer within-region scale.

3. The ancestral reconstruction does not allow for the global extinction of a lineage. While the contraction of a lineage's range through local extinction can be inferred from the reconstruction, if large numbers of taxa have gone extinct in a region this will translate into a perceived lower palaeodiversity of molecular lineages within that region. Palaeodiversities may therefore be underestimated. There is known variation in extinction rates among the five regions. Extinction of reef-associated fauna has been described in previous studies for the East Pacific and Atlantic (McCoy & Heck, 1976; Budd, 2000; Bellwood & Wainwright, 2002; O'Dea *et al.*, 2007), the Indian Ocean (Renema *et al.*, 2008), and may have been high in the Central Pacific during periods of sea-level change (Paulay, 1997; Fauvelot *et al.*, 2003). The only region where high past extinction rates have not been recorded on reefs is in the IAA (but see Springer & Williams, 1994; Williams & Duda, 2008). This may result in the IAA being inferred as a centre of origin for deeper lineages, when in fact they were probably peripheral to a widespread ancestral range.

The reconstruction of the widespread ancestral root of the Labridae reflects the widespread records of fossil labrids in the West Tethys (D.R.B., unpublished data). This offers some confidence in the palaeo-reconstructed distribution (Fig. S3, Appendix S2). However, the pomacentrids may provide some evidence of the effect that extinction has had on biogeographic interpretations. The reconstruction of the pomacentrid root origin in the IAA is contrary to the fossil record with two pomacentrid representatives in the Eocene of West Tethys (Bellwood & Sorbini, 1996; Bellwood, 1999), which indicates the presence but not, necessarily, the origin of pomacentrids in the West Tethys. Therefore, while the reconstruction of the Labridae provides support for the shift from a widespread Tethys palaeodistribution to the IAA, the conflicting pomacentrid reconstruction is potential evidence for extinction in the West Tethys.

4. There is also a strong likelihood that clade diversity within these families is not related to the age of the clade itself. In the absence of a relationship between clade age and clade richness, clade diversity can be limited by other ecological factors (Rabosky, 2009). If the regional diversity of a lineage is limited by ecological factors, the regional capacity for diversification will be influenced by changes in ecological limits rather than by length of time a clade has had to diversify. Habitat area is one such factor that can influence the carrying capacity of region. While lineages in different regions may experience the same rate of speciation and/or extinction, the capacity for cladogenesis may be regulated by habitat area. While this may not alter the inferred ancestral patterns, it does limit the interpretation. Reef area has been shown to be a major factor in explaining observed variation in the richness of coral reef species in the IAA (Bellwood & Hughes, 2001; Bellwood *et al.*, 2005). However, on an evolutionary scale reef area may also be a factor regulating diversity, by giving clades an extended growth phase before carrying capacity is reached (see Rabosky, 2009), rather than underpinning exceptionally high rates of diversification. If so, this extended growth phase appears to extend throughout the Miocene (Fig. 4), where several significantly diverse clades arise (Cowman & Bellwood, 2011). In this respect, the diversification of reef fishes in the IAA during the Miocene may be the result of expanding reef area elevating the regions capacity to support biodiversity.

5. The final caveat, and potentially the most important, is 'the pull of the present' (Pybus & Harvey, 2000). This has been discussed as a bias arising from lineages arising in the recent past being less likely to go extinct than lineages in the distant past. In a historical biogeographic context it can be seen as a bias in the likelihood of an inferred lineage arising within a specific location. Ancestral origination within the IAA may therefore arise purely from it being a location of overlapping extant ranges. In this way factors that have resulted in the accumulation, survival or maintenance of species in the IAA will result in the reconstruction of origination in the IAA. The conflict between maintenance and origination is an old one with little resolution. However, the hopping hotspot theory (Renema *et al.*, 2008) does provide some support, with fossil evidence of a shift in invertebrate fossil diversity from the Tethys to the IAA. However, the lack of independent evidence of origination of fishes in the IAA (endemics or fossils; Bellwood & Meyer, 2009a) is a concern and therefore conclusions from the reconstruction must be taken as an indication only. Solid independent evidence, preferably fossil, is urgently required.

CONCLUSIONS

For the first time, temporally congruent patterns in origination and dispersal of molecular lineages highlight global patterns of historical biodiversity of reef fishes within five major tropical marine regions. The Atlantic and East Pacific regions have been largely independent and isolated from the Indo-Pacific from the Oligocene, but have had a minor influx of Indo-Pacific biota. Within the Indo-Pacific, the IAA has played important roles as a centre of lineage accumulation, survival and origination both sequentially and simultaneously. Those lineages that survived in the IAA while others went extinct elsewhere are the driving forces behind current biodiversity in the Indo-Pacific. While ancestral reconstruction requires careful interpretation, it has allowed insights into the changing role of the largest marine biodiversity hotspot. Diversity of reef fishes in the IAA hotspot potentially began as a location within a widespread range that gradually accumulated ancestral lineages, for which it provided a refuge during a period of extinction in adjacent ancestral habitat. Surviving lineages in the IAA proliferated and formed the basis for extensive recolonization of the Indian and Pacific Ocean realms.

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SUPPORTING INFORMATION

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

Appendix S1 Supplemental tables. Table S1 shows species richness for each family by clade and by region with percentage of taxa sampled in the present study. Table S2 shows areas incorporated in five major biogeographic regions. Table S3 shows presences/absences of fish species in major marine biogeographic regions. Table S4 gives an overview of DEC model results for likelihood comparisons.

Appendix S2 Supplemental figures. Figure S1 illustrates regional inheritance scenarios considered in the DEC model implemented in Lagrange. Figure S2 illustrates DEC model constraints used in Lagrange analyses. Figures S3–S5 show resulting biogeographic reconstructions overlaid on chronograms of the Labridae, Pomacentridae and Chaetodontidae (modified from Cowman & Bellwood, 2011).

BIOSKETCHES

Peter Cowman is a researcher at James Cook University. His interests include vertebrate evolution and genomic research. His current research focuses on the use of bioinformatics methods to study the evolution of reef fishes and associated biodiversity patterns.

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