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The biogeography of tropical reef fishes: endemism and provinciality through time

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ABSTRACT

The largest marine biodiversity hotspot straddles the Indian and Pacific Oceans, driven by taxa associated with tropical coral reefs. Centred on the Indo-Australian Archipelago (IAA), this biodiversity hotspot forms the ‘bullseye’ of a steep gradient in species richness from this centre to the periphery of the vast Indo-Pacific region. Complex patterns of endemism, wide-ranging species and assemblage differences have obscured our understanding of the genesis of this biodiversity pattern and its maintenance across two-thirds of the world’s oceans. But time-calibrated molecular phylogenies coupled with ancestral biogeographic estimates have provided a valuable framework in which to examine the origins of coral reef fish biodiversity across the tropics. Herein, we examine phylogenetic and biogeographic data for coral reef fishes to highlight temporal patterns of marine endemism and tropical provinciality. The ages and distribution of endemic lineages have often been used to identify areas of species creation and demise in the marine tropics and discriminate among multiple hypotheses regarding the origins of biodiversity in the IAA. Despite a general under-sampling of endemic fishes in phylogenetic studies, the majority of locations today contain a mixture of potential paleo- and neo-endemic fishes, pointing to multiple historical processes involved in the origin and maintenance of the IAA biodiversity hotspot. Increased precision and sampling of geographic ranges for reef fishes has permitted the division of discrete realms, regions and provinces across the tropics. Yet, such metrics are only beginning to integrate phylogenetic relatedness and ancestral biogeography. Here, we integrate phylogenetic diversity with ancestral biogeographic estimation of lineages to show how assemblage structure and tropical provinciality has changed through time.

Key words: biodiversity, biogeography, provinciality, assemblage similarity, coral reef fishes, endemism, hotspot.

CONTENTS

I. INTRODUCTION

The distribution of tropical fishes and their enigmatic association with reef-building corals has long been of interest in biodiversity science. While tropical reefs only account for 0.1% of the ocean's surface, over 6,300 species of fish (~40% of all marine fishes; Parravicini *et al.*, 2013) and over 790 zooxanthellate species of coral (~30% of all coral species; Veron *et al.*, 2009) are found therein. A latitudinal cline in reef-associated diversity mirrors that observed in terrestrial groups (Willig, Kaufman & Stevens, 2003; Hillebrand, 2004; Tittensor *et al.*, 2010), while a longitudinal decline in species richness can be identified away from a bullseye of species richness centred in the Indo-Australian Archipelago (IAA). The IAA forms a large area of multitaxon diversity (Tittensor *et al.*, 2010). There are several other names and delineations for this biodiverse region (Fig. 1A; for review see Hoeksema, 2007). The IAA has a broad geographic spread and encompasses the world's most complex archipelago (Bellwood, Renema & Rosen, 2012), housing the vast continental reefs of Southeast Asia, Indonesia, the Philippines, Papua New Guinea and the Great Barrier Reef (Bellwood & Hughes, 2001). However, there are a number of characteristics of the IAA hotspot that have confounded the study of its genesis (Cowman, 2014). In addition to its central hotspot and the associated gradient in fish diversity, multiple endemic centres exist, mostly on its periphery (Fig. 1A; Roberts *et al.*, 2002; Hughes, Bellwood & Connolly, 2002), with the bulk of the diversity pattern being formed by medium- and wide-ranging species. Due to a dominance of soft barriers to gene flow across the Indo-Pacific (Cowman & Bellwood, 2013*b*), many species are able to maintain continuous ranges from the east coast of Africa to the west coast of the Americas (Lessios & Robertson, 2006). Permeable, or transient barriers have resulted in vicariance among clades and species sister pairs, with population structuring present across Indo-Pacific provinces for some species, but not others (Craig *et al.*, 2007; Horne *et al.*, 2008; Gaither *et al.*, 2009). Regional assemblages and biogeographic structures in species composition have been identified (Fig. 1B; Kulbicki *et al.*, 2013), but the extent and position of boundaries is variable according to the authors and the techniques employed (Spalding *et al.*, 2007; Floeter *et al.*, 2008; Kulbicki *et al.*, 2013; Keith *et al.*, 2013; Briggs & Bowen, 2013). The delineation of both genetic barriers and boundaries for regional assemblages are important steps in evaluating conservation priorities in both terrestrial and marine environments (Whiting & Lawler, 2000; Olson *et al.*, 2001; Carpenter *et al.*, 2011; Toonen *et al.*, 2011). Such regional schemes can also inform a deep-time understanding of the historical processes that have shaped past and present-day biodiversity patterns (Renema *et al.*, 2008; Bowman *et al.*, 2010; Cowman & Bellwood, 2013*a*; Bowen *et al.*, 2013; Bender *et al.*, 2013).

The conflict between marine endemism and biodiversity hotspots, diversity gradients and provinciality, has made it difficult to discern the underlining processes generating and maintaining biodiversity patterns on deep and shallow timescales. However, during the last decade intersection among fields of molecular phylogenetics, palaeontology and biogeography has allowed researchers to examine processes underpinning the evolution of coral reef ecosystems and the biodiversity they support.

II. BIODIVERSITY IN THE MARINE TROPICS

(1) What constitutes a marine biodiversity hotspot?

The description of terrestrial biodiversity hotspots based on plant endemism and a measure of habitat degradation has been commonplace since the late 1980s (Myers, 1988; Myers *et al.*, 2000). Such descriptions have provided a valuable tool in the conservation of biodiversity across terrestrial taxonomic groups with regular updates on both the status of these hotspots and the addition of new ones (www.conservation.org). Yet, in the marine realm, the designation of biodiversity hotspots has proved difficult with often conflicting results (Roberts *et al.*, 2002; Hughes *et al.*, 2002; Mora, Tittensor & Myers, 2008). The conflict arises from incongruence between centres of endemism and centres of total species richness (Fig. 2; Hughes *et al.*, 2002), a pattern that can also be seen on land in birds (Orme *et al.*, 2005). How one defines an endemic species also impacts observed patterns of endemism (Fig. 2B–D; Hughes *et al.*, 2002; Mora *et al.*, 2008). Although marine biodiversity hotspots have been delineated based on endemism and threat assessment (Fig. 1A; Roberts *et al.*, 2002; Parravicini *et al.*, 2014), some areas of higher species richness of wider ranging taxa (e.g. the Great Barrier Reef) are not considered 'true' hotspots by this definition. Indeed, there is ample evidence to show that the majority of endemic centres of biodiversity are peripheral when compared to the centre of highest diversity across the Indo-Pacific (Fig. 2; Bellwood *et al.*, 2012). The centre of highest biodiversity (the 'bullseye' in the biodiversity gradient) for fishes lies within the IAA (Fig. 2A). How the IAA hotspot was formed, and its role in generating diversity across the Indo-Pacific has been a contentious topic with multiple hypotheses and little consensus (but see Cowman & Bellwood, 2013*a*; Bowen *et al.*, 2013).

Today, the IAA marine biodiversity hotspot and its associated gradients span two-thirds of the global tropics. However, on an evolutionary timescale it represents a pattern that has been shaped across at least the last 50 million years (Renema *et al.*, 2008). The global hotspot in marine biodiversity literally moved across the globe, even beyond the Indo-Pacific, and so a global context is needed to reveal its origins. The re-centring of the biodiversity hotspot and the eastward shift in its diversity gradient is linked to a series of tectonic, eustatic, climatic, oceanographic and geologic (TECOG) events (Bellwood *et al.*, 2012). These TECOG events have altered the distribution of carbonate platforms and modified the rates of speciation and extinction of ancestral fish lineages (Cowman & Bellwood, 2011; Dornburg *et al.*, 2015). The combination of palaeontological data and molecular phylogenies has allowed us to track the evolution of the IAA hotspot, but questions still remain regarding the dominant processes of biodiversity creation and maintenance, inside and outside of the IAA (Cowman, 2014).

Although much biodiversity research has focused on the description of patterns of a particular system or specific group, during the last five years there has been an increasing effort to quantify biodiversity in terms of assemblage differences and species turnover among locations along the diversity gradient (Leprieur *et al.*, 2012; Kulbicki *et al.*, 2013; Mouillot *et al.*, 2013; Parravicini *et al.*, 2014). These metrics are also being explored at the population level in an effort to identify significant areas of genetic diversity (Liggins *et al.*, 2015). While this can be a difficult task (Mouillot *et al.*, 2013) and often question-driven, it is an essential part of biogeographic science. Understanding how and why biodiversity changes along a gradient and how regional and local species pools are structured has a vital part to play in the guidance of conservation initiatives (Whittaker *et al.*, 2005). In the case of tropical reef assemblages there are a number of schemes that delineated realms, regions, provinces and ecoregions based on shared environmental traits (Spalding *et al.*, 2007), composition of endemic taxa (Briggs & Bowen, 2012, 2013) and measures of species dissimilarity (Floeter *et al.*, 2008; Kulbicki *et al.*, 2013). The scheme presented by Kulbicki *et al.,* (2013) (Fig. 1B) integrates a large database of geographic ranges for over 6,300 reef-associated fishes (Parravicini *et al.*, 2013). The resulting scheme appears to reflect historical differences among regions (Cowman & Bellwood, 2013*a*), with present-day biodiversity best predicted by past habitat stability and fragmentation (Pellissier *et al.*, 2014). However, it remains unclear whether any provincial scheme based on current species distributions has had macroevolutionary significance in the past (Cowman, 2014). To investigate the historic relevance of extant biogeographic delineations a phylogenetic perspective is required, incorporating estimates of ancestral biogeographic ranges.

Questions regarding centres of endemism and biodiversity of reef fishes, the categorization of regional assemblages and their ancestral biogeography require further discussion and analysis. Herein, we present an overview of the recent literature and advances on these topics, alongside new analyses of assemblage dissimilarity through time.

(2) The available data

Although phylogenies for the major groups that are classically considered ‘reef fish families’ remain incomplete (Cowman, 2014) the most iconic families that have been calibrated with fossil data have provided much insight into early diversification and trophic evolution on coral reefs. The fossil records for these reef fish groups, while sparse, still provide critical evidence for the morphological and ecological expansion of reef-associated fish lineages (Goatley, Bellwood & Bellwood, 2010; Friedman, 2010).

The combination of both the fossil record and molecular phylogenies has given us a broad understanding of the different phases in the evolutionary relationships between fishes and coral reefs (Bellwood *et al.*, 2015; Bellwood, Goatley & Bellwood, 2016). Recent efforts have resulted in a large database of species ranges and detailed species checklists for locations across the global tropics (Kulbicki *et al.*, 2013; Parravicini *et al.*, 2013). The combination of these data with phylogenetic hypotheses for those sampled reef fish groups are providing significant insight into the origins of biodiversity patterns and the ancestral biogeography of global tropical assemblages.

III. THE NATURE OF ENDEMISM IN THE MARINE TROPICS

(1) What is a marine endemic species?

An endemic species can be defined as a species that has an exceptionally small geographic range and as such presents a priority for conservation (Myers *et al.*, 2000). This view of endemic species being of exceptional importance for conservation is related to the 'double jeopardy' concept – a terrestrially biased observation of a strong positive link between geographic distribution and abundance (Blackburn, Cassey & Gaston, 2006) that has formed a basis for the assessment of extinction risk (Pimm *et al.*, 2014). However, such a link may not exist for reef corals and associated fishes, where the abundances of endemic and pandemic species are equally broad (Hughes *et al.*, 2014), with some endemic species showing higher recruitment in certain locations (DeMartini & Friedlander, 2004). Endemics have also traditionally been viewed as representing young species at their location of origin, with their use in demarking terrestrial biodiversity hotspots validated by concordant patterns of total diversity across multiple groups (Myers *et al.*, 2000; Mittermeier *et al.*, 2005, 2011). Yet, across the tropics there is no concordance between centres of endemism and centres of total biodiversity in reef-associated fishes (Fig. 2) or reef-building corals (Hughes *et al.*, 2002). It has been difficult to classify a marine endemic species, especially because of the subjectivity in defining what is an 'exceptionally small' range. In the marine realm, there is also the issue of habitat continuity, particularly in coral reef systems where the distribution of habitat is often patchy with varying degrees of distance between patches. Previous assessments of reef fish endemism have taken a regional or provincial approach (Randall, 1998; Mora *et al.*, 2003; Floeter *et al.*, 2008; Cowman, 2014) or defined endemism by per cent of all geographic range areas recorded (Connolly, 2005; Kulbicki *et al.*, 2013) or by absolute area, which has generally been defined as areas less than the size of the Hawaiian archipelago (1.3×10^6 km^2; Bellwood & Meyer, 2009*b*) but smaller areas have been used (0.5×10^6 km^2; Hughes *et al.*, 2002). By comparing different endemic schemes based on the largest fish geographic database to date (Fig. 2B–D) we can identify both conflict and agreement among assigned centres of endemism and their relationship to centres of biodiversity.

Overall, the centre of highest total biodiversity is located in the Coral Triangle/Sunda Shelf areas (Fig. 2A), which is characterized by low endemic species richness (Fig. 2B–D). Conflict with previous studies likely stems from the size and delineation of locations (Mora *et al.*, 2003). Here, we consider the ecoregional scheme of Spalding *et al.* (2007), which may not reflect biogeographic boundaries and true genetic connectivity across localities, particularly in the ecoregions that define the Coral Triangle (Treml *et al.*, 2015). However, these patterns are similar to previously reported patterns for an earlier dataset based on location checklists (Parravicini *et al.*, 2013) with similar (but not concordant) patterns reported for endemic coral species richness (Hughes *et al.*, 2002). Longitudinal peripheral locations stand out as having equal or higher density of endemic species compared to the central hotspot (top margin plots in Fig 2B–D), and in having endemic species in higher proportions of the total species pool (Fig. 3A). It is interesting to note that the Great Barrier Reef (GBR) appears to have low endemism across any scheme, but is very high in species richness of medium- and wide-ranging taxa across multiple groups (Roberts *et al.*, 2002). Given the concerns regarding the health and status of the GBR (Hughes, Day & Brodie, 2015), conservation efforts are also important for areas that support wide-ranging species, not considered by traditional hotspot analysis (Roberts *et al.*, 2002; Hughes *et al.*, 2002).

(2) The birth and death of endemic species

An endemic species can represent a lineage at the beginning of its evolutionary life (neo-endemic) or the end of its life before becoming extinct (paleo-endemic; Bellwood &

Meyer, 2009*b*). The range of a neo-endemic species should reflect its location of inception, i.e. its position when as a sub-population it became spatially and/or genetically isolated from its parent lineage, through any number of allopatric, sympatric or peripatric scenarios (Gaston, 2003; Coyne & Orr, 2004; Rocha *et al.*, 2005*b;* Hodge *et al.*, 2013). Paleo-endemics on the other hand, arise through range contraction relating to processes of extinction, i.e. a former widespread species becomes locally extinct across its range, with its current endemic position reflecting its last site of survival. A third scenario can also be imagined, where an endemic species arose in a particular location, and due to some ecological or geographic constraint has remained there to the present day without significantly expanding or contracting its range (e.g. endemics in the Red Sea; DiBattista *et al.*, 2016*a*) Such 'ecological' endemics may be particularly suited to their native range and as such could become locally dominant compared to pandemic congeners, perhaps supporting the observed lack of pattern between geographic extent and abundance (Hughes *et al.*, 2014). Distinguishing between paleo-, neo-, or ecological endemism requires temporal, biogeographic and ecological insight into their origins and persistence.

Whether endemic species are at the beginning of their evolutionary life or at the end has called into question their value in delineating locations of significant species accretion, marine biodiversity hotspots, and their role in the origins of Indo-Pacific tropical biodiversity (Bellwood & Meyer, 2009*a*; 2009*b*; Briggs, 2009; Bowen *et al.*, 2013). However, understanding how endemism has arisen through processes of local speciation and/or pandemic extinction is an important aspect of how biodiversity patterns are generated in marine systems. How endemic lineages have arisen through time has implications for both the relationship between lineage age and geographic range, and the primary modes by which speciation occurs in coral reef systems (Hodge *et al.*, 2012; Hodge, van Herwerden & Bellwood, 2014). Determining the geographic distribution of paleo- and neo-endemism should provide an outline of areas or time periods that have been important for species origin (macroevolutionary sources) or areas that represent species survival and/or extinction (macroevolutionary sinks). Source and sink areas for biodiversity may not be mutually exclusive (Bowen *et al.*, 2013), adding another dynamic facet to the accretion and maintenance of tropical biodiversity.

(3) Temporal patterns in tropical marine endemism

Given adequate fossil evidence for a lineage it may be possible to distinguish between paleo- and neo-endemism (Bellwood & Meyer, 2009*b*). Without such fossil records, it remains to be seen if such endemic processes can be recorded in dated molecular phylogenies. If the assumption that neo-endemics are represented by relatively young lineages and paleo-endemics by comparatively older lineages holds true, then dated phylogenies of reef-associated fishes may allow us to examine the distribution of paleo- *versus* neo-endemism across the tropics. From a list of over 600 species classified as having an endemic range (based on the top 10% of all sampled species when ranked from smallest to largest range size; Parravicini *et al.*, 2014) only ~17% of these species have an associated age estimate from a published, calibrated time tree (Fig. 3B). This incomplete phylogenetic and taxonomically biased sampling (Table 1) is a primary obstacle to investigating temporal patterns of endemism that requires further attention in the future. A secondary obstacle is to decide what evolutionary age distinguishes a paleo- from a neo-endemic. Here, we use a cut-off of less than or equal to 2.6 million years ago (Ma) for a neo-endemic with greater than 2.6 Ma defining a paleo-endemic (Fig. 3B). This marks the beginning of the Quaternary, a time period characterized by over 30 glacial-interglacial cycles associated with repeated cooling and warming which had consequences for reef habitat stability and the diversification of many associated fish lineages (Pellissier *et al.*, 2014). While there are many extant lineages of Quaternary age and younger (of various geographic size) the majority of extant reef-associated species date to the Miocene (~23–5.3 Ma) and Pliocene (~5.3–2.6 Ma) epochs (Cowman, 2014; Hodge *et al.*, 2014; Bellwood *et al.*, 2016). For these 17%, there appears to be very little temporal signal in the ages of endemic lineages (Fig. 3B).

Although there is a general trend of increasing numbers of endemic lineages towards the present day, this is most likely an artefact of increasing node density and ‘the pull of the present’ (Pybus & Harvey, 2000). When comparing the distribution of neo- *versus* paleo-endemism there are as many species in our neo-endemic cut-off period as there are from 2.6–5.2 Ma (~23% of the sample in each time period), with many more paleo-endemics distributed throughout the Miocene epoch (~48% of the whole sample). From a geographic perspective, the patterns of endemism are also not clear. Fig. 3A displays the proportion of each ecoregion assemblage that is made up by endemics, and when those endemic taxa have a published age estimate, whether it represents neo-endemism, paleo-endemism or a mixture of both. In addition to there being higher numbers of endemic reef fishes in peripheral locations in the Indo-Pacific and the Atlantic realms, fish endemism in this sampled data set forms a higher proportion of local assemblages. In the Pacific, proportions of endemics in location assemblages are higher in island areas such as Hawaii (16.5%), the Galapagos (13%), Easter Island (32%) and Juan Fernández Island (73%). These locations have varying degrees of isolation from the core Indo-Pacific biodiversity hotspot with faunal breaks recognized in some taxonomic assemblages (e.g. corals; Keith *et al.*, 2013). In the Atlantic, locations such as St. Helena and Ascension Islands, and Cape Verde display higher proportions of endemics (24% and 12%, respectively) when compared to coastal regions. It must be noted that published estimates of fish endemism in these Pacific and Atlantic locations do vary from the data examined here (estimated endemism in each location 25%, 11.7%, 22%, 87.5%, 26%, 30%, respectively; Randall, 2007; Allen, 2008; Floeter *et al.*, 2008; Randall & Cea, 2011; Friedlander *et al.*, 2016).

These discrepancies highlight the impact a definition of endemism can have on assessments of local endemism. An extreme case of this can be seen in a recent assessment of endemism in the Red Sea (DiBattista *et al.*, 2016*b*). DiBattista *et al.* (2016*b*) calculated 12.9% endemism for the entire Red Sea region, while our estimates of numbers of endemics are low or zero for each of our defined categories (Fig. 2B–D). Aside from minor taxonomic sampling differences, this is likely due to the geographic size cut-off in our per cent endemism definition (<12,550 km^2 – top 10% of species ranges ranked from smallest to largest) and the splitting of the Red Sea into two ecoregions under our ecoregion assessment (Northern and Central, and Southern Red Sea; Spalding *et al.*, 2007). If we consider a larger area cut-off of 5×10^5 km^2 (*cf.* Hughes *et al.*, 2002), per cent endemism based on this data set increases to ~23% in the entire Red Sea province. Variation in ecoregional assessments for the Caribbean region (Robertson & Cramer, 2014) and the North and East coast of Brazil (Floeter *et al.*, 2008) will result in different estimates for local and regional endemism. Future examination of patterns of reef fish endemism may require the integration of both local and regional-scale assessments (*cf*. Borsa *et al.*, 2016), incorporating issues related to geographic scale and how endemism is identified.

In terms of lineage ages, there is a dramatic lack of phylogenetic sampling of endemic species within Central Indo-Pacific and coastal Atlantic locations (Fig. 3A). This is probably a general artefact of the likelihood of sampling an endemic species along the biodiversity gradient, and the difficulties associated with sampling peripheral locations. For those locations where endemic age estimates are available, some broad patterns emerge. The majority of ecoregions show either a mix of both paleo- and neo-endemism (e.g. Hawaii, Agulhas Bank, Natal, Cape Verde), or are completely paleo-endemic (e.g. Galapagos, Juan Fernández, Easter Island, Kermadec Island). Only two ecoregions contain species whose lineage age is less than 2.6 Ma: Marshall and Society Islands, however only one lineage is sampled in each case and both areas have very low endemism (<3%). The majority of species defined as paleo-endemic are found in the Tropical East Pacific and Atlantic regions. This may be evidence of higher turnover of assemblages over time in these regions with older endemic ages linked to the high rates of extinction observed there (Budd, 2000). The mixture of endemic ages in the Indo-Pacific realm reflects a complex biogeographic and vicariant history. On the other hand, in the Indo-Pacific there appears to be more stable reef habitat in the last 3 million years that has provided a possible refuge from extinction for older lineages, with fragmentation and isolation of distant stable habitat patches driving younger speciation (Cowman & Bellwood, 2011; Pellissier *et al.*, 2014). Our general pattern of mixed endemic ages in the majority of Central Indo-Pacific areas may reflect the broader pattern of lineage ages observed across the Indo-Pacific, where areas that have been in close proximity to stable reef refugia in the last 3 million year, display larger differences in the ages of reef fish lineages found there (Pellissier *et al.*, 2014). The effect of stable reef habitat can also be noted in the phylogenetic structure of assemblages where more stable areas are more phylogenetically clustered (Leprieur *et al.*, 2016*a*).

The paleo- *versus* neo-endemism discussion can be likened to that of the museum/cradle analogy, where locations that act as a museum can harbour older lineages through increased survival or isolation (macroevolutionary sinks, or ‘graveyards’ for diversity), while cradles of diversity act as location of species inception (macroevolutionary source, or ‘wellspring’ of diversity; Bowen *et al.*, 2013). There is ample evidence to show that tropical coral reefs have acted as both museums and cradles for biodiversity on different temporal and geographic scales (Kiessling, Simpson & Foote, 2010; Cowman & Bellwood, 2011; Bellwood *et al.*, 2012; Briggs & Bowen, 2013). The museum/cradle pattern of biodiversity evolution has also been associated with the latitudinal diversity gradient (LDG) in both marine (Jablonski, Roy & Valentine, 2006) and terrestrial settings (McKenna & Farrell, 2006; Moreau & Bell, 2013). Although many hypotheses have been used to examine the LDG, their utility in explaining the longitudinal gradient in this marine system has been limited (Rosen, 1984). For the longitudinal gradient, several cornerstone hypotheses have generally been discussed (Bellwood *et al.*, 2012; Barber & Meyer, 2015). But it is only in the last five years where dated phylogenies for the groups that form this pattern have been used to assess these long-standing hypotheses from a temporal perspective.

(4) Endemism and ‘centres of’ – hypotheses still requiring data

The popular perceptions of the IAA hotspot (or the more restricted Coral Triangle region) as a significant centre of species origin (CoOr; Ekman, 1953), a centre of overlap among Indian and Pacific biotas (CoOl; Woodland, 1983), or a centre of species accumulation/survival (CoAc/CoSr; Ladd, 1960; Heck & McCoy, 1978) have been assessed using dated phylogenies and ancestral biogeographic estimation. Some of these hypotheses (or variants of them) have held the distribution of endemic species across the Indo-Pacific gradient as a distinguishing factor (Potts, 1985). Originally summarized by Potts (1985) for coral species, the assumptions and implications of each of these cornerstone and subsequently derived models are numerous (reviewed by Bellwood *et al.*, 2012).

For the CoOr model, there should be a preponderance of young endemics in the centre of the hotspot forming a ‘fountain’ or cradle for new species, with the gradient in richness the result of older species expanding their range, or gradually becoming displaced by superior competitors from the centre (Stehli & Wells, 1971; Briggs, 2000). The predictions of the CoOl model are less aimed towards the age of endemics and more towards the location of species origin (Bellwood *et al.*, 2012), being on the peripheral oceanic islands (Rosen, 1984). Overall, there should be more small or endemic ranges on either side of biogeographic boundaries, with wide-ranging sister pairs of species overlapping in the centre of the hotspot (Gaither & Rocha, 2013). But, the CoOl model assumes symmetry in speciation forcing factors either side of biogeographic boundaries. In the case of the Indian and Pacific Oceans there is a strong asymmetry in patterns of isolation (or connectivity). While the Pacific is dominated by stepping stone processes, the Indian Ocean provides a continuum of continental masses. These result in very different distributions of endemism, with the exception that in both oceans endemism tends to increase in peripheral regions (Red Sea and South West Indian Ocean; Hawaii, Marquesas, Easter Island and Kermadec in the Pacific). The CoAc model, similar to the CoOl model, has species arising on the peripheral oceanic islands and gradually moving into the centre, but does not require geographic overlap of closely related species.

No single 'centre of' process appears to be responsible for the current temporal and geographic pattern of endemic reef fishes (Fig. 3), although important age estimates for endemic taxa in the hotspot centre are still required. The majority of locations seem to support both old and young endemics. Similarly, published evidence in the temporal and geographic structuring of species and populations reflect patterns of IAA origination (Timm & Kochzius, 2008), overlap (Hubert *et al.*, 2012; Gaither & Rocha, 2013) and accumulation (Kool *et al.*, 2011) in different taxa. But previous studies across fishes, corals and molluscs fail to show any broadscale evidence of any of the core models (Halas & Winterbottom, 2009) despite these groups showing similar patterns of tropical diversity (Roberts *et al.*, 2002). The underlying process appears more dynamic with multiple roles played by both centres of endemism and centres of biodiversity (Bowen *et al.*, 2013) that are likely to act on different timescales (Renema *et al.*, 2008; Cowman & Bellwood, 2013*b*; Pellissier *et al.*, 2014).

Other models of Indo-Pacific biodiversity evolution have included the distribution of widespread species (Connolly, 2005) and the role played by extinction (McCoy & Heck, 1976; Barber & Bellwood, 2005). The mid-domain effect (MDE; Connolly, 2005) seeks to explain the position of a hotspot 'bullseye' pattern by the random placement of geographic ranges in a bounded domain. In the case of the Indo-Pacific, the MDE explains much of the variation in species richness for fishes and corals among tropical locations (Bellwood *et al.*, 2005). But significant deviations from a MDE expectation can also be identified in both groups, where the Red Sea/West Indian Ocean and the IAA hotspot stand out as having significantly higher species richness than predicted, while much of the Pacific Ocean is depauperate (Connolly, Bellwood & Hughes, 2003). The explanatory power and null expectations of the MDE are useful, but still lack an historic perspective (Bellwood *et al.*, 2012).

The 'centre of survival' model (CoSr) is a more pluralistic variant of the CoAc model that provides a shift in focus from rates of speciation to rates of extinction (Heck & McCoy, 1978). Under the CoSr model, speciation can occur at any time or location, but more lineages tend to survive inside the IAA hotspot than outside where extinction is higher (Barber & Meyer, 2015). Support for the role of the IAA hotspot as a significant centre for lineage survival has come from integrating time-calibrated phylogenies with ancestral biogeographic estimation (Cowman & Bellwood, 2013*a*; Dornburg *et al.*, 2015) and from population-level data (Evans *et al.*, 2016). Coral reef occupation appears to provide a refuge effect in some taxa (Cowman & Bellwood, 2011; Sorenson, Santini & Alfaro, 2014) with coral reef stability important for the survival of old lineages and the fragmentation of habitat linked to younger diversification in the reef fish families Labridae, Pomacentridae and Chaetodontidae (Pellissier *et al.*, 2014). Our assessment of endemism here may also highlight the primary role of the IAA as a centre of survival. The lower number of endemics in the centre of the hotspot may be an artefact of elevated rates of range expansion through higher concentrations of stable reef area and connectivity leading to more small- to medium-sized ranges that are larger than the endemic range definition. Deviations from the MDE expectation may be concordant with the CoSr, where the enriched IAA is the result of more medium- and small-range species present there (Connolly *et al.*, 2003), but overall rates of origination may not be significantly higher than elsewhere. Recent assessment of the rates of diversification in the clownfish genus *Amphiprion* showed no significant difference in rate of speciation among the Indian and Pacific Ocean radiations (Litsios *et al.*, 2014). When comparing the biogeographic histories of the Atlantic and the IAA hotspot there are similar patterns of origination, but it is the survival and subsequent cladogenesis of ancestral lineages and connectivity across the Indo-Pacific domain that have elevated biodiversity within the IAA (Cowman & Bellwood, 2013*a*; Bellwood *et al.*, 2015).

IV. ANCESTRAL BIOGEOGRAPHY AND BIODIVERSITY

The tropical world, restricted to the lower latitudes since ~37 Ma by the Circum-Antarctic Current (Kamp *et al.*, 1990), is broken up into three major longitudinal realms – the Atlantic, the Indo-Pacific and the Tropical East Pacific. A series of barriers have separated these realms sequentially over the past 65 million years: (*i*) the East Pacific Barrier (EPB) – a 5000 km expanse of open ocean forming a 'soft' but effective barrier throughout the past 65 million years (Bellwood & Wainwright, 2002); (*ii*) the Terminal Tethyan Event (TTE) – a land barrier at the northern tip of the Red Sea marking the final closure of the ancient Tethys Seaway and the low latitude connect between the Atlantic and Indian Ocean, dated between 18 and 12 Ma (Adams, Gentry & Whybrow, 1983; Steininger & Rogl, 1984) with evidence of earlier closures (Rogl, 1998); (*iii*) the Isthmus of Panama (IOP) – the final raising of the land bridge is estimated at between 3.1 and 2.8 Ma (Coates & Obando, 1996; O'Dea *et al.*, 2016) with an extended geological and biological history as far back as the Miocene (Farris *et al.*, 2011; Montes *et al.*, 2015; Bacon *et al.*, 2015*a*). These barriers have left a marked signal in broad regional measures of assemblage dissimilarity of reef-associated fishes (Floeter *et al.*, 2008; Kulbicki *et al.*, 2013). Both 'soft' and 'hard' barriers can leave a strong signal of vicariance in the evolutionary history of reef-associated lineages (Lessios, 2008). For the wrasses (Labridae), damselfishes (Pomacentridae) and butterflyfishes (Chaetodontidae) an assessment of vicariance by Cowman & Bellwood (2013*b*) found that the temporal signal of hard and soft barriers can be quite different, reflecting the history of the isolating mechanism. While these historical barriers have been very effective in isolating these realms, there have been several reports of barrier breaches by lineages (with subsequent speciation) and prolonged genetic connectivity among populations (Rocha *et al.*, 2005*a*; Lessios & Robertson, 2006; Bowen *et al.*, 2006). The assemblages that are found in each realm today are the product of a long history of tectonic and climatic turmoil. Changes in the configuration of coral reefs and global provinciality over the past 60 million years can be seen in the fossil and phylogenetic records of associated fish lineages.

(1) The Atlantic and Indo-Pacific – worlds apart

A deep split between the extant Atlantic and the Indo-Pacific reef fish assemblages is seen in species checklists (Floeter *et al.*, 2008; Kulbicki *et al.*, 2013, 2014) and in several phylogenetic analyses (Barber & Bellwood, 2005; Hodge *et al.*, 2013; Cowman & Bellwood, 2013*b*). Although many cladogenetic splits occur around the timing of the TTE, there is evidence that points to early divergences across this barrier (Cowman & Bellwood, 2013*b*) and fossil indications of earlier endemic reef-associated fauna both in the ancestral Tethys Sea and Caribbean regions (Coates, 1973; Hallam, 1973). Today there are a few notable fish taxa absent from the Atlantic that are present in the Pacific [rabbitfishes (family Siganidae); fusiliers (family Caesionidae); and unicornfishes (genus *Naso*)], and *vice versa* (the blenny family Labrisomidae and the parrotfish genus *Sparisoma*). There are also several genera that show disjunct distributions that indicate either extinction in the West Atlantic or colonization of the East Atlantic from the Indian Ocean. In the case of the surgeonfish genus *Naso,* a putative sister-lineage fossil from the Caribbean (Tyler & Sorbini, 1998) provides direct evidence of extinction in the Atlantic realm promoting assemblage differences. Other reef-associated fish genera such as *Cirrhitus* (hawkfish)*, Girella* (sea chubs) and *Prionurus* (sawtail surgeonfish) are found in the Indo-Pacific, including the Tropical East Pacific, but are not present in the West Atlantic.

Within the Atlantic, some genera have highly skewed distributions. There are 156 genera that occur in the New World (both sides of tropical America) but not in the East Atlantic [e.g. grunts (*Anisotremus*, *Haemulon*), porgies (*Calamus*), cleaner-gobies (*Elacatinus*), and wrasses (*Halichoeres*/*Iridio* clades)], while 84 genera display the opposite pattern [e.g. gobies (*Gobius*, *Thorogobius*, *Wheelerigobius*), blennies (*Lipophrys*), porgies (*Pagellus*, *Spicara*) and wrasses (*Symphodus*)] (Floeter *et al.*, 2008; Levy *et al.*, 2011). Other genera, such as *Malacoctenus* (blennies), *Mycteroperca* (groupers), *Sparisoma* (parrotfishes) and *Stegastes* (damselfishes), are much more diverse in the West Atlantic (and the Tropical East Pacific) than in the East Atlantic. However, the genera *Diplodus* (porgies), and *Parablennius* and *Scartella* (blennies) are more speciose in the East Atlantic than in the West Atlantic. At least 18 East Atlantic genera occur in the Indo-Pacific but are not found in the West Atlantic or Tropical East Pacific (e.g. the wrasse genus *Coris*, the emperor genus *Lethrinus* and the sweetlips genus *Plectorhinchus*). These East Atlantic/Indo-Pacific genera indicate either a relatively recent connection *via* southern Africa (Bowen *et al.*, 2006) or more ancient relictual lineages remaining from an ancestral Tethyan hotspot (Barber & Bellwood, 2005). However, extinction associated with the collapse of the Tethyan hotspot and the more recent Messinian Salinity Crises in the Mediterranean (Harzhauser *et al.*, 2007; Renema *et al.*, 2008) will have blurred the biogeographic origins of those clades.

(2) The hopping hotspot

The collapse of the ancestral Tethys hotspot and the survival of lineages in emerging habitat in the Indo-Pacific laid the foundation of modern reef biodiversity (Renema *et al.*, 2008). The fossil record of scleractinian corals shows expansion in the Miocene that is paralleled by accelerated cladogenesis in associated fish lineages (Cowman & Bellwood, 2011). While the fossil record of reef-associated fishes does not show a clear signal of this ancestral collapse, recent methods combining fossil and extant taxa in an ancestral biogeographic assessment show the potential movement of lineages in the family Holocentridae (squirrel and soldier fishes) from a Tethyan hotspot to an Indo-Pacific one during the Oligo-Miocene (Dornburg *et al.*, 2015). This 'hopping hotspot' pattern described by Renema *et al.* (2008) highlights how the collapse of ancestral reef habitat is reflected in the distribution of fossil diversity across taxa and the temporal history of molecular lineages ('as hotspots hop, their taxa slide': Bellwood *et al.*, 2012, p. 231). These deep-time distributional changes in biodiversity, numerous hard and soft dispersal barriers, and variation in reef habitat stability mean that provincial delineation of the marine tropics requires discrete temporal investigation.

V. PROVINCIALITY OF THE MARINE TROPICS

Several biogeographic schemes have been superimposed onto the backdrop of the Indo-Pacific diversity gradient. These have been based on numerous criteria (Spalding *et al.*, 2007; Kulbicki *et al.*, 2013; Keith *et al.*, 2013; Briggs & Bowen, 2013), but as yet there has been little attempt to account for evolutionary relationships or biogeographic processes. Several studies have employed dated phylogenies and extant geographic distributions to estimate ancestral biogeographic ranges (Tavera, Balart & Bernadi, 2012; Cowman & Bellwood, 2013*a*; Litsios *et al.*, 2014; Dornburg *et al.*, 2015). A popular biogeographic model for these studies has been the dispersal, cladogenesis and extinction model (DEC) of Ree & Smith (2008). Recently, this model has been extended, allowing the incorporation of a number of other biogeographic scenarios (Matzke, 2013). The conventional likelihood algorithms implemented in the DEC model remain computationally limited (Landis *et al.*, 2013) and biogeographic inference across more than 10 areas becomes unmanageable (Ree *et al.*, 2005). The number of areas can be increased if strict assumptions are made about area occupancy (Webb & Ree, 2012), but more often geographic distribution data is condensed into less than 10 area assignments, reducing its spatial resolution. However, a recent paper by Landis *et al.* (2013) outlines a Bayesian approach to ancestral biogeographic estimation across hundreds of areas (BayArea). While this approach does make some strict assumptions and only models a restricted number of biogeographic scenarios (Matzke, 2013) it has the advantage of not being limited by area allocation, allowing biogeographic inference at a much finer scale. In theory, one could assign areas in a gridded manner where biogeographic areas are not well defined (Landis *et al.*, 2013).

In the study of reef fish ancestral biogeography, a number of different area definitions have been used (Tavera *et al.*, 2012; Litsios *et al.*, 2014; Dornburg *et al.*, 2015). The main differences among the area schemes used are the delineation of discrete provinces within the Indo-Pacific, inclusion of the Coral Triangle as an independent area, and divisions within the Atlantic realm. Kulbicki *et al*. (2013) outlined a method for delineating tropical regions and provinces based on the dissimilarity of reef fish species assemblages. Their approach followed the methodological framework proposed by Kreft & Jetz (2010). This statistical approach for assigning areas for biogeographical assessment based on assemblage differences could be used as an initial step in an ancestral biogeographic analysis to achieve a meaningful, taxon-specific delineation of geographic space. Although Kulbicki *et al*. (2013) did not incorporate phylogenetic history, methods do allow for measures of turnover among locations based on lineages distributed across a phylogenetic tree (Leprieur *et al.*, 2012). By measuring lineage turnover, we can examine provinciality base on phylogenetic assemblage dissimilarity. Further, by using the BayArea approach to estimate ancestral ranges at internal nodes on a phylogeny we can compare the phylogenetic clustering of present-day assemblages with the phylogenetic clustering of lineages through time.

Here, we examine regional dissimilarity, accounting for phylogenetic relatedness, across 111 tropical ecoregions (*cf.* Spalding *et al.*, 2007) for 11 globally distributed reef-associated fish families (Apogonidae, Acanthuridae, Chaetodontidae, Holocentridae, Labridae, Lutjanidae, Pomacentridae, Pomacanthidae, Sparidae, Tetraodontidae, and Zanclidae). These families vary in richness from the monotypic family Zanclidae to the very diverse Labridae with over 630 species. Dated phylogenies for these families were obtained from a number of published sources (Cowman & Bellwood, 2011; Choat *et al.*, 2012; Frédérich *et al.*, 2013; Santini *et al.*, 2013; Santini, Carnevale & Sorenson, 2014; Sorenson *et al.*, 2013; Rabosky *et al.*, 2013; Dornburg *et al.*, 2015), with geographic distributions taken from the largest database of reef fish species ranges (Parravicini *et al.*, 2013). The individual family phylogenies and their associated presence/absence of species across the 111 ecoregions were used for biogeographic analyses in the BayArea program. The resulting biogeographic reconstruction and associated phylogeny was then truncated at 3 million year increments back to 27 Ma. At each time point the biogeographically reconstructed ranges and the associated phylogenetic tree was used to cluster ecoregion assemblages based on phylogenetically informed dissimilarity. In order to obtain a metric independent from the richness of lineages, we only used the turnover component of phylogenetic dissimilarity. The results of the phylogenetic dissimilarity clustering for present-day assemblages and across nine, 3 million year time slices are discussed below.

(1) Tropical provinciality in the present

The present-day provinciality of tropical fish assemblages (Fig. 4) when accounting for phylogenetic relationships shows many similarities with the results of Kulbicki *et al.* (2013), even though the 11 families examined here are only a subset of the geographic data they examined. There is a basal split between the Atlantic and Indo-Pacific realms, with the Tropical East Pacific (TEP) and Eastern Atlantic (EA) also defined regions (Fig. 4). However, unlike the results of Kulbicki *et al*. (2013), the TEP is phylogenetically more similar to the rest of the Indo-Pacific than to the Atlantic. This probably reflects the number of species that are found both in the large Indo-Pacific and TEP realms (32 species in this analyses) and sister lineages presumably separated by the East Pacific Barrier. Accounting for phylogenetic history has resulted in other dramatic changes within the Indo-Pacific. Comparing the geographic schemes in Figs 1B and 4A there is a large expansion of the region previously named the Central Indo-Pacific (CIP) by Kulbicki *et al*. (2013). This cluster (red in Fig. 4A) now engulfs the majority of the Indian and western Pacific Ocean, stretching from Madagascar and coastal India in the west, to the Hawaiian Archipelago and Pitcairn Islands in the east. Ecoregions along the East African coast are clustered together with the Red Sea locations. There is also a cluster containing assemblages from the Ogasawara Islands in the northeastern Pacific and Easter, Juan Fernández and Desventuradas Islands in the far eastern Pacific Ocean. Clustering of Atlantic assemblages is similar to that found by Kulbicki *et al*. (2013), with the exception of the Gulf of Guinea in the West African Coast standing out as separate to the East Atlantic cluster (Fig. 4).

The expansion of the CIP to encompass the Indo-West Pacific (IWP hereafter) is not unexpected. Previous schemes have outlined a large Indo-Pacific assemblage (Briggs & Bowen, 2012) and even in the original analysis of Kulbicki *et al*. (2013) the entire Indo-Pacific is characterized by very low internal dissimilarity. Accounting for phylogenetic similarity among lineages in this analysis has captured the phylogenetic connections between CIP and Central Pacific lineages. The outline of the Indo-Malay-Philippine region (IMP, Fig. 1A; Carpenter & Springer, 2005) previously united these two provinces. Previous broad-scale biogeographic analyses have shown that the diversity of fishes in the Central Pacific is derived from the expansion of lineages of IAA origin (Cowman & Bellwood, 2013*a*). More interesting is the extent of the incursion of this new IWP cluster into the Indian Ocean to include Madagascar, Coastal India and Sri Lanka – regions that have been considered closely associated with Indian Ocean, African and Red Sea assemblages (Spalding *et al.*, 2007; Keith *et al.*, 2013; Mouillot *et al.*, 2013; Borsa *et al.*, 2016). This appears to be the result of range expansion from the IAA to the west with wide lineage ranges and subsequent speciation reducing phylogenetic dissimilarity (Fig. 5).

The clustering of islands separated by over 13,000 km is more curious. Examination of the lineages found in the cluster containing the Ogasawara, Easter, Juan Fernández and Desventuradas Islands (Fig. 5), shows that it is made up of widespread lineages dispersed throughout the phylogeny, and by some small-range species that appear to have evolved through peripheral isolation processes (*cf.* Hodge *et al.*, 2012) on these islands far from the biodiversity hotspot centre. This clustering may also reflect some anti-tropical ranges found in several lineages sampled (e.g. *Pseudolabrus*, *Bodianus*, *Chromis*; Randall, 1981) a pattern also seen in previous clustering analyses (see supplemental material Kulbicki *et al*., 2013). In the Atlantic, the assemblage of fishes found in the Gulf of Guinea stands apart from the rest of the East Atlantic cluster with phylogenetically dispersed wide-ranging lineages and peripheral speciation processes defining local assemblages differing from those at a regional scale (Fig. 5).

(2) Tropical provinciality in the past

Throughout the last 30 million years, shallow tropical marine habitats have undergone massive reconfiguration. As a result, the distribution of and connections among assemblages in the past may be quite different to what we see in the present day. By incorporating estimates of ancestral ranges, we may be able to examine the changing biogeographic structure of tropical reef fish assemblages. Fig. 6 illustrates the results of phylogenetic lineage dissimilarity analyses at 3 million year intervals from 3 Ma to 27 Ma with corresponding dendrograms illustrating the clustering structure of 111 tropical ecoregional assemblages.

Moving back in time, at 3 Ma, we see less phylogenetic separation of reef fish assemblages either side of the Americas (Fig. 6A). The TEP is more closely aligned with the West Atlantic (WA) assemblages than those in the Indo-Pacific, in contrast to the present-day clustering analysis (Fig. 4). This points to a greater similarity of assemblages either side of the Isthmus of Panama. Although many geminate pairs pre-date the final closure of the Isthmus at 3.1 Ma (Lessios, 2008) the link between the TEP and the WA here is likely due to the lack of subsequent lineage diversification in the last 3 million years within clades separated by the Isthmus. The link between these two regions is more apparent at 6 Ma (Fig. 6F) where a decline in phylogenetic dissimilarity between the WA and TEP leads to a clustering of assemblages at Juan Fernández and Desventuradas islands in the far eastern Pacific with assemblages on the East Brazilian Coast. Such disjunct ranges (eastern Brazilian coast and Pacific islands) have previously been noted in some clades of gastropods that lack coastal East Pacific congeners (Vermeij, 2001). Given the complex geological and biological history of the Isthmus of Panama (Farris *et al.*, 2011; Bacon *et al.*, 2015*a;* reviews by Leigh, O'Dea, & Vermeij, 2014; Bagley & Johnson, 2014) extinction of marine lineages on both sides of the barrier may have led to disjunct distributions of extant clades (Marko, Eytan & Knowlton, 2015), biasing phylogenetic dissimilarity estimates and the temporal signal of biogeographic processes. Examples of such disjunct distributions linked to extinction on either side of the Isthmus are the sparid species *Archosargus pourtalesii* found only in the Galapagos with its closest relatives only in the Atlantic (McCosker, 1987), and the wrasse *Halichoeres rubrovirens* from Trindade Island (South Atlantic) with its closest relative in the TEP (Rocha, Pinheiro & Gasparini, 2010).

Recent discussion on the age and evolutionary influence of the Isthmus of Panama (Leigh *et al.*, 2014; Bacon *et al.*, 2015*a*; O'Dea *et al.*, 2016) has highlighted its extended biological history for some terrestrial and marine lineages, but cautions against the use of incomplete and biased data sets (Lessios, 2015; Marko *et al.*, 2015; but see Bacon *et al.*, 2015*b*). The analyses presented here are likely to be hindered by both undersampling and extinction. However, from the assemblage perspective it is interesting that (with the exception of Juan Fernández and Desventuradas islands) the TEP and the WA are retained as separate, phylogenetically dissimilar clusters throughout the last 27 million years, linked as sister-areas based on the presence/absence of particular genera (Floeter *et al.*, 2008) but not classified as phylogenetically similar in the present day by extant assemblages. The influence of Indo-Pacific lineages can be seen in the clustering of extant lineages (Fig. 4) reflecting those lineages that have been able to maintain genetic connection across the East Pacific Barrier (Lessios & Robertson, 2006). Between 27 Ma and 18 Ma (Fig. 6F–I) the Caribbean assemblages show greater dissimilarity from other Atlantic or Eastern Pacific ecoregions. This is likely a result of the high turnover of assemblages found there at this time and subsequent periods of extinction (Budd, 2000). For example, the extinct fossil genera *Eonaso* (Tyler & Sorbini, 1998) of Antigua, *Armbourgthurus* of Iran (Tyler, 2000), *Sorbinithurus* of Monte Bolca, Italy (Tyler, 1999), and *Marosichthys* of the Celebes in the west Pacific (Tyler, 1997) highlight an ancestral pan-tropical distribution of the Nasinae (Acanthuridae) lineage, while its single living genus *Naso* is restricted to the Indo-Pacific. The extinction of the three fossil genera means these putative ancestral assemblage connections are not sampled in the deeper parts of the phylogeny. Moving forward in time, it is the diversification and dispersal of surviving lineages sampled in the phylogeny that influence assemblage similarity among regions. Further insight into the deep-time affinity of tropical reef assemblages will require the integration of the fossil and geological records of associated taxa.

On the far side of the Indo-Pacific there are significant fluctuations in provinciality within the Indian Ocean region and its boundary with the IWP cluster (Fig. 6A–D). Prior to 3 Ma the Red Sea was an independent province from the East African coast cluster. At earlier time steps the East African coast cluster both includes and excludes Madagascar and coastal India. At 12 Ma (Fig. 6D) the southeastern coast of Africa (Delagoa, Agulhas Bank and Natal) forms a cluster dissimilar from the other Indian Ocean assemblages. Between 27 Ma and 15 Ma an entire Indian Ocean cluster that includes all Red Sea, East African coast, Madagascar and Indian coast assemblages appears to be stable, with minor differences for some assemblages in the IWP cluster at 18 Myr and 27 Myr (Fig. 6F,I).

Based on these temporal clustering analyses the Indian Ocean and IWP assemblages are phylogenetically closer than they are to any TEP or Atlantic assemblage from the 15 Ma time step to the present. At 18 Ma, the IWP and TEP assemblages are more phylogenetically similar to each other than they are to the Indian Ocean cluster (Fig. 6F) and at 21 Ma the Indian Ocean cluster is reconstructed to be more phylogenetically similar to an East Atlantic cluster (Fig. 6G). A number of clades display deep vicariance across an Atlantic/Indian Ocean divide (e.g. *Holacanthus*; Alva-Campbell *et al.*, 2010), but the timing of these vicariance events does not appear to be concordant among fish families (Cowman & Bellwood, 2013*b*). The biogeographic clustering analysis described here suggests that this ancestral phylogenetic link between the Indian Ocean and East Atlantic could be a phylogenetic signal of the remnants of a Tethys-like assemblage, at a time when the ancient seaway around northern Africa would have supported a shallow-water reef habitat. Evidence from the fossil record of foraminifera (Renema *et al.*, 2008) highlights the Arabian region as a centre of paleo-biodiversity for reef-associated taxa, an intermediate step in the eastward shift in marine biodiversity at that time. For reef fishes, the earliest fossil records for many ancestral forms lie in the Eocene deposits of Monte Bolca (Italy), a *lagerstätten* that contains both Atlantic and Indo-Pacific taxa in an area close in proximity to the ancestral Tethyan hotspot (Bellwood *et al.*, 2016). At 27 Ma the signal of an ancient Tethyan province is more apparent with the Indian Ocean cluster including reconstructed assemblages of the Gulf of Guinea and the Sahelian upwelling ecoregion. The clustering of assemblages to form a Tethyan province during this period not only highlights the effect of plate tectonics on tropical reef biodiversity dynamics but also the phylogenetic history of reef fish lineages (Leprieur *et al.*, 2016*b*).

(3) Analytical considerations

Implementing the BayArea program for ancestral biogeographic reconstruction allows a finer geographic resolution than previous methods and provides the opportunity to examine dissimilarity clustering at various time points. However, there are a number of limitations to the program in its current form that require care when interpreting results. The reconstruction is based on a single phylogenetic reconstruction with no ability to incorporate phylogenetic uncertainty or account for unsampled lineages. Inclusion of unsampled lineages could alter the patterns presented here. Similarly, there is no way to account for extinct lineages in the analysis, or use fossil data in the reconstruction, which is permitted in other maximum likelihood approaches (Matzke, 2013). Furthermore, the BayArea analysis is conducted under a static geological history, i.e. the dispersal model cannot currently account for tectonic drift, sea-level changes, or the formation of barriers (Landis *et al.*, 2013). In particular, for reef-associated lineages the stability of reef habitat through time has been an important factor influencing patterns of phylogenetic similarity (Leprieur *et al.*, 2016*a*). Our reconstruction did not treat land masses as dispersal barriers, which may have resulted in reconstructing excessively wide ranges and unrealistic dispersal events. In the oldest time steps (Fig. 6H, I) the clustering of the eastern Pacific islands within an Indian Ocean cluster appears to imply such possible analytical limitation. However, even with this limitation the phylogenetic clustering of ancestral ranges seems to provide a clear pattern of provincial rearrangement, with a signal of both the closure of the Panama Isthmus and the Tethys seaway. This suggests that past and present patterns of phylogenetic similarity can provide insight into the biogeographic history of tropical assemblages.

VI. FUTURE DIRECTIONS

The biodiversity of tropical reef systems has a complex pattern, with a history that has been blurred by tectonic rearrangement and climatic shifts that have altered rates of speciation, extinction, dispersal, and thus genetic connections among local and regional assemblages. However, the combination of molecular phylogenies, fossil dating and ancestral biogeographic estimation can allow us to trace the origins of biodiversity across the globe. Here we show that including ancestral range reconstructions across many discrete locations can result in a fine-scale biogeographic history on internal nodes of a phylogenetic tree. This estimated biogeographic history, based entirely on present-day ranges and the cladogenetic history of extant molecular lineages, can provide insight into the historical connections among assemblages and the delineation of provinces over shallow and deep timescales. The processes promoting marine endemism remain unclear, both through lack of phylogenetic sampling and ambiguous definitions of an endemic range. A more informative method of endemism classification based on range size categories may provide an alternative approach to the study of local and regional endemism (Borsa *et al.*, 2016). Overall, a primary obstacle to overcome in future research on the biogeographic history and biodiversity of reef (and many other) systems is the lack of phylogenetic sampling and resolution of taxa that form these patterns.

There has been an incremental increase in the phylogenetic sampling of iconic reef fish families (e.g. Chaetodontidae, Labridae, Pomacentridae; Cowman, 2014, and references therein) while phylogenetic relationships in other reef-associated families are only now beginning to receive significant phylogenetic attention (e.g. Blennidae, Gobiidae; Hundt *et al.*, 2014; Thacker, 2015). In general, fishes have a legacy of a significantly lower rate of phylogenetic resolution compared to other vertebrate lineages in the last two decades (Thomson & Shaffer, 2010). However, large-scale phylogenetic efforts with a focus on the deeper relationships and systematics of fishes (Near *et al.*, 2012; Betancur-R. *et al.*, 2013; Rabosky *et al.*, 2013) are providing a framework to allow macroevolutionary questions to be investigated at deeper timescales. For coral reefs in particular, these 'top-down' approaches are revealing the early origins and tempo of diversification of fish families on coral reefs (Price *et al.*, 2014, 2015). The extant biodiversity patterns we see on reefs today arose from the expansion of coral-dominated reef habitat during the Miocene (23–5 Ma) and its influence on the diversification of its associated fish fauna (Bellwood *et al.*, 2015). Sampling and sequencing of genetic data are needed from the 'bottom-up' to focus on filling the taxonomic gaps in species-level phylogenies. New phylogenomic methods allowing the capture of hundreds of unlinked loci (Faircloth *et al.*, 2013) that can be used across evolutionary scales (Faircloth *et al.*, 2012) promise to provide unparalleled ability to reconstruct species-level phylogenies.

With complete species-level phylogenies, future research could include temporal and biogeographic data to explore how lineages have diversified to form present-day assemblages. The methods we outline here could be extended to incorporate a dynamic geographic model whereby dispersal among locations changes through time to reflect tectonic movement (Landis *et al.*, 2013), or in the case of reef habitat the isolation or collapse of habitat under different sea-level conditions (Pellissier *et al.*, 2014). In addition to describing patterns of provinciality and historic connections among assemblages, a more in-depth understanding of how diversity has evolved would be gained by quantifying rates of speciation, extinction and dispersal among locations. Rate estimation and rate-shift analyses have been used to explore the tempo and mode of several groups with reef affinities (Alfaro, Santini & Brock, 2007; Cowman & Bellwood, 2011; Litsios *et al.*, 2012). More recently, newly developed methods are being used to examine variation in rates of speciation, extinction and dispersal (or transition) among species and its correlation with geography or life history (Jetz *et al.*, 2012; Rabosky *et al.*, 2013; Morlon, 2014).

During the last 20–30 million years (Oligocene to Miocene epochs) we see the functional development of reef fishes both in fossils (Bellwood *et al.*, 2014) and phylogenies (Cowman, Bellwood & van Herwerden, 2009; Lobato *et al.*, 2014). From a functional aspect, high diversity in coral reef systems does not appear to beget functional redundancy (Mouillot *et al.*, 2014). With fewer species supporting critical but vulnerable functional roles, it is important to understand how these functions have evolved along lineages and whether those lineages are adequately protected under current conservation efforts (Mouillot *et al.*, 2016). From a marine conservation standpoint, it is critical to consider the different types of biodiversity that can and should be protected. Although the focus herein is the biogeographic origins of biodiversity in terms of species richness and assemblage differences, an equally important aspect of coral reef fish evolution is in the origins and distribution of functions critical for reef health. Life-history traits of reef species and populations display interesting geographic patterns (Luiz *et al.*, 2013; Selkoe *et al.*, 2016) that have yet to be fully explored for their evolutionary impact on past and present assemblage patterns. Ancestral biogeography combining assessments of functional evolution on coral reefs should remain an active area of research and development in the future.

VII. CONCLUSIONS

(1) Defining important areas for biodiversity conservation in the marine tropics has proved more difficult than in terrestrial systems. The IAA marine biodiversity hotspot is recognized as an important repository of biodiversity for reef-associated fishes and other organisms, but its origins still remain a matter of debate. For reef-associated fishes, centres of total species richness are not concordant with centres of endemism. The origins of complex patterns of endemic and wide-ranging species, richness gradients and provincial assemblages can be explored using dated phylogenies combined with methods to estimate ancestral biogeographic ranges.

(2) Although phylogenetic sampling of endemic lineages is generally low (<20%), the evolutionary origins of endemic-range species points to multiple processes acting in concert to generate biodiversity across the Indo-Pacific. Most locations tend to have both neo and paleo-endemic lineages, with a slight trend of older endemic taxa in higher

proportions in more peripheral locations (Fig. 2). In relation to prevailing hypotheses concerning the origins of Indo-Pacific biodiversity, temporal patterns of endemism favour the IAA as a centre of survival, but its relative role in the origination of species remains unclear due to undersampling of endemic lineages there.

(3) Accounting for measures of phylogenetic diversity in the delineation of present-day assemblages across the tropics highlights the importance of connectivity among locations and the impact of habitat stability during the Quaternary. Expansion of lineages from the Central Indo-Pacific to adjacent locations has resulted in lower phylogenetic dissimilarity across a larger Indo-West Pacific province, but coastal Africa and the Tropical East Pacific remain separate clusters within the larger Indo-Pacific realm. Distant islands in the Pacific, peripheral to the biodiversity hotspot are linked by phylogenetically distinct lineages that may not taxonomically overlap. The basal split between the Atlantic and Indo-Pacific highlights deep taxonomic divides and phylogenetic distance (Fig. 5).

(4) The past 30 million years has seen a massive reconfiguration in the provinciality of reef fish assemblages. The cladogenetic history of several diverse reef fish families displays fine-scale spatial arrangements that reflect both recent and deep-time alterations in regional connectivity, isolation and lineage turnover. Phylogenetic dissimilarity clustering of reconstructed assemblages highlights the influence of the Isthmus of Panama land bridge and a deep-time connection between the Atlantic and Indian Ocean assemblages *via* the ancient Tethys Seaway (Fig. 6), a pattern only seen previously in fossils. Assemblages in the Caribbean display deep-time phylogenetic dissimilarity which may reflect higher rates of extinction.

(5) In the absence of adequate fossil data, dated phylogenies and ancestral biogeographic estimation may provide a glimpse at past assemblage differences. Molecular phylogenetics and its utility as a tool to explore biogeographic and biodiversity patterns is entering a new era. Cross-disciplinary research integrating phylogeny, palaeontology, biogeography and functional assessments of reef-associated fishes will allow further insight into how modern reef biodiversity was formed and what aspects are important for its survival. The combination of genomic data sets and more sophisticated analytical techniques will allow inference at the level of entire assemblages. Considering the dire consequences facing coral reef biodiversity under a changing climate, future research

focused on the evolution of coral reef biodiversity should aim to answer some important questions: where has it come from, how is it maintained, and, where will it go?

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Table 1. Geographic and phylogenetic sampling of endemic taxa by family. The number of species with geographic data across 13 common reef-associated families with the per cent of those taxa that are present in a phylogeny with age estimates in parentheses. '5% End' and '10% End' are the number of species that are defined as endemic in the top 5% or 10% of species ranked from smallest to largest geographic range size across the entire data set. 'Total GASPAR' is the number of species found in the 111 tropical ecoregion of the GASPAR data set (Parravicini *et al.*, 2013).

Family	**Species (% Phylogeny)**	**5% End**	**10% End**	**Number of species with age estimate**
Acanthuridae	83 (75.9%)	-	1	-
Apogonidae	305 (25.25%)	9	17	-
Blenniidae	333 (27.03%)	22	42	4
Carangidae	99 (57.58%)	2	2	2
Chaetodontidae	127 (75.59%)	9	15	5
Gobiidae	722 (13.85%)	40	55	2
Holocentridae	71 (59.15%)	5	7	1
Labridae	448 (43.08%)	30	52	13
Lutjanidae	83 (55.42%)	-	-	-
Mullidae	49 (16.33%)	1	5	-
Pomacanthidae	86 (48.84%)	7	15	2
Pomacentridae	366 (55.19%)	27	44	7
Sparidae	99 (70.71%)	8	16	10
Total GASPAR	6182 (32.77%)	322	604	103

Figure Legends

Fig. 1. (A) Biodiverse regions in the marine tropics modified from Gaither & Rocha (2013). IAA, Indo-Australian Archipelago following Bellwood & Hughes (2001) and Renema *et al*. (2008); CT, Coral Triangle following Veron *et al*. (2009); IMP, Indo-Malay-Philippine biodiversity hotspot following Carpenter & Springer (2005); InP, Indo-Polynesian biogeographic province modified from Briggs & Bowen (2013); EH, endemic 'biodiversity hotspots' based on endemism and assessments of threat following Roberts *et al*. (2002). (B) Tropical regions delineated bases on dissimilarity measure (Kulbicki *et al*., 2013). CIP, Central Indo-Pacific; CP, Central Pacific; EA, East Atlantic; TEP, Tropical East Pacific; WA, West Atlantic; WIO, West Indian Ocean. Global maps are drawn in Mollewide projection.

Fig. 2. Patterns of reef-associated fish biodiversity relating to (A) total species richness, (B) endemic species richness based on the top 10% and (C) the top 5% of species ranked from smallest to largest range size in the sampled data set (Parravicini *et al.*, 2013). (D) Fish endemic species richness based on species that are restricted to a single ecoregion. Ecoregion scheme follows Spalding *et al.* (2007). The top margin of each map displays a density plot for each measure across longitude. Maps drawn in Mollewide projection.

Fig. 3. (A) Proportion of endemic reef fish species (top 10% of smallest ranges) found across tropical ecoregions. Size of circles indicates per cent of assemblage made up by endemic species. Colour of circle denotes if those species are considered neo-endemics (orange, ≤ 2.6 Ma), paleo-endemics (purple, >2.6 Ma) or a mixture of both (green). Number next to each coloured point indicates the number of neo- and paleo-endemics with age estimates at that ecoregion. Ecoregions where no age estimates were available are in white, and ecoregions with no endemic species based on the 10% definition are not shown. (B) Temporal distribution of endemic lineages and whether they are considered neo- or paleo-endemic. Bin widths represents 0.3 million years and *y*-axis is scaled to per cent of all endemic age estimates sampled (103 lineages total).

Fig. 4. Tropical provinciality of extant reef fish assemblages based on phylogenetic dissimilarity clustering methods. (A) Map of ecoregions; colour indicates their association with a particular cluster. (B) Dendrogram showing the clustering of ecoregions based on phylogenetic dissimilarity. Coloured branches are linked to cluster colours in A. E* indicates the clustering of distant Pacific Islands linked by endemic taxa formed through peripheral isolation processes (see text). Cluster analysis produces a quantitative, hierarchical classification of the dissimilarity among species assemblages, but is sensitive to the dissimilarity measure and the classification algorithm chosen. Amongst the myriad of dissimilarity indices available (most reviewed in Koleff *et al.*, 2003) we chose a metric based on species turnover as these are insensitive to variation in species richness, which may blur biogeographic patterns. Since our analysis was conducted across lineages and evolutionary time, instead of a turnover measure based on species we chose a recently developed measure of turnover based on lineages across the phylogenetic tree (Leprieur *et al.*, 2012) as this has the advantage of giving different weight to the dissimilarity among assemblages while accounting for phylogenetic distance among lineages. Clustering using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm achieved the best performance and was retained for further analysis in time slices (see Fig. 6).

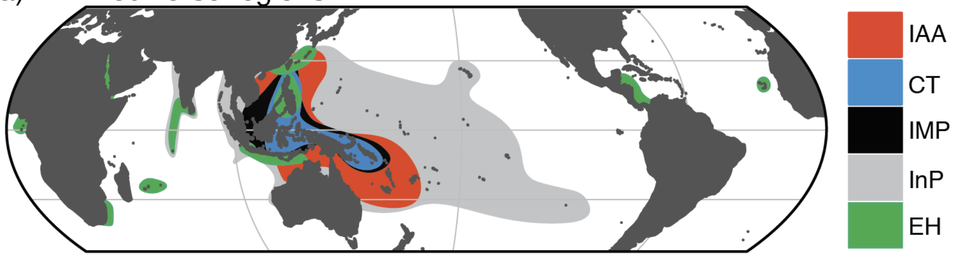
Fig. 5. Composite time-calibrated phylogenetic tree for 11 reef-associated fish families and their presence/absence in present-day phylogenetic dissimilarity clusters (see Fig. 4). Colours at tips correspond to cluster colours in Fig. 4. Geological epochs are denoted on the time axis (Pe: Pleistocene; Pi: Pliocene).

Fig. 6. Tropical provinciality through time at 3 million year time steps (3–27 Ma). Each panel displays the global continental reconstruction for that time period, the reconstructed ecoregion clusters based on phylogenetic dissimilarity of lineages with ancestral biogeographic estimation, and the associated cluster dendrogram with corresponding cluster colours. Light- and dark-grey backgrounds indicate whether the time step is found in the Pliocene, Miocene or Oligocene epochs. For each dendrogram, the optimal number of biogeographic clusters was determined by applying the Kelley–Gardner–Sutcliffe

penalty function (KGS). This function maximizes differences between the groups and cohesiveness within the groups. Its minimum value corresponds to the optimal number of clusters (Kelley *et al*., 1997; Hattab *et al*., 2015).

Figure 1

(a) Biodiverse regions



(b) Marine tropical regions

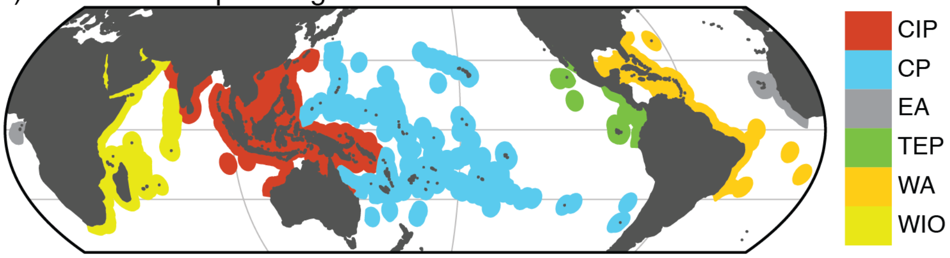
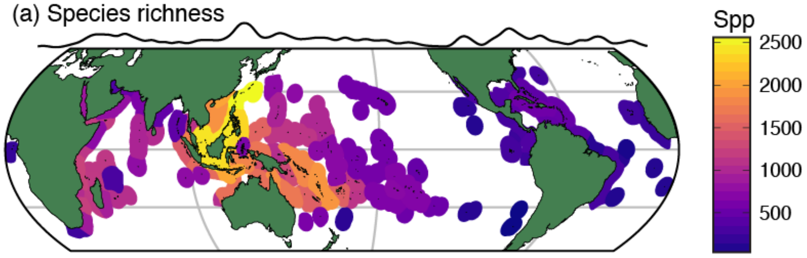
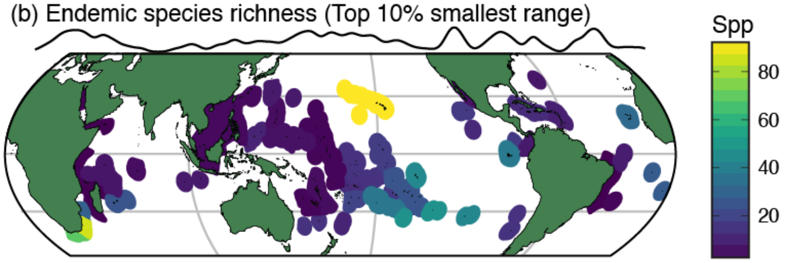


Figure 2

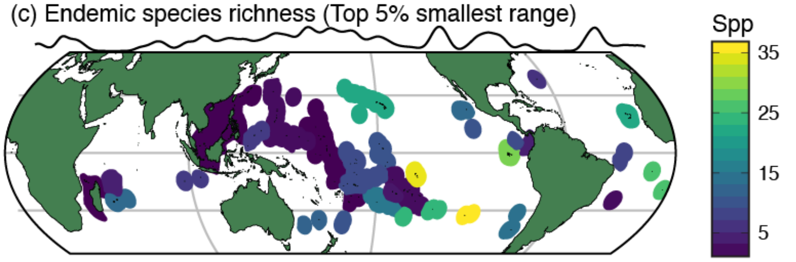
(a) Species richness



(b) Endemic species richness (Top 10% smallest range)



(c) Endemic species richness (Top 5% smallest range)



(d) Endemic species richness (by ecoregion)

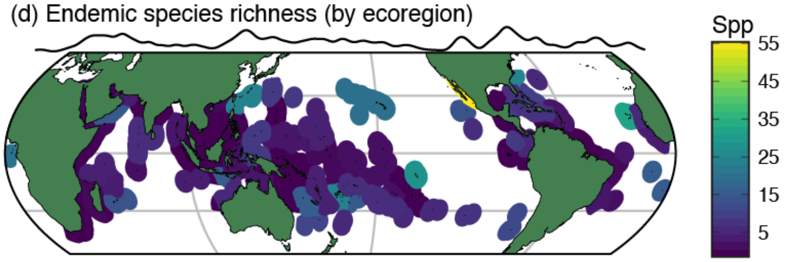


Figure 3

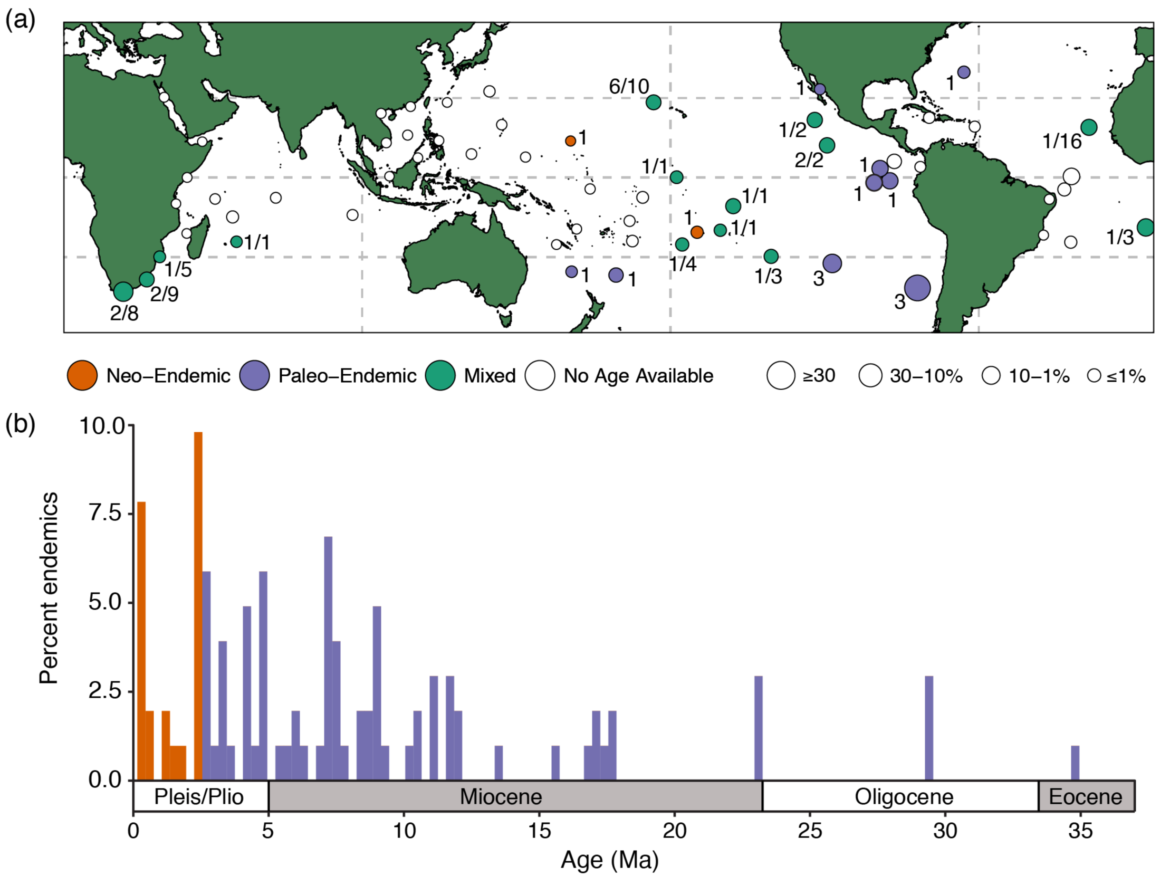
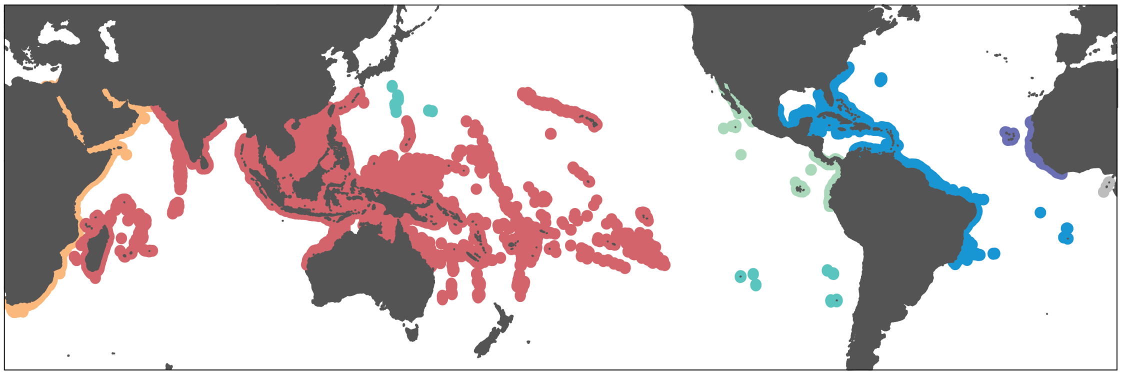

(a)
6/10
1
1/1
1/1
1
1/1
1/4
1/3
3
3
1
1
1/2
2/2
1
1
1
1
1
1/16
1/3
1/1
1/5
2/9
2/8
Neo–Endemic
Paleo–Endemic
Mixed
No Age Available
≥30
30–10%
10–1%
≤1%
(b)
Percent endemics
10.0
7.5
5.0
2.5
0.0
Pleis/Plio
Miocene
Oligocene
Eocene
0
5
10
15
20
25
30
35
Age (Ma)

Figure 4

(a) Map of present day assemblage clusters – 7 clusters



(b) Phylogentically informed cluster diagram of assemblage dissimilarity

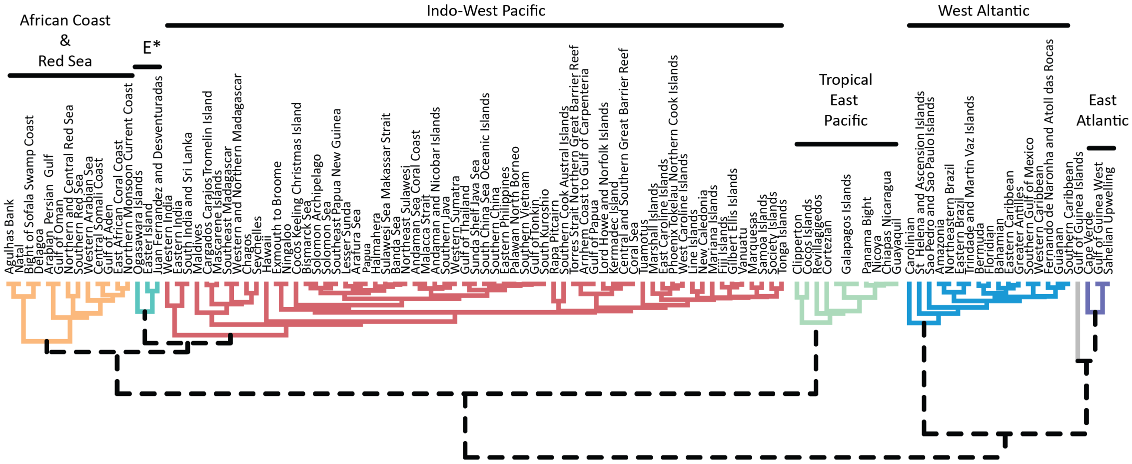


Figure 5

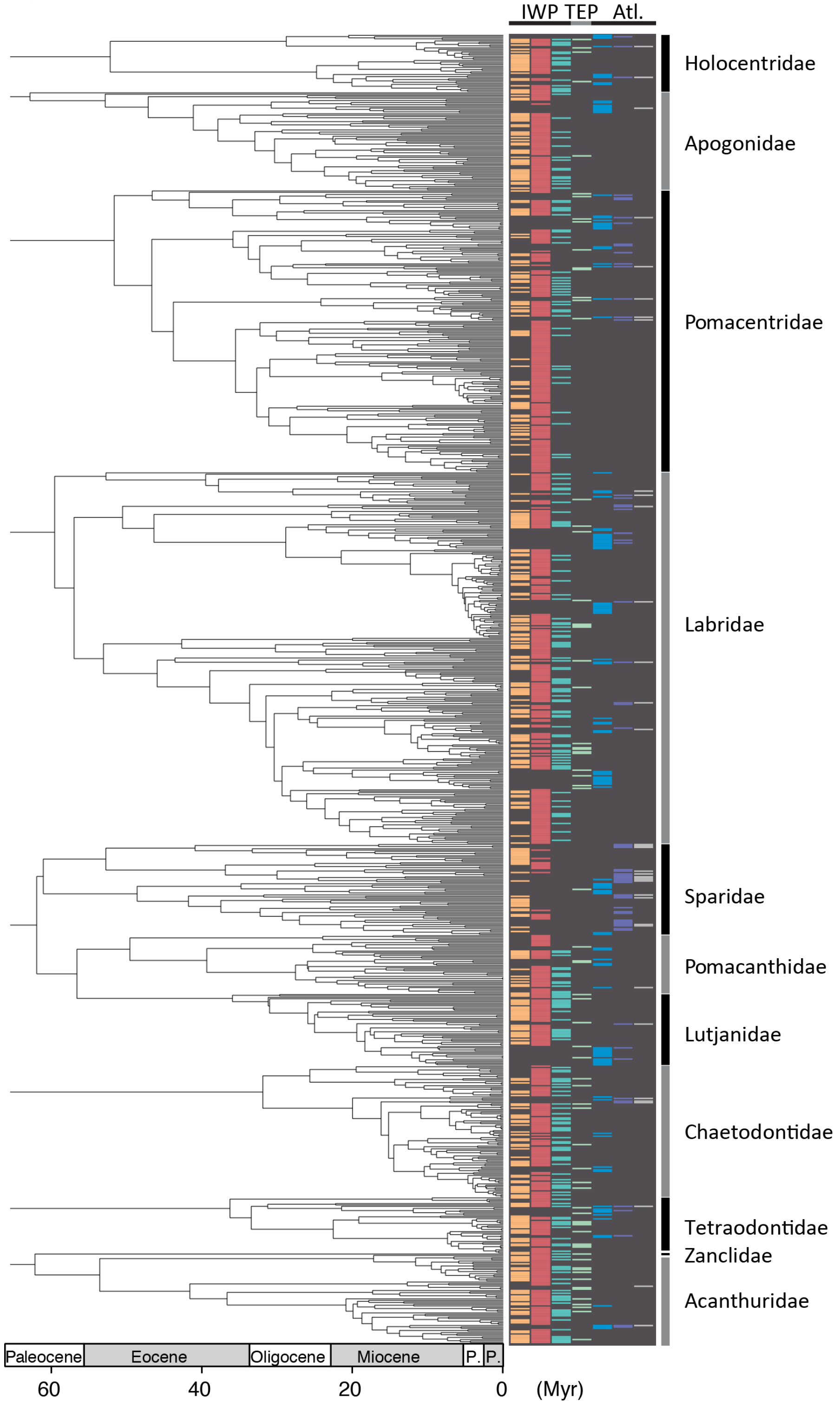
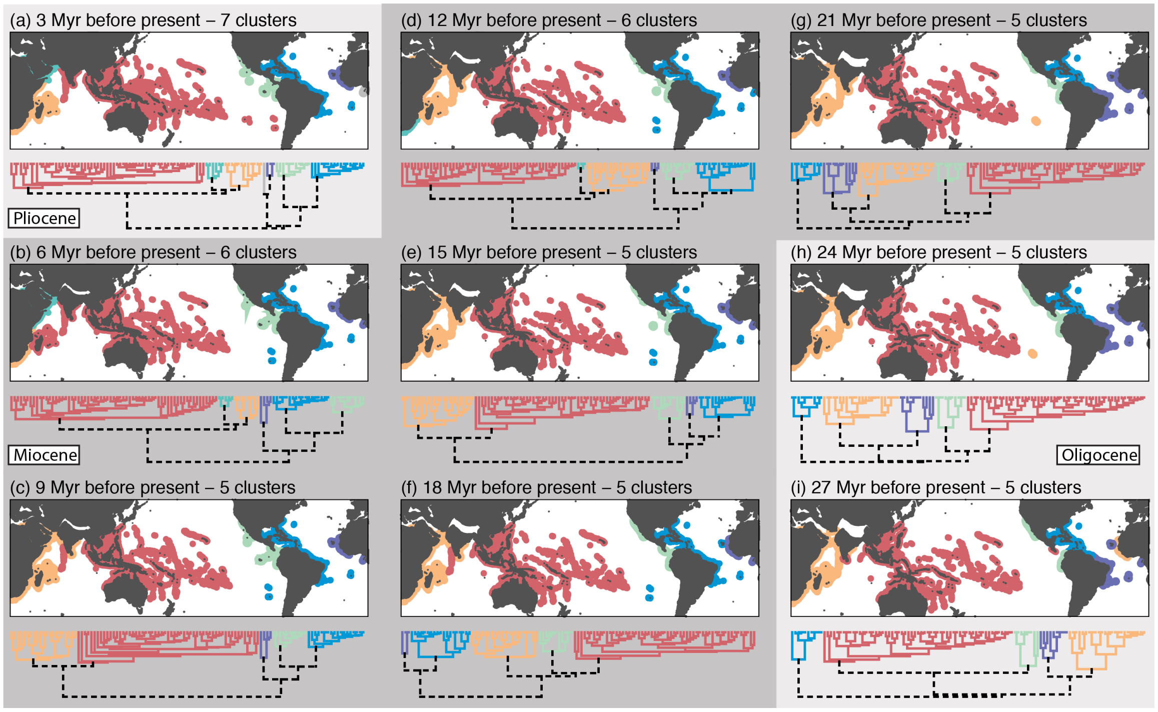

IWP
TEP
Atl.
Holocentridae
Apogonidae
Pomacentridae
Labridae
Sparidae
Pomacanthidae
Lutjanidae
Chaetodontidae
Tetraodontidae
Zanclidae
Acanthuridae
Paleocene
Eocene
Oligocene
Miocene
P.
P.
60
40
20
0
(Myr)

Figure 6


(a) 3 Myr before present – 7 clusters
Pliocene
(b) 6 Myr before present – 6 clusters
Miocene
(c) 9 Myr before present – 5 clusters
(d) 12 Myr before present – 6 clusters
(e) 15 Myr before present – 5 clusters
(f) 18 Myr before present – 5 clusters
(g) 21 Myr before present – 5 clusters
(h) 24 Myr before present – 5 clusters
Oligocene
(i) 27 Myr before present – 5 clusters