HOTSPOTS OF CENOZOIC TROPICAL MARINE BIODIVERSITY

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Abstract Hotspots of tropical marine biodiversity are areas that harbour disproportionately large numbers of species compared to surrounding regions. The richness and location of these hotspots have changed throughout the Cenozoic. Here, we review the global dynamics of Cenozoic tropical marine biodiversity hotspots, including the four major hotspots of the Indo-Australian Archipelago (IAA), western Tethys (present Mediterranean), Arabian Sea and Caribbean Sea. Our review supports the 'Hopping Hotspots' model, which proposes that the locations of peak biodiversity are related to Tethyan faunal elements and track broadscale shallow-marine habitats and high coastal complexity created by the collision of tectonic plates. A null

hypothesis is the 'Whack-A-Mole' model, which proposes that hotspots occur in habitats suitable for high diversity regardless of taxonomic identity or faunal elements. Earlier 'Centre-of' theories (e.g. centres of origin with diversity decreasing with distance from supposed areas of exceptionally high rates of speciation, for which easy connection to adjacent regions to the east and west is important) were based on the analysis of recent biotas with no palaeontological foundation, and may better explain diversity dynamics within a hotspot rather than those between hotspots. More recently, however, human disturbance is massively disrupting these natural patterns.

Introduction

Tropical oceans support several fold more biodiversity than any other marine region (Reaka-Kudla 1997, Bouchet et al. 2002, Plaisance et al. 2011), including the ~30% of all marine species found in coral reef ecosystems alone (Costello et al. 2015, Fisher et al. 2015). Biodiversity hotspots are areas that contain disproportionately large numbers of species (species richness) compared to surrounding regions (Jefferson & Costello 2020, Manes et al. 2021). For example, within the tropics and subtropics, the Indo-Australian Archipelago (IAA) is characterised by the highest marine species richness and endemicity for numerous taxonomic groups, such as corals, molluscs, crustaceans and fishes (Bouchet et al. 2002, Hoeksema 2007, Tittensor et al. 2010, Plaisance et al. 2011, Bellwood et al. 2012, Asaad et al. 2018a, b). However, the richness and geographical location of biodiversity hotspots have changed over the Cenozoic (last 66 Myrs [million years], the latest geologic era that has much better fossil records than the, older, Mesozoic and Paleozoic eras) (O'Dea et al. 2007, Renema et al. 2008, Yasuhara et al. 2017a, Di Martino et al. 2018).

Palaeontological studies of biodiversity hotspots have been conducted in the western Tethys, Arabian, Caribbean and Indo-Pacific regions. The western Tethys has a long history of palaeontological research and accumulation of fossil data (McKenzie 1982, 1991a,b, Popov et al. 2001, Harzhauser et al. 2002, Popov et al. 2002, 2004, Harzhauser et al. 2007). The Panama Palaeontology Project and subsequent studies have described Neogene (23.0–2.6 Ma [million years ago]) biodiversity dynamics of the Caribbean in detail (Coates & Collins 1999, Jackson & Johnson 2000, O'Dea et al. 2007, Johnson et al. 2008, Di Martino et al. 2018). The IAA has been studied less, despite being the location with the highest modern-day diversity (Renema et al. 2008, Di Martino et al. 2015, 2019, Johnson et al. 2015b, Yasuhara et al. 2017a, Harzhauser et al. 2018), although pioneering studies and re-investigations of their fossil collections and localities exist (e.g. Martin 1919, Gerth 1923, van der Vlerk & Umbgrove 1927, Gerth 1933, Kingma 1948, Keij 1966, Beets 1986, Leloux & Wesselingh 2009). Further palaeontological studies have been conducted recently by international collaborations, including the Throughflow Project (Reich et al. 2014, Di Martino et al. 2015, Johnson et al. 2015a, Kusworo et al. 2015, Santodomingo et al. 2015, 2016, Yasuhara et al. 2017a, Shin et al. 2019). In addition to palaeontological studies (Wilson & Rosen 1998, Renema et al. 2008), molecular studies have improved our understanding of the evolutionary processes and mechanisms behind the development of IAA hotspot (Williams & Duda Jr 2008, Bellwood et al. 2017). However, extinction in the ancient Caribbean Sea, western Tethys and Arabia (Johnson et al. 2008, Renema et al. 2008) has made it difficult to study the macroevolutionary dynamics of these ancient hotspots using molecular techniques alone. In addition, ongoing anthropogenic ecosystem degradation is making biodiversity studies increasingly difficult in the Anthropocene (Waters et al. 2016) by obscuring or even erasing the natural baseline condition (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003, Lotze et al. 2006, Halpern et al. 2008, 2015, 2019).

Renema et al. (2008) proposed the Hopping Hotspots model to explain the Cenozoic history of multiple biodiversity hotspots, arguing that the tropical biodiversity hotspot has migrated from the western Tethys via the Arabian Peninsula to the IAA during the Cenozoic (Renema et al. 2008).

The Caribbean region was not included in this model, although strong biogeographic ties between the Caribbean and Mediterranean existed until the end of the Oligocene (Cheetham 1968, Budd et al. 2011). Cenozoic biogeographic relationships (i.e. similarities and differences of faunal compositions) between these four (western Tethys, Arabian, IAA and Caribbean) hotspots have never been synthesized fully or updated since work in the 1960–1990s, which often had a stratigraphic rather than a biogeographic perspective (Adams 1967, McKenzie 1967, 1982, Adams et al. 1983, Adams 1987, McKenzie 1991a,b). These earlier studies also focused almost entirely on foraminifera and ostracods to the exclusion of other informative taxa. The extent to which human activities have degraded natural biodiversity patterns is also poorly established, complicating comparison of recent and fossil biogeographic patterns.

In short, a global synthesis of the Cenozoic history of tropical marine biodiversity and biogeography is still lacking, preventing a holistic understanding of the dynamics and mechanisms behind the regional waxing and waning of tropical biodiversity. Here we review the Cenozoic history of tropical biodiversity hotspots from a palaeontological perspective. Our main aims are to: (1) describe present-day total marine biodiversity patterns, including all coastal taxa, and assess their consistency with marine biodiversity patterns of groups with high fossilisation potential and good fossil records (such as bivalves and corals); (2) provide an in-depth and up-to-date review of the Cenozoic history of marine biodiversity and biogeography in the western Tethys, Arabian Sea, Indo-Australian Archipelago and Caribbean Sea; (3) synthesize the ecological and evolutionary dynamics of Cenozoic hotspots globally and their likely mechanisms and drivers; (4) summarise available evidence of human-induced degradation in the IAA and Caribbean regions; and (5) identify research opportunities and future directions for uncovering the underlying mechanisms driving the locations of hotpots through time. We mainly focus on Cenozoic marine patterns in the microfossil and macrofossil records such as ostracods, foraminifera, molluscs, corals and bryozoans. Here we firmly establish that palaeontological data are essential for understanding the current as well as ancient geographic distribution of biodiversity.

Present-day global biodiversity patterns

Global patterns and hotspot regions

Broadly speaking, marine species richness increases from high to low latitudes, referred to as the latitudinal biodiversity gradient (Tittensor et al. 2010, Chaudhary et al. 2016, 2017, Reygondeau 2019, Gagné et al. 2020, Rogers et al. 2020, Yasuhara et al. 2020b) (Figure 1). However, species richness is longitudinally heterogeneous within the relatively diverse tropics. The highest marine species richness is found in the IAA, with more diversity than in other tropical regions such as the Caribbean Sea and western Indian Ocean (Tittensor et al. 2010, Plaisance et al. 2011, Reygondeau 2019, Gagné et al. 2020, Rogers et al. 2020) (Figure 1). Species richness in the Caribbean is higher than in other areas in the Atlantic, but much lower than in the IAA hotspot (Tittensor et al. 2010, Rogers et al. 2020) (Figure 1). The Mediterranean Sea, which in the past represented the western Tethys hotspot, is no longer in the tropics (Leprieur et al. 2016). The Mediterranean does not currently have significant warm-water coral reef systems, but has more species than the adjacent Atlantic ocean (Costello et al. 2010) (Figure 1). The present-day Arabian region, including the Red Sea, Gulf of Aden and Persian Gulf, has lower biodiversity than the IAA (Figure 1) but higher biodiversity than the Caribbean for some taxa (e.g. Scleractinia; Veron et al. 2009) and comparable or somewhat lower biodiversity for other groups (e.g. fishes; Miloslavich et al. 2010, Sonnewald & El-Sherbiny 2017) (Figure 1). These trends, however, may be related to comparatively low sampling effort and high levels of endemism in the Arabian region (Sonnewald & El-Sherbiny 2017).
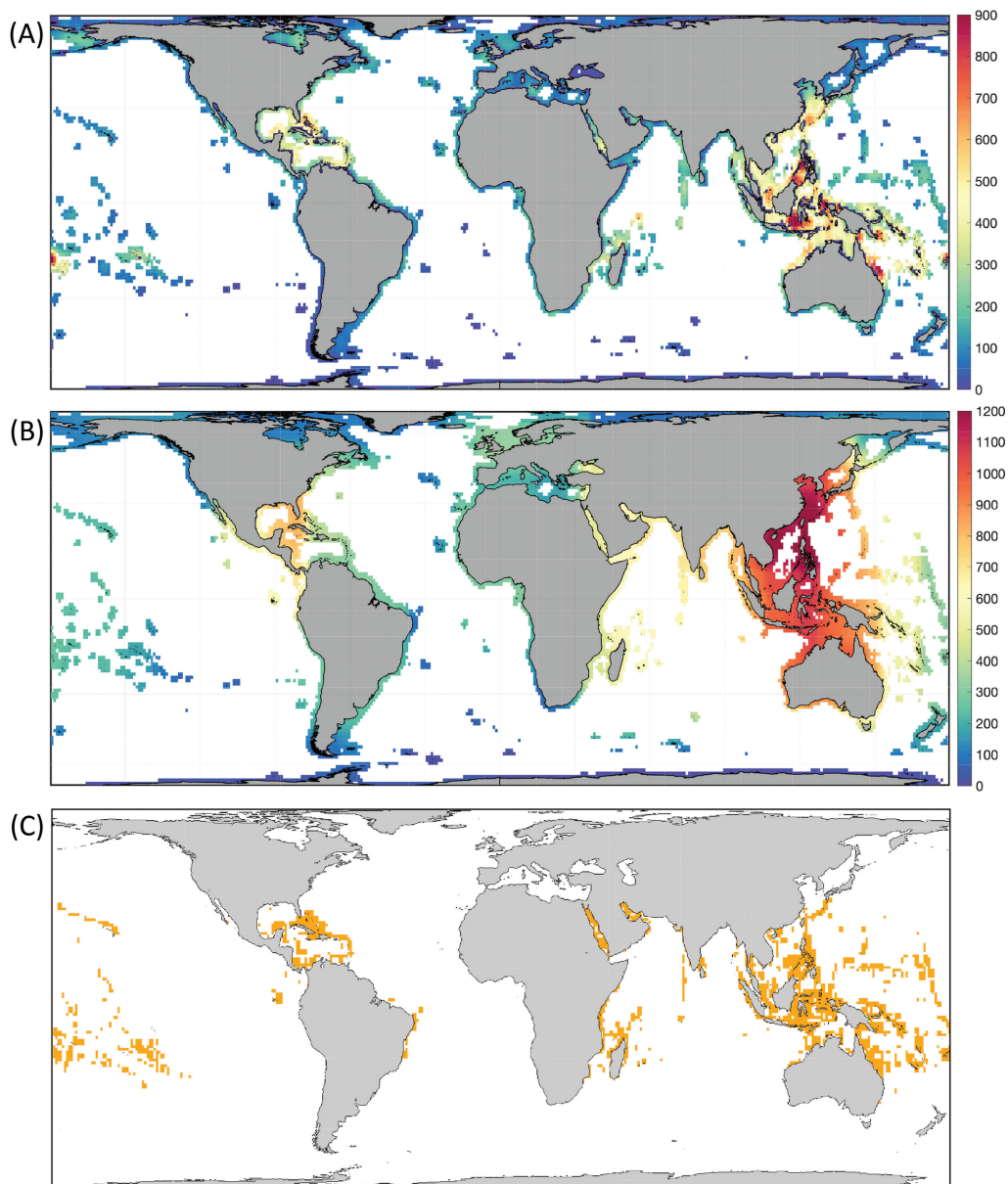
Figure 1 Present-day global biodiversity patterns. Species richness heat maps of (A) all coastal taxa (Reygondeau 2019, Reygondeau & Dunn 2019, Gagné et al. 2020, Reygondeau et al. 2020, Rogers et al. 2020) and (B) bivalves (Jablonski et al. 2013). (C) Coral reef distribution (orange) is shown to visualise habitat availability for tropical shallow-marine biodiversity (Zhao et al. 2020).

Fossilisation potential of global patterns

Among taxonomic groups with well-preserved fossil records, the most comprehensive synthesis of present-day biodiversity data is available from bivalves (Belanger et al. 2012, Jablonski et al. 2013), followed by reef corals (Hughes et al. 2002, Keith et al. 2013, Veron et al. 2015, Kusumoto et al. 2020). Bivalve and coral diversity show a distinct IAA hotspot and
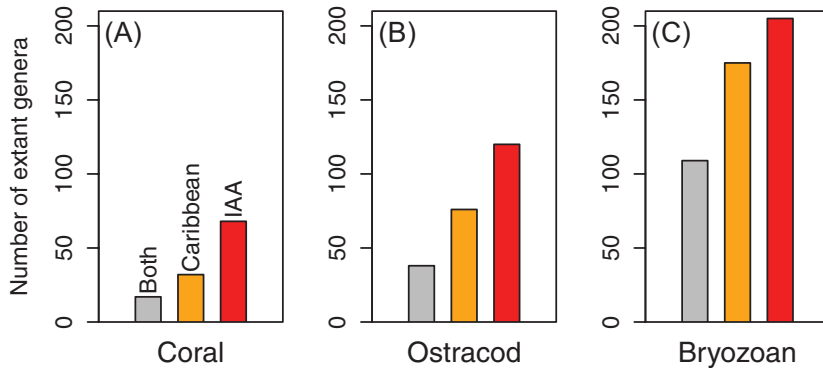
Figure 2 Comparison of IAA and Caribbean generic diversity for corals (Kusumoto et al. 2020) (A), ostracods (Yasuhara et al. 2017a and references therein, Chiu et al. 2020) (B), and bryozoans (data compiled in April 2020 from the website Recent and Fossil Bryozoa of Philip Bock, available at www.bryozoa.net) (C), illustrating richness of extant genera distributed in the Caribbean Sea (orange) and the IAA (red) as well as that of shared genera between the Caribbean Sea and IAA (grey). These data for taxonomic groups with high fossilisation potential consistently show higher extant diversity in the IAA than in the Caribbean Sea.

less diverse Caribbean Sea and western Indian Ocean (Veron et al. 2009, Jablonski et al. 2013) (Figure 1), patterns consistent with those of total marine and coastal biodiversity (Tittensor et al. 2010). Indeed, many additional taxonomic groups with a good fossil record (larger benthic foraminifera [LBF], ostracods and bryozoans) show higher diversity in the IAA than in the Caribbean (Figure 2), mirroring the pattern of total marine biodiversity. Taxonomic groups with a good fossil record are also known to show consistent biodiversity responses with other taxonomic groups (e.g. Jackson & Johnson 2000, Renema et al. 2008, Di Martino et al. 2018, Chiu et al. 2020). Thus, their fossil records may be reliable proxies for total tropical marine biodiversity trends prior to the timescale of modern observations.

History of major biodiversity hotspots

How has present-day tropical diversity emerged? To address this question, we review the regional Cenozoic history of one present-day (IAA), one waning (Caribbean) and two vanished (western Tethys and Arabian) biodiversity hotspots. Figure 3 shows the Cenozoic timescale and the names and ages of geological periods, epochs and stages, as well as names of palaeogeographical and palaeobiogeographical regions mentioned in this paper. A global summary of the Cenozoic events and biodiversity patterns are shown in Figures 4–7 and Table 1.

Vanished hotspots of the Tethys

Introduction

The Tethys Ocean included two Cenozoic biodiversity hotspots, the western Tethys and Arabia. Diversity in these regions is not high today, but they were the global centre of marine diversity during the early Cenozoic. These two hotspots have a dynamic Cenozoic history. Note that while the IAA and Caribbean regions were a part of the Tethys Ocean during the Paleogene (66–23 Ma), we treat these hotspots in the next sections separately, because these regions were hotspots primarily in the Neogene after the disappearance of the Tethys Ocean.

The Tethys was originally defined as an equatorial ocean that was present prior to the uplift of the Alpine-Himalayan mountain ranges (Suess 1893, Sengor 1985). The Tethys originated at the
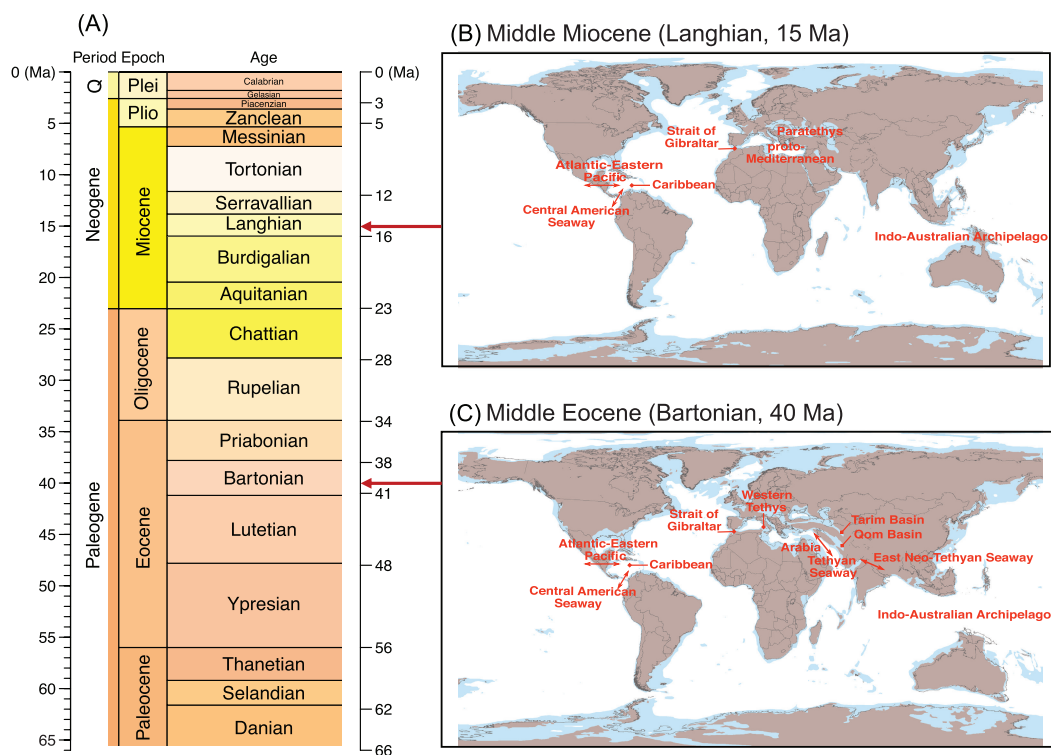
Figure 3 Geological timescale and (palaeo)geographical regions. (A) Cenozoic timescale (Walker et al. 2018, Gradstein et al. 2020). Overview of palaeogeographical and palaeobiogeographical regions on middle Miocene (B) and middle Eocene maps (C). Palaeogeographical maps (light blue denotes shallow-marine areas) based on Kocsis & Scotese (2021). Note that the east Neo-Tethyan seaway is not represented in the middle Eocene palaeogeographical map of Kocsis & Scotese (2021), but should have existed, because the Indian subcontinent had not yet collided with the Eurasian continent at that time (Harzhauser et al. 2002, Wang et al. 2020).

eastern edge of the Pangea supercontinent in the Permian with the drifting of the Cimmerian Plates away from Gondwana (Golonka 2002). Pangea broke apart during the Triassic and Jurassic, separating into Laurasia (North America and Eurasia) to the north and Gondwana (Antarctica, India, South America, Australia, Africa) to the south. This process opened a circumtropical marine connection between the Pacific and Atlantic Ocean basins across the Tethys.

The northward movement of the African, Indian and Australian plates resulted in a continuous narrowing of the vast Tethys Ocean since the Late Cretaceous (~80 Ma). This narrowing allowed water mass exchange at low latitudes between the Atlantic, Indian and Pacific oceans until the beginning of the Neogene (Harzhauser et al. 2007, Bialik et al. 2019). The western Tethys remained biogeographically connected to the Caribbean (west-central Atlantic Ocean) to the west and the east Tethys region (Indo and western Pacific) to the east until the end of the Paleogene (Cheetham 1968, Budd et al. 2011). Together, these regions constituted a broad Tethyan biogeographic realm that continued south as far as Southeast Asia and Madagascar during the Paleogene (Cowman & Bellwood 2013a, Hou & Li 2018, Yasuhara et al. 2019a) (Figure 3).

The Caribbean (western Atlantic or tropical American) region has been considered as its own distinct biogeographic unit (e.g. Harzhauser et al. 2002, Renema 2002, 2007). However, some Caribbean species had broad distributions from the east Tethys through the western Tethys to the Caribbean during the Eocene (e.g. Cheetham 1968, Givens 1989, Ivany et al. 1990, Matsumaru
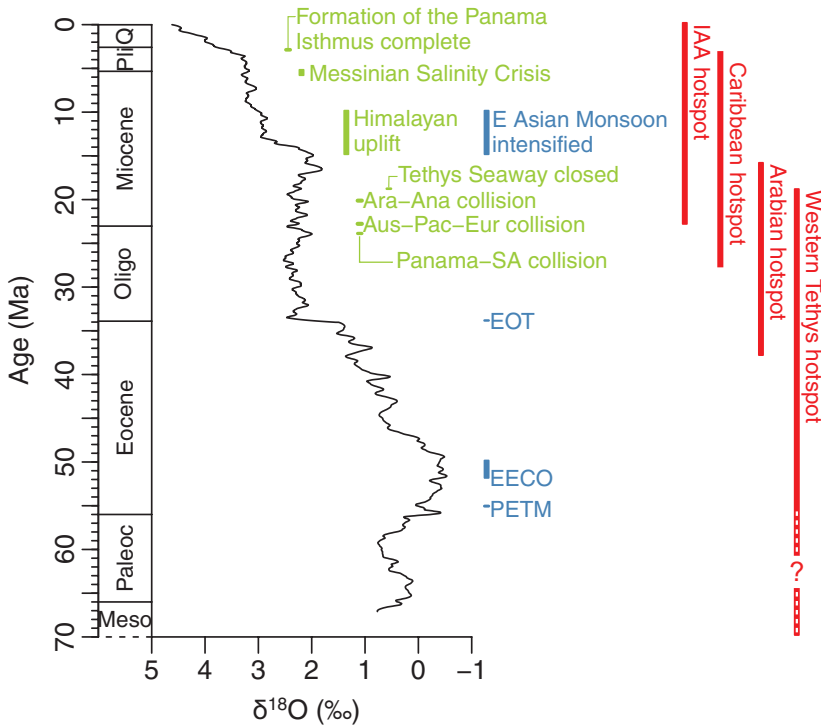
Figure 4 Cenozoic global changes and major events associated with biodiversity hotspots. Global deep-sea oxygen isotope records are from Westerhold et al. (2020). The figure is modified after Yasuhara et al. (2020a). Major tectonic-related events (green) include the Panama-South America (SA) collision (~24 Ma) (Farris et al. 2011), Australia-Pacific-Eurasia (Aus-Pac-Eur) collision (~23 Ma) (Renema et al. 2008), Arabia-Anatolia (Ara-Ana) collision (~20 Ma) (Renema et al. 2008), Tethys Seaway closure (~19 Ma) (Harzhauser et al. 2007, Yasuhara et al. 2019b), Himalayan uplift latest phase (15–10 Ma) (Tada et al. 2016), Messinian Salinity Crisis (5.96–5.33 Ma) (Krijgsman et al. 1999) and completion of the Formation of the Panama Isthmus (~3 Ma) (O'Dea et al. 2016, Jaramillo 2018). Major climatic events (blue) include Paleocene–Eocene thermal maximum (PETM, 55.5 Ma) (Cronin 2009), early Eocene climatic optimum (EECO, 52–50 Ma) (Cronin 2009), Eocene–Oligocene transition (EOT, ~34 Ma) (Cronin 2009) and late Miocene East Asian Monsoon intensification (15–10 Ma) (Tada et al. 2016). Biodiversity hotspot durations (red) include those of the western Tethys, Arabian, Caribbean and IAA hotspots (Figure 7, Table 1).

1996, Harzhauser et al. 2002, Shahin 2005, Renema 2007, Yamaguchi & Kamiya 2009, Budd et al. 2011, Yasuhara et al. 2019a). This broad circumtropical Tethys faunal element in the Eocene was characterised by a warm-water, tropical to subtropical fauna and flora that included taxa with broad geographic distributions (e.g. Harzhauser et al. 2002, 2007, Renema et al. 2008, Cowman & Bellwood 2013a, Hou & Li 2018, Yasuhara et al. 2019a). The faunal similarity between the western Tethys and the Caribbean in the Eocene varies among taxonomic groups. For example, similarity is substantial in gastropods (Harzhauser et al. 2002) but more limited in LBF (Renema 2002, 2007).

Western Tethys hotspot: Paleogene biogeography and biodiversity

Global tropical marine biodiversity peaked in the western Tethys (present Mediterranean) during the Eocene, at least when considering LBF (Renema 2007) (Figures 4–7). High diversity is also recorded for molluscan and ostracod faunas during the Eocene (Oppenheim 1894, 1896, 1901, 1909, 1912, Keij 1957, Ducasse et al. 1985, Guernet et al. 2012), but up-to-date and quantitative syntheses are lacking. Close to the Eocene/Oligocene boundary (~34 Ma), LBF suffered a large extinction
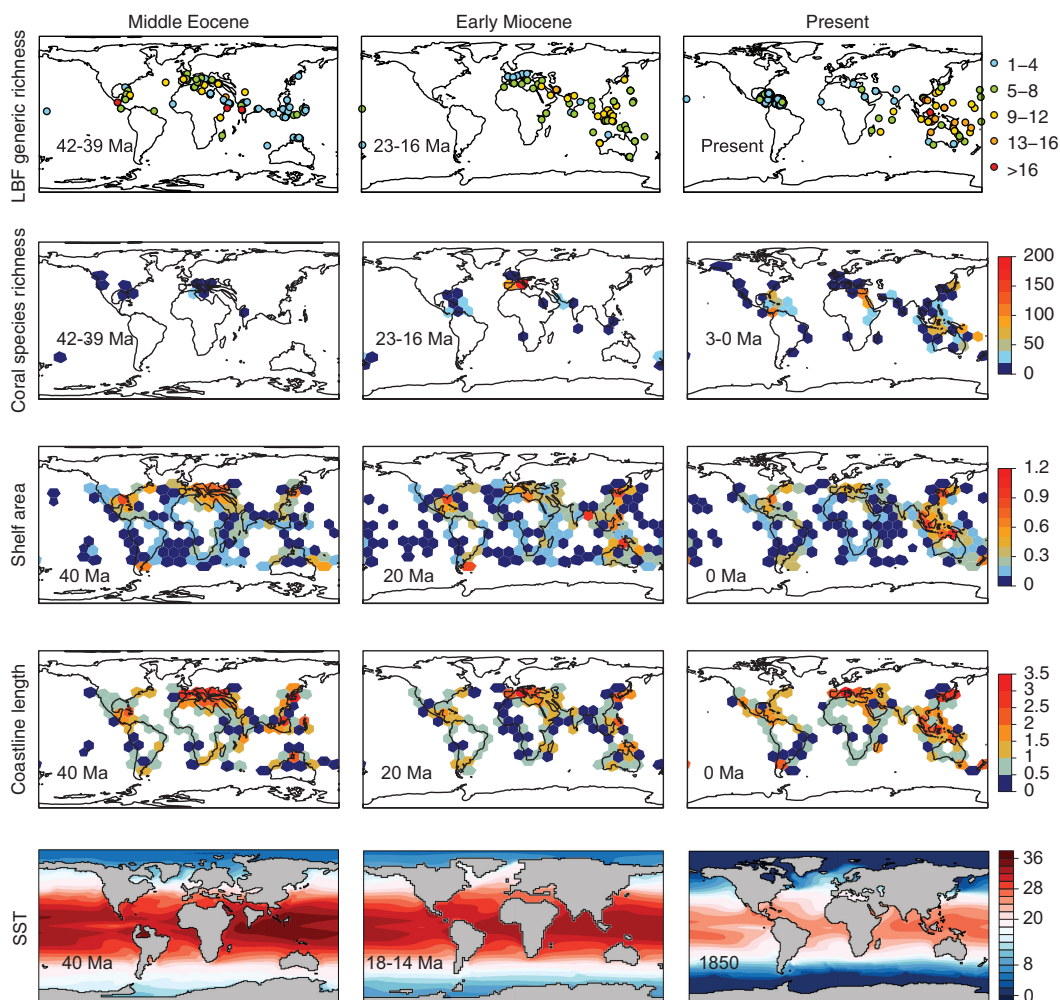
Figure 5 LBF diversity, coral diversity, shelf area, coastline length and sea surface temperature (SST) time slices. LBF data are based on Renema et al. (2008) with our own additional compilation: present (Culver and Buzas 1982 and references therein, also Buzas et al. 1977, De Araújo & De Jesus Machado 2008, Baker et al. 2009); Miocene and Eocene (Robinson 1974, de Mello e Sousa et al. 2003, Robinson 2003, Bowen Powell 2010, Baumgartner-Mora & Baumgartner 2016, Serra-Kiel et al. 2016, Cotton et al. 2018, 2019, Torres-Silva et al. 2019, Cotton Unpublished). Coral data were downloaded from Palaeobiology Database on 28 January 2021 (requested taxa: Scleractinia; identification resolution: species; filters: certain genus and species identification only, regular taxa only). See Section 'Role of shallow-marine habitat size and complexity' for the details of shelf area and coastline length reconstructions. Sea surface temperature reconstructions are from Hutchinson et al. (2018), Feng (2019) and Danabasoglu et al. (2020).

(Adams et al. 1986, Cotton & Pearson 2011) that marks the initial decrease in western Tethys diversity (Renema 2007) (Figures 6 and 7). LBF diversity continued to decrease through the Oligocene to early Miocene at ~19 Ma, leading to the final disappearance of the western Tethys hotspot (Figures 4, 6 and 7, see Section 'End of the Tethys').

Changing patterns in the generic composition of the western Tethys reef coral fauna suggest a gradual decrease in faunal exchange with the western Atlantic-Caribbean near the end of the
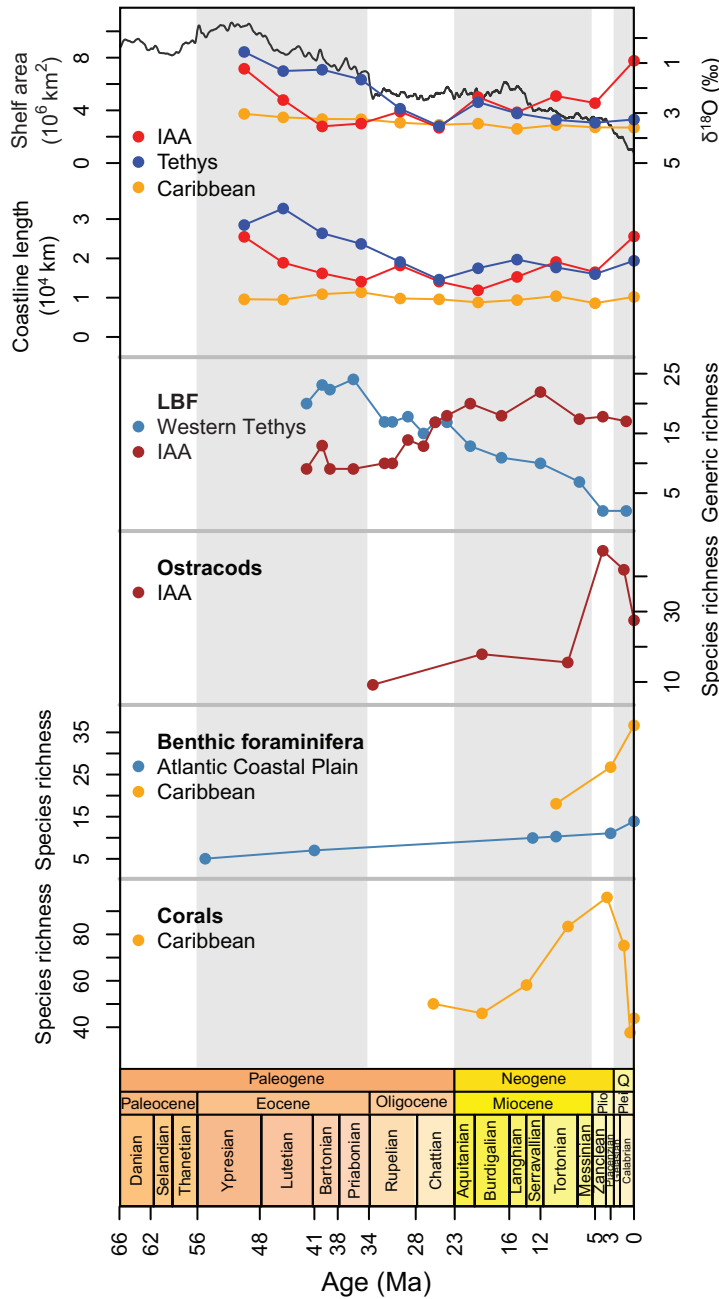
Figure 6 Diversity trends during the Cenozoic. Plots show (from top to bottom): shelf area (see Figure 10 and Section 'Role of shallow-marine habitat size and complexity' for details) and a global climate curve (Westerhold et al. 2020); coastline length (see Figure 10 and Section 'Role of shallow-marine habitat size and complexity' for details); and diversities of LBF (western Tethys and IAA, Renema 2007), ostracods (IAA, Yasuhara et al. 2017), benthic foraminifera (Fisher's alpha used for the species richness proxy; Caribbean with temperate north-western Atlantic as a reference; Buzas et al. 2002), and corals (Caribbean; Johnson et al. 2008, Chao et al. 2014). We followed Chao et al.'s (2014) method to calculate Hill numbers ($q=0$, minimum coverage) for the coral biodiversity estimates, using abundance data from Johnson et al. (2008).
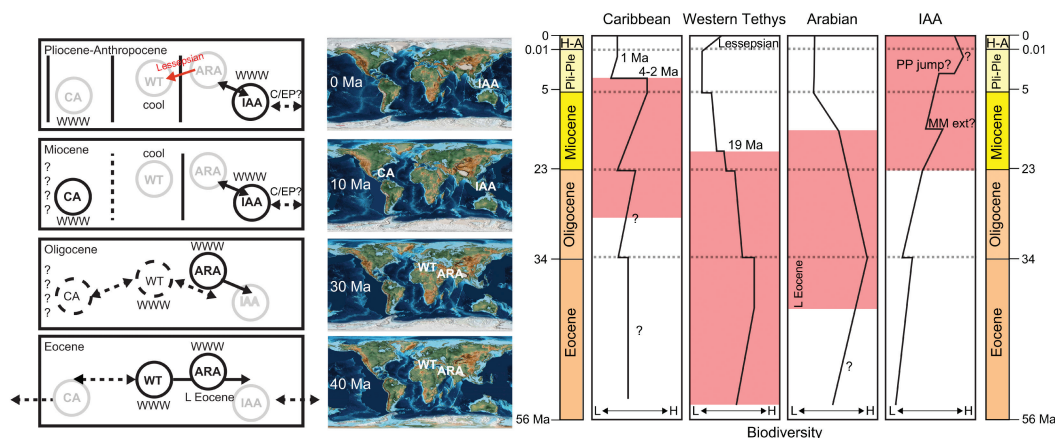
Figure 7 Hypothetical and schematic summary of global hotspots dynamics. (Left) Schematic diagrams summarising hotspots dynamics. 'WWW' indicates major continent-continent collision. Solid and dotted arrows: solid and limited connectivity/dispersal, respectively. Vertical solid and dotted bars: solid and limited separation, respectively. Questions mark indicate uncertainty. Solid circles: hotspot presence (dotted circle indicates limited diversity or uncertainty). Grey circle: hotspot absence. CA, Caribbean hotspot; WT, western Tethys hotspot; ARA, Arabian hotspot; IAA, Indo-Australian Archipelago hotspot; C/EP, central and/or eastern Pacific. (Middle) Palaeogeographical maps (Scotese 2016). (Right) Hypothetical summary of diversity trajectories of four biodiversity hotspot regions (mainly based on the taxonomic groups with good quantitative fossil records, i.e. LBF and ostracods, but also referred to other major taxonomic groups such as molluscs, corals and bryozoans). Biodiversity is shown in a relative sense (H, high; L, low). Red indicates a hotspot period. Question marks indicate uncertainty. Pli-Ple, Pliocene–Pleistocene; H-A, Holocene–Anthropocene. The Caribbean region is characterised by relatively low diversity in the Eocene, Eocene–Oligocene extinction, (uncertain) Oligocene diversification, Oligocene–Miocene coral loss (extinction event?), Miocene–Pliocene diversification (likely by increased habitat heterogeneity by diminished interoceanic seaways), major extinction event at ~4–2 Ma that basically eliminated this hotspot (likely via productivity collapse related to the establishment of the Panama Isthmus), rapid diversification since the extinction event (by oligotrophication and coral reef development; magnitude uncertain) and stable diversity for the last one Myrs. The Western Tethys region is characterised by high Eocene diversity, Eocene–Oligocene extinction, gradual diversity decline in the Oligocene (via suitable habitat decline; the hotspot shifts to Arabia in the late Eocene–Oligocene), Oligocene–Miocene extinction, final disappearance of the hotspot at ~19 Ma (by the final closure of the Tethys Seaway), further diversity decline in the middle and late Miocene (by global and regional cooling), Miocene–Pliocene (Messinian) extinction and diversity increase by Lessepsian migration from the Indian Ocean. The Arabian region is characterised by Eocene diversification, high diversity in the late Eocene, high but declining Oligocene diversity, and Miocene diversity decline with final hotspot disappearance in the middle Miocene (by habitat loss due to the final closure of the Tethys Seaway). The IAA is characterised by low (but increasing) Eocene diversity, Eocene–Oligocene extinction, Oligocene diversification, hotspot establishment at the early Miocene (~23 Ma; by increased suitable habitats by the collision), strong Miocene diversification punctuated by the middle Miocene extinction (MM ext; at least in LBF), Pliocene–Pleistocene diversity jump (the PP jump, related to cyclic glacial-interglacial sea-level changes; exact timing uncertain), and (uncertain) recent diversity decrease (by Anthropocene human-induced degradation or large late Pleistocene glacial-interglacial sea-level changes, at least in ostracods). See main text and Table 1 for further details.

Oligocene (Perrin 2002, Perrin & Bosellini 2012). This decrease is considered to reflect a major oceanographical change in the Central Atlantic, which led to the breakup of pan-tropical ocean circulation (Perrin 2002, Perrin & Bosellini 2012). Consistent with the corals, the fossil record of LBF shows the last Caribbean-western Tethys faunal exchange during the Oligocene at ~32 Ma (BouDagher-Fadel & Price 2010). The same is true of bryozoans (Cheetham 1968). Molecular phylogenies of scleractinian corals previously classified in the families Faviidae and Mussidae, however,

Table 1 Summary of the Cenozoic tropical biodiversity hotspots

	Western Tethys	Arabian	IAA	Caribbean	Remarks
Eocene	Hotspot. But Arabian diversity became higher than the Eocene. Marginal basins such as the Tarim Basin and east Neo-Tethyan seaway had rich marine faunas, but with relatively low diversity.	Hotspot. Especially in the late Eocene, diversity was higher than the western Tethys. Faunal connection with the western Tethys.	Non-hotspot. Temperature too high?	Non-hotspot? Temperature too high?	Certain faunal elements show circumtropical distribution, indicating certain connection of all of these hotspots in the Eocene. But note that degree of pandemism/endemism depends on taxonomic groups and LBF shows high endemism and large difference between western Tethys and Caribbean faunas.
Oligocene	Extinction at E/O. Transition to non-hotspot. Paratethys Sea appeared at around the E-O boundary; enhancement of fragmentation of broad Tethys region.	Hotspot. But molluscan data indicate unstable/hypersaline environments in the late Oligocene. Decreased faunal connection with the western Tethys in the late Oligocene.	Non-hotspot. Extinction at E/O.	Extinction at E/O. Initiation of suitable habitat and so hotspot. Reef loss at O/M.	The faunal connection between the western Tethys and Caribbean is more limited compared to the Eocene, but still exists by the end of the Oligocene, even in LBF that show higher endemism than other organisms.
Miocene	Closure of the Tethyan Seaway (19 Ma) finally eliminated this hotspot. Cooling and perhaps Messinian Salinity Crisis (5.96–5.33 Ma) further decreased the diversity of Proto-Mediterranean fauna at the end of the Miocene.	Hotspot sustained by the middle Miocene. Faunal connection with the IAA. Then hotspot gradually disappeared by the middle-late Miocene due to habitat loss by the Arabia-Eurasia collision. Increasingly unstable/hypersaline environment in the early Miocene.	Hotspot initiation at ~23 Ma due to the collision of Australia with Pacific arcs and the Southeast Asian margin. End mid-Miocene (~11.6 Ma) extinction (in LBF).	Hotspot. High productivity. Mio-Pliocene diversification.	In the early Miocene, the Indian Ocean showed strong provincialism with 4 different provinces, in contrast to the homogenous fauna throughout the Indian Ocean for the last 10 million years from the late Miocene to the present. Basic biogeographic distributions have been similar for the last 10 million years.
Plio-Pleistocene	Non-hotspot. Non-tropical and likely too cold.	Non-hotspot.	Hotspot. Diversity jump via biological pump; successive cycles of sea-level change caused repeated habitat disconnection and reconnection. Indonesian Throughflow restriction from 10 to 4.4 or 1.6 Ma may have also allowed diversification.	Hotspot finally eliminated by the extinction event at ~4–2 Ma; productivity collapse and delayed extinction. Final closure of shallow-marine connection of the Central American Seaway (3 Ma). Reef proliferation and diversity increase since 2 Ma.	Exact timing of Plio-Pleistocene diversity jump remains elusive.
Holocene/Anthropocene/present	Non-hotspot. Non-tropical. Too cold. Lessepsian migration.	Non-hotspot.	Hotspot. Modern diversity and distribution likely affected by Anthropogenic forces (aka reef ecosystem degradation), but data deficient.	Reef proliferation and diversity increase since 2 Ma. Modern diversity and distribution affected by Anthropogenic forces (aka reef ecosystem degradation). Data deficient to quantify the anthropogenic diversity loss.	A subordinate centre of coral reef biodiversity in the northern Mozambique Channel between East Africa and Madagascar in the Indian Ocean.

indicate a deeper divergence between the dominant Atlantic and Indo-West Pacific lineages before the end of the Eocene (= before ~34 Ma) that had been obscured by conventional (only based on macromorphological characters) coral taxonomy (Fukami et al. 2004, Budd et al. 2012, 2019).

Marginal basins of the Tethys

Marginal basins of the Tethys show lower biodiversity compared to the core western Tethys hotspot in general (Renema et al. 2008). The Paratethys Sea (Figure 3) originated around the Eocene/Oligocene boundary (~34 Ma) as a northern satellite basin of the Tethys Ocean due to the uplift of the Alpine mountain chains and disintegrated during the Pliocene. The sea reached maximum extent during the early Miocene and stretched from the Rhône Basin in France towards Inner Asia (Rögl 1998) (Figure 3). During the Oligocene–Miocene, convergence of the Afro-Arabian and Eurasian plates initiated a complex pattern of changing seaways and land bridges between the eastern and western Tethys Ocean and the Paratethys Sea. These palaeogeographical changes were amplified by sea-level fluctuations in the range of ~50–60 m associated with Antarctic ice-sheet dynamics at the time (Harzhauser et al. 2007, Reuter et al. 2009, Miller et al. 2020). The Paratethys Sea is characterised by moderate biodiversity, outside of the core Tethyan hotspots of the western Tethys and Arabia, at least in LBF (Renema et al. 2008). However, the Paratethys Sea has a rich fossil record (Walkiewicz 1977, Radwańska 1984, Stolarski 1991) and harboured high biodiversity, for example, of gastropods (Baluk 1975, Bałuk 1995, 2006, Scarponi et al. 2015), as documented for recently revised taxonomic groups (Harzhauser et al. 2002, Harzhauser & Landau 2017, 2019, 2021a, b).

The Tarim Basin (Figure 3; in the western part of Xinjiang province, north-western China) was a semi-enclosed sea and a north-western branch of the Tethys seaway in the Paleogene before the establishment of the Paratethys Sea (Xi et al. 2016). The Tarim Basin fostered a rich marine invertebrate and microfossil fauna in the Paleogene but disappeared due to marine regression by the end of the Eocene (Bosboom et al. 2014, Cao et al. 2018, Jiang et al. 2018). The biodiversity of this sea is not well quantified but does not seem high judging from published data (Bosboom et al. 2014, Cao et al. 2018, Jiang et al. 2018).

The eastern Neo-Tethyan seaway (Figure 3) is the shallow-marine basin between the Eurasian continent and Indian sub-continent before the India-Asia collision (Figure 3). This seaway is characterised by relatively low LBF and ostracod biodiversity during the Eocene (Renema et al. 2008, Wang et al. 2020) and remained opened until at least ~36 Ma (Wang et al. 2020).

Arabian hotspot: late Eocene–Miocene

Renema et al. (2008) considered the Arabian hotspot to be distinct from the western Tethys hotspot from the late Eocene into the Miocene. During the late Eocene, LBF biodiversity was highest in the Arabian region (Renema et al. 2008, Serra-Kiel et al. 2016) (Figure 7). Indeed, even in the late middle Eocene (42–39 Ma), some Arabian sites record higher LBF diversity than those of the western Tethys based on our new data compilation (Figure 5). Arabian biodiversity remained highest during the middle Miocene, while western Tethys biodiversity had already diminished by that time (Renema et al. 2008) (Figures 4 and 7). The Arabian hotspot shares faunal elements with the western Tethys hotspot in the late Eocene and with the IAA hotspot in the Miocene (Renema et al. 2008) but also exhibits endemism in the Eocene (Lunt 2003), Oligocene and Miocene (Harzhauser et al. 2007, Ozcan & Less 2009).

Restriction and closure of the Tethyan Seaway: the demise of the Arabian hotspot

Marine connections through the Tethyan Seaway became gradually restricted from the late Oligocene to the early Miocene as detailed below. In the late Oligocene (Chattian, 28–23 Ma), gastropod faunas from the Kutch Basin (northwestern India, northern coast of the eastern Tethys) indicate a moderate, but still traceable, faunal exchange via the Tethyan Seaway with the western Tethys (Harzhauser et al. 2009). However, comparison of molluscan faunas from the late Oligocene

(Chattian) Warak and earliest Miocene (Aquitanian) Ghubbarrah formations in south-eastern Oman with coeval faunas from north-western India and Pakistan reveals the initial blockage of dispersal pathways for the shallow-marine biota along the Afro-Arabian margin (Harzhauser 2007, Harzhauser et al. 2009).

Along with this biogeographic development, extensive parts of the Arabian shelf sea became increasingly restricted in the south-eastern Oman region during the late Oligocene and finally emerged in the earliest Miocene (early Aquitanian, ~22.5 Ma), linked to rifting cessation and commencement of seafloor spreading in the Gulf of Aden at that time (Reuter et al. 2008). The dynamic interplay between tectonics and sea-level caused the stepwise interruption of the marine connection (Tethyan Seaway) between the western and eastern Tethys in the region that later become the Zagros Mountains and Mesopotamia (Arabia) during the early to middle Miocene (Harzhauser et al. 2007). Frequent changes from normal marine to hypersaline facies are documented in the late Oligocene–early Miocene Asmari Formation, which was deposited on a carbonate platform in the foreland of the Zagros orogenic belt (Iran), representing the inner part of the Tethyan Seaway (Mossadegh et al. 2009). Following the general shallowing-upward trend in the Asmari Formation, a change from normal marine to hypersaline conditions occurred during the late Oligocene (late Chattian) (Mossadegh et al. 2009). Hypersaline conditions with episodes of even higher salinity followed during most of the early Miocene (Aquitanian) (Mossadegh et al. 2009). Such a dynamic environment is unlikely to sustain high-level biodiversity. Larger benthic foraminiferal, gastropod and bivalve evidence indicates that the Arabian biodiversity hotspot finally collapsed in the middle or late Miocene as a result of habitat loss largely caused by regional uplift of the Arabia-Eurasia collision and the closure of Tethyan Seaway (Kay 1996, Harzhauser et al. 2007, Renema et al. 2008).

End of the trans-Tethyan marine connection

In the north-eastern sector of the Tethyan Seaway (Eurasian margin), the marine gateways to the Qom Basin (central Iran; Figure 3), which was connected to the western Tethys and Tethyan Seaway, gradually ceased during the early Miocene (Aquitanian and early Burdigalian) due to the compressive tectonic regime (Reuter et al. 2009). This favoured deposition of evaporites in the basin during the third-order sea-level lowstands at 21.4 and 20.4 Ma (Reuter et al. 2009). It is therefore assumed that the total breakdown of western Tethys connectivity in Aquitanian gastropod assemblages from SE Oman (Harzhauser 2007) and north-western India (Kutch Basin; Harzhauser et al. 2009) and in the Aquitanian–Burdigalian echinoid fauna of southern Iran (Hormuz Strait; Kroh et al. 2011) was related to an excessively saline environment throughout the Tethyan Seaway (Reuter et al. 2009). This saline environment interrupted east–west dispersal of shallow-marine biota such as molluscs and corals (Reuter et al. 2009). A shift back to normal marine conditions took place during the latest Aquitanian in the Zagros Basin and was followed by frequent changes from normal marine to slightly hypersaline in the early Burdigalian (Mossadegh et al. 2009). Although this phase coincided with the re-appearance of western Tethys gastropod taxa in northwestern India (Kutch Basin; Harzhauser et al. 2009), the Burdigalian gastropod faunas of southern Iran (Makran) and of southwestern India (Kerala Basin) exhibit no faunal affinity to the western Tethys (Harzhauser et al. 2007, Harzhauser 2014) (Figure 8). In addition, the Mediterranean and Indo-Pacific reef coral faunas shared no species after the Aquitanian (McCall et al. 1994, Schuster & Wielandt 1999, Perrin & Bosellini 2012). This lack of faunal relations point to considerable dispersal limitation via temporary and rather ineffective dispersal pathways from the western to the eastern Tethys during the Burdigalian. In line with this biogeographic pattern, the trans-Tethyan marine connection was finally interrupted during the Burdigalian third-order sea-level low stand at 19.2 Ma (Reuter et al. 2009) (Figures 4 and 7). The progressive narrowing of the Tethyan Seaway culminated in the extensive distribution of terrestrial and hypersaline sedimentary facies in the Iranian Qom, Esfahan-Sirjan and Zagros basins at the end of the Burdigalian (Reuter et al. 2009). Development of these facies documents the
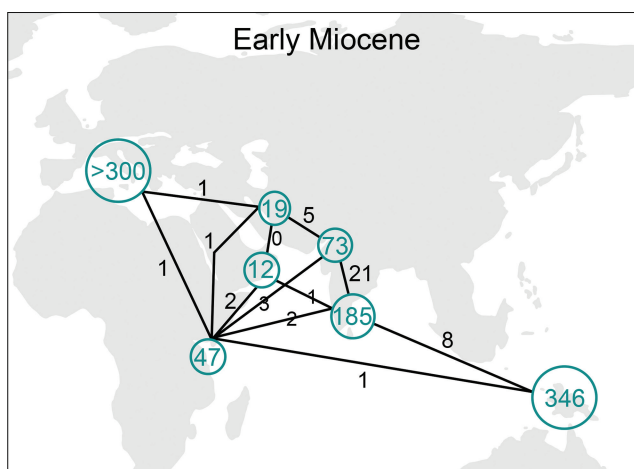
Figure 8 Diversity distribution of Early Miocene gastropod faunas. The numbers in the circles indicate the numbers of species described. Numbers over the lines indicate the number of shared species between regions. The pattern suggests a strong provincialism. Data from Harzhauser (2007, 2009, 2014), Harzhauser et al. (2009, 2017) and Leloux and Wesslingh (2009). Palaeogeographical map for 20 Ma and from Kocsis and Scotese (2021).

emergence of the *Gomphotherium* Landbridge at ~19 Ma, which allowed for the first exchange of terrestrial biota between Eurasia and Africa, but formed a biogeographic barrier for marine organisms (Harzhauser et al. 2007, 2009, Reuter et al. 2009). Although eustatic sea-level rise related to the middle Miocene climatic optimum (MMCO), a global warming event at ~17.0–14.5 Ma (Figure 4), might have re-opened the seaway for a short time via the Mesopotamian Trough (Rögl 1998, 1999), biogeographic separation between Mediterranean and Indo-West Pacific shallow-marine faunas persisted until the opening of the Suez Canal and the Lessepsian migration (Por 1978, Harzhauser et al. 2007, Rilov & Galil 2009, Perrin and Bosellini 2012, Albano et al. 2021).

End of the Tethys

With the final closure of the Tethyan Seaway during the early Miocene (~19 Ma; Harzhauser et al. 2007), the western Tethys vanished and gave rise to the proto-Mediterranean Sea (Harzhauser et al. 2002) (Figures 4–7). Some original western Tethys biota such as tridacnine bivalves (Harzhauser et al. 2008), strombid gastropods (Harzhauser et al. 2007), *Parascolymia* corals (Reuter et al. 2015) and Platinistidae dolphins (Barnes 2002) migrated into the eastern Tethys prior to the closure of the Tethyan Seaway and contribute to the enormous present-day biodiversity of the Indo-West Pacific (Figure 9). Generic richness of zooxanthellate corals markedly declined in the Mediterranean reef coral province during the Miocene. The reason for the decline in reef coral diversity was likely regional climate cooling from tectonically-induced northward shift of the Mediterranean region and global climatic change (Bosellini & Perrin 2008, 2010, Perrin & Bosellini 2012, 2013). This gradual cooling in the Miocene caused the disappearance of almost all zooxanthellate colonial corals (except for *Cladocora caespitosa*) from the Mediterranean Sea and the end of the (sub)tropical Mediterranean coral reef province until the onset of the Pliocene (Perrin & Bosellini 2013, Vertino et al. 2014). The geologically short-term (5.96–5.33 Ma) Messinian Salinity Crisis (MSC: Figures 4 and 7) additionally caused a massive disruption to marine life in the Mediterranean Sea, but small *Porites* reefs were still present in the Messinian post-evaporitic Terminal Complex in the western Mediterranean Sea (Vertino et al. 2014).

With the closure of the Tethyan Seaway, the Indian Ocean became a geographic entity in the Miocene. The data on Oligocene and early Miocene shallow-marine gastropods from central (Qom
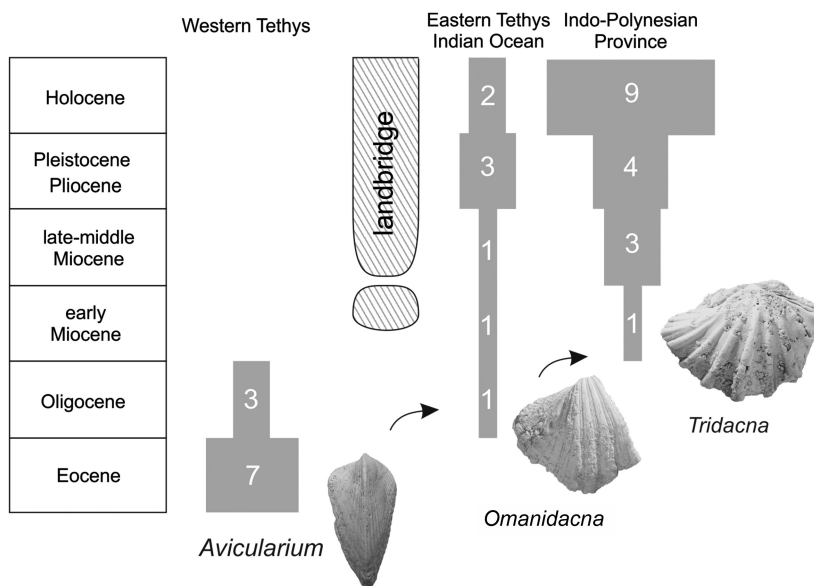
Figure 9 Evolutionary history of tridacnine bivalves. They evolved during the Eocene in the north eastern Atlantic and the western Tethys and spread to the eastern Tethys during the Oligocene. Numbers indicate species richness. Data from Harzhauser et al. (2007).

Basin) and southern (Makran) Iran, Oman, Tanzania and northwestern (Kutch Basin) and south western (Kerala Basin) India document a complex pattern of faunal relations among these areas with high rates of endemism (Harzhauser 2007, 2009, Harzhauser et al. 2009, Harzhauser 2014, Harzhauser et al. 2017) (Figure 8). Thus, a distinct early Miocene bioprovincialism can be postulated during the switch from the eastern Tethys to the Indian Ocean with a Central East African Province, an east African-Arabian Province, a western Indian Province and a Proto-Indo-Polynesian Province in the east (Harzhauser 2007, 2009, 2014). Correspondingly, Oligocene and early Miocene reef coral faunas from eastern Africa (Somalia) show a low similarity with southern and central Iran and no relation to Indonesia at species level (Reuter et al. 2019). This early Miocene palaeobiogeographical pattern differs fundamentally from the pattern of the Indian Ocean as a rather homogeneous single province that persisted during the last 10 Myrs (late Miocene–present; Costello & Chaudhary 2017, Kocsis et al. 2018).

Present-day Indian Ocean

Today, reef coral diversity peaks in the IAA, but a subordinate centre of coral reef biodiversity (across diverse taxa such as corals, mantis shrimps and LBF) occurs in the northern Mozambique Channel between east Africa and Madagascar (Reaka et al. 2008, Obura 2012, Veron et al. 2015, Förderer et al. 2018, Kusumoto et al. 2020) (Figure 1). This subordinate centre is maintained by the inflow of the South Equatorial Current, which brings coral larvae from the IAA (Obura 2012). The high compositional similarity at species level between a late Miocene (~7–6 Ma, Messinian) reef coral fauna from southern Tanzania (Rovuma Basin) and the living coral fauna of eastern Africa shows that the community structure of reef corals remained largeley unchanged in this area since the late Miocene (Reuter et al. 2019). The different biogeographic affinities of Oligocene–early Miocene and late Miocene–recent east African coral faunas indicate that this regional centre of reef coral biodiversity

in the western Indian Ocean did not exist in its present form during the early Miocene. Its high diversity may have developed by the faunal connection of the region to the IAA during the middle to late Miocene (Reuter et al. 2019). The end of bioprovincialism corresponds with the onset and intensification of the Miocene Indian Ocean Equatorial Jet between 14 and 9 Ma in response to the narrowing of the Indonesian Gateway (Gourlan et al. 2008). This precursor of the South Equatorial Current is thought to have caused high biogeographic connectivity across the Indian Ocean (Reuter et al. 2019) and, thus, facilitated the formation of the east African hotspot of reef coral diversity as an offshoot of the Coral Triangle (Reuter et al. 2019).

Strengths, weaknesses and opportunities

Our knowledge of the western Tethys and Arabian hotspots is high for certain taxonomic groups such as molluscs, but there is no synthetic quantification of biodiversity trends in space and time. Renema et al. (2008) used LBF as a proxy, but the resolution of their palaeobiogeographical maps (regarding number of time slices and data points) was not sufficient to show details throughout the broad Tethys region. Consequently, we do not know when and how peak biodiversity shifted from the western Tethys to Arabia. Details for marginal regions such as the Tarim Basin, Qom Basins, and Paratethys Sea are also not well resolved. There is a pressing need for rigorous standardised assessments for other taxonomic groups, including molluscs, corals, bryozoans and ostracods.

Another major problem in understanding these hotspots is a dearth of information about Paleocene biogeography and biodiversity that preceded the above transitions. Some migration events are known during the Paleocene–Eocene transition (Speijer et al. 2012, Beasley et al. 2021). For example, the ostracod genus *Alocopocythere* is known to disperse from west Africa to the western Tethys region, and poleward shift is known in several taxa such as planktonic foraminifera (e.g. *Acarinina sibaiyaensis*) and the dinoflagellate cyst genus *Apectodinium*. However, aside from these events, we lack synthesis of Paleocene Tethys palaeobiogeography, with studies focusing mostly on taxonomy of individual taxa (e.g. in ostracods: Al-Furaih 1980).

Indo-Australian Archipelago (IAA)

Miocene origin

The Indo-Australian Archipelago region began to host substantial biodiversity (hotspot initiation) from the early Miocene (~23 Ma ago), following relatively low diversity in the Paleogene (Renema et al. 2008, Bellwood et al. 2012, Yasuhara et al. 2017a, Prazeres & Renema 2019) (Figures 4–7). With senescence of the western Tethys hotspot, narrowing of the Tethyan Seaway and contraction of the tropics to lower latitudes after the Eocene (Renema et al. 2008, Bribiesca-Contreras et al. 2019), Tethyan relicts of corals and reef fishes are believed to have shifted their distribution to the IAA during the Oligocene–Miocene. Both groups exhibited rapid lineage diversification in the IAA (Bellwood et al. 2017), resulting in the formation of the modern IAA faunal province (Titterton & Whatley 1988, Keith et al. 2013, Costello et al. 2017, Kocsis et al. 2018). After extinction of a number of widespread and long-ranging taxa at the Eocene/Oligocene boundary (Renema 2007, Cotton et al. 2014, Prazeres & Renema 2019), the diversity of LBF increased in the Oligocene and plateaued from the early Miocene to the present (Adams 1965, Adams et al. 1986, Renema 2007, Prazeres & Renema 2019) (Figures 6 and 7), with a change in faunal characteristics in the early Miocene (rise of the modern fauna) and highest diversity in the middle Miocene, where both the 'old faunal' and an already upcoming modern fauna merged (Renema et al. 2015, Prazeres & Renema 2019). After, LBF experienced a substantial extinction during the middle Miocene (~11.6 Ma) (Renema 2007) (Figures 6 and 7). Fossil corals and ostracods show substantial Miocene diversification (Renema et al. 2008, Johnson et al. 2015b, Renema

et al. 2016, Yasuhara et al. 2017a) (Figures 6 and 7). Based on molecular data, the Miocene origin of the vast majority of modern fish genera has been believed to have played an important role in the development of the IAA hotspot (Bellwood et al. 2017). These lines of evidence consistently support an early Miocene initiation of the IAA hotspot. However, IAA diversity may have been lower than Caribbean diversity at that time (Di Martino et al. 2018), and Oligocene–early Miocene fossil data remain sparse in the IAA region (McMonagle et al. 2011, Reich et al. 2014, Yasuhara et al. 2017a), which means taphonomic or sampling biases may affect observed diversity patterns. Indeed, Paleogene IAA diversity was already high in LBF that have more complete fossil records compared to other taxonomic groups (Renema 2007). Although numerous molluscs have been described from the Miocene of the IAA (e.g. Indonesia, Leloux & Wesselingh 2009, see Harzhauser et al. 2018 for a literature survey), collecting is still fragmentary and biogeographic analyses and critical revisions are largely lacking.

The apparent Oligocene–Miocene increase in IAA shallow-marine biodiversity coincided with tectonic activity that formed the complex island archipelagos of the IAA region, with a dynamic mosaic of oceanic arc and microcontinental fragments (Renema et al. 2008, Leprieur et al. 2016, Hall 2017). In particular, the collision of the south-east Eurasia margin with the Australian and Pacific plates at ~23 Ma was critical in developing this vast area of complex habitat (Kuhnt et al. 2004, Renema et al. 2008, Hall 2011). Thus, an extensive array of shallow seas provided suitable habitats for corals on shallow carbonate platforms, and the geographic complexity of this region provided barriers for vicariance events, which may have together facilitated the colonisation of Tethyan relicts and diversification of new lineages as suggested by molecular studies (Pandolfi 1992, Dornburg et al. 2015, Bellwood et al. 2017, Bribiesca-Contreras et al. 2019). An example of a vicariance event within the IAA is the biogeographic separation of the late Miocene gastropod fauna from the South China Sea from those of the Java Sea, the Makassar Strait and the Celebes Sea (Harzhauser et al. 2018). This biogeographic pattern was triggered by a landmass stretching from the Asian mainland across Borneo from the Oligocene to the Pliocene (Lohman et al. 2011). With the formation of the IAA hotspot, the basic framework of modern biodiversity and biogeographic patterns in tropical oceans emerged in the Miocene (Titterton & Whatley 1988, Renema et al. 2008, Keith et al. 2013, Bellwood et al. 2017) (Figures 5 and 7).

Pliocene–Pleistocene biodiversity jump

Another important period of significant diversity increase in the IAA hotspot occurred during the Pliocene–Pleistocene, known as the Pliocene–Pleistocene biodiversity jump (Hoeksema 2007, Renema et al. 2008, Renema 2010, Bellwood et al. 2012, Yasuhara et al. 2017a, Shin et al. 2019) (Figures 6 and 7). In terms of corals and reef fishes, both fossil and phylogenetic evidence indicates rapid species-level diversification during this interval (Bellwood et al. 2017). Molecular evidence further suggests that coral reef biodiversity approximately doubled in the last 5 Ma (Bellwood et al. 2017). In addition, microfossil groups, including ostracods and LBF, show a consistent Pliocene–Pleistocene diversity increase (Renema 2007, Yasuhara et al. 2017, Shin et al. 2019). During the Pliocene and Pleistocene, the IAA hotspot played a more important role as the macroevolutionary source from which shallow-marine lineages diversified and dispersed into the Indian Ocean and Central Pacific regions (Cowman & Bellwood 2013b, Cowman et al. 2017). It is widely recognised that Pliocene–Pleistocene eustatic sea-level fluctuations are the most important mechanism of diversity increases (Bellwood et al. 2005, Briggs 2005, Hoeksema 2007, Bellwood et al. 2012, Yasuhara et al. 2017a). Successive cycles of sea-level change caused repeated disconnection and reconnection of small marine basins during lowstands and highstands, which in turn influenced habitat area and affected ocean currents within the geographically complex IAA region through a relatively short geological time (Pandolfi 1992, Hoeksema 2007, Bellwood et al. 2012, Yasuhara et al. 2017). Due

to these dynamic eustatic and oceanographic processes, isolation of populations may have promoted speciation, but also increased the risk of extinction. Subsequent reconnection may have then facilitated the accumulation of peripheral species in the centre of biodiversity (Renema et al. 2008, Bellwood & Meyer 2009, Bellwood et al. 2012). Movements and/or expansion of the geographic distributions of shallow-marine species may have also led to an overlap zone in their geographic ranges, resulting in high species richness (Bellwood et al. 2012). However, it is uncertain if glacially-forced isolation was long enough to prompt speciation. In addition, diversification (Renema 2010, Yasuhara et al. 2017, Prazeres & Renema 2019, Shin et al. 2019) may predate the onset of the large glacial-interglacial sea-level variations at ~2.6 Ma (Lisiecki & Raymo 2005, Yasuhara et al. 2020b).

Switching the Indonesian Throughflow (ITF: warm ocean current running from the Pacific to Indian Ocean) on and off may have also driven Pliocene–Pleistocene diversification in the IAA. Gallagher et al. (2009) presented evidence for Indonesian Throughflow restriction between 10 and 4.4 Ma, and between 4 and 1.6 Ma. Either of these periods of restriction, which would have disrupted north-east to south-west ITF current flows from the Pacific to Indian Ocean, may have facilitated a west-to-east faunal shift from the Indian to Pacific Ocean, across the Timor and Arafura Seas, via a South Java Current flow uninhibited by the influence of the ITF. This may have resulted in the coexistence of species from the Indian Ocean and the Pacific Ocean in shallow-marine environments on the east side of a subsequently re-established Indonesian Throughflow. For example, the first records of the ostracod genera *Alocopocythere* and *Stigmatocythere* indicate that these taxa originated in the Cretaceous or early Paleogene African-Arabian-Indian region (Siddiqui 1971, Al-Furaih 1980, El Sogher et al. 1996) and went on to become widely distributed in the Eocene to Miocene of the Indian Ocean (Siddiqui 1983). The earliest records of these genera in Southeast Asia are in the Pliocene (although pre-Pliocene fossil records in this region are poor) (Hou & Gou 2007). The earliest records of *Alocopocythere* in northern Australia (east of the ITF) are in the 'Anthropocene' (Warne et al. 2006), although, again, earlier fossil faunas in this region are poorly known. Despite this patchy fossil record, if these genera migrated into the Pacific during a period of the Indonesian Throughflow restriction, migration would have occurred between 10 and 4.4 Ma or more likely between 4 and 1.6 Ma. The Indonesian Throughflow restriction may have facilitated faunal dispersal from the Indian to Pacific Ocean, subsequently resulting in the coexistence of species, or speciation in new environments after re-establishment of the Indonesian Throughflow.

Due to the incompletely known late Cenozoic ostracod fossil record of the IAA, we cannot exclude an alternate possible hitch-hiker dispersal event via recent shipping or earlier human maritime travel (Teeter 1973). Although some Tethyan ostracod genera such as *Schizocythere* are known to be widely distributed in the Asian Pacific in the Eocene (Yamaguchi and Kamiya 2009), it may be that certain Tethyan ostracod genera such as *Alocopocythere* and *Stigmatocythere* could not disperse into the Pacific until the Pliocene–Pleistocene because of the Indonesian Throughflow. Consistent with this explanation, benthic foraminifera show faunal separation between the Indian and Pacific Oceans until 4.4 Ma (Gallagher et al. 2009). These 'out of Indian Ocean' shifts might have enhanced IAA biodiversity.

In summary, incorporation of fossil and molecular data with patterns of modern species richness provide valuable insight into the origin and development of the IAA hotspot from the Miocene to the Pleistocene and the nature of biodiversity hotspots more generally. As the western Tethys hotspot senesced after the Eocene, the IAA may have inherited ancient Tethyan lineages and gradually become the key biogeographic region. The Miocene and Pliocene–Pleistocene were two critical epochs during which diversity increased, leading to the modern, bullseye-like pattern of IAA biodiversity, likely aided by the lack of substantial extinction in the region, in contrast to the Caribbean Sea as discussed below (Di Martino et al. 2018).

Strengths, weaknesses and opportunities

IAA biodiversity trends are comparatively well summarised in palaeontological and molecular data for several taxonomic groups (Renema et al. 2008, Williams & Duda 2008, Bellwood et al. 2012, Johnson et al. 2015b, Leprieur et al. 2016, Yasuhara et al. 2017). In contrast, detailed palaeobiogeographical changes in the Cenozoic IAA, and their relationship to the western Tethys, are not well understood for many taxonomic groups. With a few exceptions (Renema et al. 2008, Bromfield & Pandolfi 2012, Santodomingo et al. 2015, 2016, Mihaljević et al. 2017, Yasuhara et al. 2017a, Di Martino et al. 2018), palaeontological data and their syntheses are scanty in the IAA when compared to other hotspots. This obvious deficiency in bryozoans, corals, molluscs and ostracods will be improved with the Throughflow (Johnson et al. 2015a) and 4D-REEF (https://www.4d-reef.eu/) project samples in the near future. Given rich Pliocene–Pleistocene fossiliferous sediments in the region compared to Paleogene sediments (e.g. Yasuhara et al. 2017, Shin et al. 2019), the Pliocene–Pleistocene biodiversity jump should be better quantified.

Tropical America and the Caribbean

Continental rifting broke up Pangea, forming the proto-Atlantic Ocean as North America drifted to the north-west and opened the Central American Seaway (CAS) during the Early Jurassic (Pliensbachian) (Smith & Tipper 1986). The CAS persisted in various sizes until the Pliocene–Pleistocene. The dynamics of the resident biota in Tropical America were defined principally by regional tectonic activities leading, at first, to an ocean expansion and emergence of shallow-marine habitats. Later, general trend across all major groups shows a pattern of ever-increasing isolation and rapid *in situ* diversification until massive extinction at the beginning of the Pleistocene. Today, Tropical American biodiversity is generally low compared to the IAA, but considerably higher than in the eastern Pacific, west Africa and Brazil (Figure 1). Here we review the known geological, environmental and biotic changes that resulted in the modern-day biodiversity of Tropical America, with particular focus on the Caribbean.

Early Cenozoic tropical America

Throughout the Eocene, the eastern Pacific and western Atlantic remained connected through the CAS. Tectonic reconfigurations, uplift and emergence led to a complex arrangement of platforms. Florida formed a broad carbonate platform, with abundant LBF, echinoderms and molluscs, and isolated platforms existed across the Caribbean. However, shared faunal assemblages existed across Mexico, Florida and Cuba, characterised by the LBF lepidocyclinids and nummulitids (Frost 1974, Bowen Powell 2010, Cotton et al. 2018, Torres-Silva et al. 2019). Diverse corals are also found on the Mexican platform. Further south, LBF assemblages are found in Jamaica and the Nicaragua rise, showing higher species richness than the more northerly platforms, including multiple endemic species (Robinson 1995, Robinson et al. 2003). However, samples from Costa Rica show curiously low diversity (Baumgartner-Mora & Baumgartner 2016). Robinson (2004) suggested that the more restricted marine connections between the Gulf of Mexico and Florida (following reconstructions by Pindell 1994) would have inhibited lower to higher latitude movement from the tropical Nicaragua Rise to marginally tropical Florida and Gulf coast, and may account for the varying taxa and diversity. New data compilation of late mid-Eocene (42–39 Ma) LBF diversity in the present study shows that, while diversity was generally lower compared to the western Tethys at that time, there are a few high diversity sites (Figure 5).

The Eocene LBF assemblages of the Caribbean differ considerably to elsewhere at this time. Although the genus *Nummulites* is found in all three biogeographic provinces (i.e. western Tethys, Arabian and IAA), only two species of the genus *Nummulites* are present in the Americas, while several hundred species are present in the Tethys within the same interval (Schaub 1981, Torres-Silva

et al. 2019). The lepidocyclinids evolved in the middle Eocene in the Caribbean province and became widespread in the region, but are not seen until the Oligocene in the Tethyan region and until the late early Oligocene in the IAA (BouDagher-Fadel & Price 2010). Their dispersal is thought to have been facilitated by fluctuating sea-level in this interval (BouDagher-Fadel & Price 2010).

Few Oligocene and Miocene LBF records from the Caribbean have been published. However, as in other regions, the Eocene/Oligocene boundary is followed by a decrease in LBF diversity, which occurs with the extinction of orthophragmines and several other long ranging LBF taxa (Figure 7). Shallow water mollusc records also show a general decrease in diversity towards and in the Oligocene, particularly in warm water taxa (e.g. Hansen 1987). In the Gulf of Mexico, over 90% of taxa went extinct between the latest Eocene and Oligocene (Hansen et al. 2004). Irregular echinoids also show a large diversity decrease from the Eocene to Oligocene in Florida, while regular taxa remain relatively constant (Oyen & Portell 2001). Both the cooling and sea-level fall would likely have been detrimental to tropical shelf taxa, although studies of the timing from elsewhere suggest extinctions within the LBF were not caused directly by the decrease in shelf space (Cotton & Pearson 2011).

In the Oligocene, the previous dominance of LBF across the Caribbean declined and conditions became more favourable for corals, resulting in the region-wide formation of thick sequences of coral reefs (Johnson et al. 2008, 2009). However, these coral reefs declined at the Oligocene–Miocene transition when 50% of corals species disappeared and the rate of reef growth reduced sharply (Johnson et al. 2008, 2009) (Figures 6 and 7). The cause of this biotic turnover remains to be determined. Steinthorsdottir et al. (2021) speculated that narrowing of the Tethyan Seaway reorganised ocean currents such that cool waters entered from the Pacific through the CAS into the Caribbean, causing extinction of thermophilic reef taxa.

Increasing isolation of tropical America

In the Oligocene, the Caribbean remained marginally connected to the Tethys. However, the collision of the Afro-Arabian plates with Eurasia in the early to middle Miocene brought this circum-global tropical seaway to an end and cut the Mediterranean from the IAA and isolated the Caribbean from the rapidly growing hotspot of the IAA (Figure 7, Renema et al. 2008). Indeed, a number of major clades of marine organisms that are today shared between the modern day Atlantic and Pacific hotspots ceased to disperse and began to split around this time (e.g. Duda Jr & Kohn 2005). Moreover, many genera of reef corals formerly believed to be circumtropical are now classified in different families, with many clades restricted to the Caribbean and broader tropical western Atlantic (Fukami et al. 2004, 2008).

As global continental reconfigurations continued, the Caribbean became ever more isolated from other warm-water biogeographic realms. The Atlantic Ocean continued to spread and widen, making the crossing from west Africa and the Mediterranean Sea less likely. At the same time, the tropical western Atlantic was isolated from the eastern edge of the IAA by the largest ocean barrier in the world: the eastern Pacific Barrier (EPB) that today includes around 5000 km of almost entirely deep water that continues to act as a strong dispersal filter between the west and east Pacific (Darwin 1872, Ekman 1967, Vermeij 1987, Lessios & Robertson 2006).

The rise and fall of the productive Atlantic-Eastern Pacific biogeographic realm

The continued isolation of Tropical America from both the east and the west resulted in the formation of a unique faunal province called the Atlantic-Eastern Pacific (AEP) biogeographic realm (sometimes termed the Gatunian Faunal province) (Figure 3). The Miocene AEP extended across most of the tropical western Atlantic, including Florida to the north, Brazil to the south and Panama to the west. It continued through the CAS(s) into the Tropical eastern Pacific up to California and as far south as Ecuador (Woodring 1974, Landau et al. 2008, 2009, Aguilera Socorro et al. 2011, Pimiento et al. 2013, Aguilera et al. 2014, Leigh et al. 2014). Both taxa and ecological characteristics

were shared across this large range, with apparently long-food chain trophic systems (Pimiento et al. 2010, Alberti & Reich 2018, González-Castillo et al. 2020), abundance of filter-feeding benthic (O'Dea et al. 2007, 2016, 2018, Nebelsick et al. 2020) and pelagic (González-Castillo et al. 2020) organisms supported by strong upwelling of nutrient-rich waters (Jones & Allmon 1995, O'Dea et al. 2007, Anderson et al. 2017, Grossman et al. 2019) – a configuration that today is relegated to regions of the tropical eastern Pacific.

The productive AEP realm persisted through to the late Miocene, but even by the middle Miocene tectonic reconfigurations had initiated the transformation of the Caribbean towards the basin we know today. First, Pacific subduction uplifted the Andes and diverted the outflow of the enormous body of fresh water in South American from the Caribbean (Urumaco in northern South America) east to the Atlantic in the late Miocene (Hoorn et al. 2010). This ended the transport of land-based nutrients into the Southern Caribbean whose impacts probably reached to a ~1000 km radius (Subramaniam et al. 2008). Second, starting ~25 Ma, South America collided with the semi-emergent Panama volcanic arc causing it to fracture (Farris et al. 2011) and uplift – a process that continues today (O'Dea et al. 2016). Uplift and volcanic 'infilling' (Buchs et al. 2019) caused the interoceanic straits crossing the Panama volcanic arc to become increasingly narrow and shallow through the Miocene, as observed by evidence of (1) the shallowing of suites of sedimentary basins from Colombia to Costa Rica (Coates et al. 2004, 2005), (2) initiation of genetic, morphological and life-history divergences in marine sister taxa in the Pacific and Caribbean (Lessios 2008, O'Dea et al. 2016), (3) separations in Pacific-Caribbean deep-water oxygen isotope ratios (Sepulchre et al. 2014, Kirillova et al. 2019) and (4) an increase in the probability that continental mammals, birds, insects and reptiles could disperse over the narrowing seaways between the two American continents (O'Dea et al. 2016, Jaramillo et al. 2017).

As the narrow interoceanic seaway(s) diminished through the Miocene–Pliocene, Caribbean faunal richness accelerated (Figures 6 and 7), potentially driven by increasing habitat heterogeneity (Jackson et al. 1993, Budd et al. 1994, Johnson et al. 2007, Klaus et al. 2011, Jagadeeshan & O'Dea 2012, Grossman et al. 2019) resulting in *in situ* diversification (Vermeij 2005, Leigh et al. 2014) and providing appropriate habitat for immigrants (e.g. Siqueira et al. 2019). Evidence from the cheilostomate bryozoans – the only group whose fossil records have been compared between the Caribbean and IAA in detail – suggests that the increasing diversity observed in the Caribbean at this time paralleled that of the IAA hotspot (Di Martino et al. 2018) (Figure 7). The same may be true for reef corals that appear to exhibit only moderate diversity in the IAA during the Miocene (Santodomingo et al. 2016). In contrast, molecular analysis suggests that parrotfish diversity in the IAA was caused by *in situ* diversification, whereas immigration played a much more prominent role in the less spectacular growth of parrotfish diversity in the Caribbean (Siqueira et al. 2019).

The Miocene–Pliocene accumulation of Caribbean marine diversity is observed in the fossil records of a wide array of animal groups including corals (Johnson et al. 2008, Klaus et al. 2011), gastropods (Kohn 1990, Duda Jr & Kohn 2005, Todd & Johnson 2013), bivalves (Leonard-Pingel et al. 2012), bryozoans (Jackson & Cheetham 1994, Cheetham et al. 1998, O'Dea & Jackson 2009, Di Martino et al. 2018), decapods (Schweitzer et al. 2006) and fish (González-Castillo et al. 2020), among others (Leigh et al. 2014) (Figures 6 and 7). However, much of this diversity was soon to face extinction associated with the closure of the shallow-marine connection of the CAS between the Atlantic and Pacific Oceans approximately 3 Ma (O'Dea et al. 2016). Between 4 and 2 Ma, extinction rates across all groups peaked, resulting in the loss of 30% up to 100% of species (depending on group) by the early Pleistocene (Stanley 1986, Allmon 2001, Todd et al. 2002, O'Dea et al. 2007, Smith & Jackson 2009, Leonard-Pingel et al. 2012, Todd & Johnson 2013, Di Martino et al. 2018) (Figures 6 and 7). This regional mass extinction event was highly selective against modes of life suited to highly productive settings, such as non-zooxanthellate-assisted filter feeding, clonal reproduction and planktotrophic larvae (Johnson et al. 1995, 1996, Allmon 2001, O'Dea & Jackson 2009). This extinction pattern implicates the previously-described oceanographic declines in planktonic

productivity due to the restriction of the shallow-marine connection of the Central American Seaway as the root cause. However, several extinct bryozoan species (e.g. species of Cupuladriidae) persisted 1–2 Myrs after the diminishment of Caribbean's source of upwelling waters at ~4 Ma (O'Dea et al. 2007, O'Dea & Jackson 2009, Grossman et al. 2019), although they appear to have done so in small, isolated populations (O'Dea & Jackson 2009). The cause of this mismatch between environmental 'cause' and macroevolutionary 'effect' has yet to be resolved. Several hypotheses have been proposed, such as the random decline of metapopulations as conditions became less favourable (O'Dea et al. 2007, Smith & Jackson 2009) based on the phenomenon of extinction debt (Nee & May 1992, Tilman et al. 1997). Alternatives include the persistence of isolated pockets of nutrient-rich coastal waters (O'Dea & Jackson 2009, Grossman et al. 2019) although there is as yet no evidence of consistent environmental differences among locations to support this.

Birth of the modern Caribbean

The decline in productivity across the Caribbean also enabled coral reefs to proliferate to an extent not seen since the late Oligocene (O'Dea et al. 2007, Johnson et al. 2008, Klaus et al. 2012). The extent and rate of reef building increased sharply in the early Pleistocene, reaching rates seen in the Oligocene (Johnson & Pérez 2006, Johnson et al. 2008). This rapid reef building was, to some extent, driven by the arrival and ecological dominance of the coral genus *Acropora* in shallow Caribbean habitats around 2 Ma (Jackson 1994, Klaus et al. 2012, Renema et al. 2016). *Acropora* is characterised by rapid growth with colony extension rates many times higher than other branching coral genera and was able to thrive during the intervals of rapid sea-level change that initiated 1.8 Ma and has since intensified towards the recent.

The environmental conditions (oligotrophic and aseasonal), ecological states (fast-growing large reef tracts) and assemblages of taxa resilient to the rapid and extreme sea-level fluctuations that characterised the Pleistocene of the modern Caribbean were therefore established only within the last two million years. Since then, a few clades have experienced intense *in situ* diversifications within the Caribbean (e.g. *Polystira*; Todd & Johnson 2013, *Stylopoma*; Jackson & Cheetham 1994), but most groups appear to remain a subset of their earlier pre-extinction diversity (DiMartino et al. 2018). The last million years have seen remarkable stability in those groups whose fossil record is sufficiently well studied despite intense fluctuations in sea-level and shelf areas (Jackson 1992, Pandolfi et al. 2001) (Figure 7).

Tropical eastern Pacific: an overlooked geologically recent hotspot?

The general paradigm has been that the tropical eastern Pacific is not a biodiversity hotspot – an idea that probably stemmed from the perception that coral reefs are rare and, when they are present, they are species poor. It is true that reef building coral species are of especially low diversity in the tropical eastern Pacific, and their abundance is low when compared to the reef tracts of the Caribbean. Yet, richness of other groups (e.g. molluscs) is often comparable to the Caribbean and often exceeds it (Leigh et al. 2014) (but note that the tropical eastern Pacific is much more abundant in molluscs and so molluscan diversity could be overestimated by sampling artefact [i.e. easy to collect more specimens] [see Jackson et al. 1993, Vermeij 1993, Smith & Jackson 2009]). Ongoing work in the region is revealing high levels of previously unknown diversity, much of which is endemic, that may elevate this region to a global biodiversity hotspot (Cortés et al. 2017, Jefferson & Costello 2020). The available evidence shows that the origins of this fauna is a complex mix of high-productivity-adapted remnants of the AEP biogeographic realm (Leigh et al. 2014), descendants of lucky dispersals across the eastern Pacific barrier, and local endemics that remain poorly studied (Cortés et al. 2017).

Strengths, weaknesses and opportunities

Palaeontological studies, including those of the Panama Palaeontology Project, have documented biological patterns of diversity and ecological and evolutionary change (Jackson & Johnson 2000,

O'Dea et al. 2007, Johnson et al. 2008). Dynamics in earlier periods (e.g. Paleogene to early Miocene) are less well studied (but see Iturralde-Vinent 1998) because of a general lack of replicated sedimentary rock sequences or poor preservation in the sequences that exist. In addition, the Pleistocene records of non-reef taxa are poorly known, which leaves the precise timing of the Caribbean extinction unresolved. Indeed, smaller benthic foraminifera appear to sidestep the extinction event (Smith et al. 2013) and show strong and continuous Miocene–Present diversification (Figure 6). Filling these gaps will improve our understanding of the history of the Caribbean hotspot and allow for a more detailed comparison with other hotspots.

Summary of major Cenozoic biodiversity hotspots

The post-Mesozoic Tethys Ocean belonged to a large tropical biogeographic realm connecting all of the western Tethys, Arabian, IAA and Caribbean regions to varying degrees, but the Tethys no longer exists and these four regions are now separated by land masses and/or deep ocean (Figure 7). The hotspots associated with these four regions all have dynamic ecosystem histories. As described above and clearly shown by LBF, corals and other taxonomic groups (Figures 5 and 6), the western Tethys hotspot thrived in the Eocene, diminished in the Oligocene, and vanished in the Miocene at ~19 Ma, mainly due to isolation and regional and global cooling. The Arabian hotspot emerged in the late Eocene showing higher diversity than the western Tethys hotspot and was sustained until the middle Miocene. The IAA hotspot originated in the Miocene at ~23 Ma, further diversified in the Pliocene–Pleistocene, and, mainly because of tectonics and associated oceanography, continues to host the highest biodiversity in the oceans today. The Caribbean hotspot emerged in the Oligocene, temporarily diminished during the Oligocene–Miocene transition, then rapidly diversified in the Miocene–Pliocene and collapsed by the Pliocene–Pleistocene extinction event (Figures 4–6; see summary in Table 1 and Figure 7).

Hotspot dynamics and drivers: global perspectives

Although plausible drivers of diversity changes in each hotspot have been discussed above, the explanations tended to be descriptive. Comparing differences and similarities in their histories may help to better constrain the common driver(s) and testable hypotheses of tropical biodiversity. Thus, here we try to contextualise these hotspots globally.

Hopping Hotspots or Whack-A-Mole?

The Hopping Hotspots model (Renema et al. 2008) (Table 2) is the first integrative hypothesis to explain the spatiotemporal dynamic of multiple biodiversity hotspots. This hypothesis proposes that marine biodiversity hotspots have 'hopped' or shifted across almost half of the globe throughout the Cenozoic: from the western Tethys (present Mediterranean) during the Eocene, to the Arabian region during late Eocene–early Miocene, and eventually to the IAA region from the early Miocene onwards to track suitable shallow-marine habitats created by major tectonic movements (Renema et al. 2008). Each hotspot has an initiation and, in the case of the western Tethys and Arabian hotspots, a demise.

During the Eocene, the large western Tethys was connected to the Indian Ocean. The Indian subcontinent in the middle of the Indian Ocean had not yet collided with the Eurasian continent (Harzhauser et al. 2002, Wang et al. 2020). The western Tethys, a tectonically active and geographically complex ocean surrounded by the European, African, Arabian and Indian plates, fostered high biodiversity at that time (i.e. western Tethys hotspot) (Renema et al. 2008). After, the Tethys Ocean gradually narrowed by the collision of the African with the Eurasian continent, and the Tethys Seaway to the Indian Ocean was closed in a stepwise fashion by the Miocene at ~19 Ma

Table 2 Comparison of hypotheses and how to test their relative importance

	Hopping Hotspots	Whack-A-Mole
In short	Certain taxa with high diversity or high diversification potential hopped from the western Tethys, through Arabia to the IAA (Indo-Australian Archipelago) to the east, and to the Caribbean to the west, and prospered in each region.	Moles (=biodiversity hotspots) rise and fall individually, without moving from hole to hole. High diversity regions have occurred in suitable habitats capable of many species or speciation events.
Cause of hotspot dynamics	Suitable habitat created in tectonically active, collision regions (large habitat size/shelf area, high habitat/coastline complexity); pumping out Tethyan elements from a senescent hotspot to newborn hotspots.	Suitable habitat created in tectonically active, collision regions (large habitat size/shelf area, high habitat/coastline complexity).
Assumption	Certain Tethyan taxa (e.g. genera) are responsible for hotspots and their high diversity.	Certain Tethyan elements (e.g. genera, families) are unrelated to hotspots and their high diversity.
How to test? Eocene biogeography	Key taxa might not yet extend to the IAA and Caribbean regions. Or, key taxa may have reached these regions but not yet diversified due to lack of suitable habitat size and complexity.	Whack-A-Mole will be supported if the endemism is extremely low among the western Tethys, Arabia, IAA and the Caribbean, although high endemism itself will not reject this hypothesis.
How to test? Key elements	Key taxa are responsible for hotspots' high diversity.	Absence of common key taxa among hotspots.
How to test? Oligocene–Miocene biogeography	There should be enhanced migration of key taxa from the western Tethys and Arabia to the IAA and perhaps Caribbean.	There may be less migration in general compared to the Eocene, when the western Tethys and Arabia had more connection to the IAA and Caribbean.
How to test? Pre-extinction Caribbean fauna	The key taxa in the pre-extinction Caribbean should exhibit phylogenetic relationships with those of the Eocene western Tethys.	The key elements of pre-extinction Caribbean biodiversity should have functional/ecological similarity to those of the Eocene western Tethys.
How to test? Modern IAA fauna	The key taxa of the modern IAA should exhibit phylogenetic relationships with those of the Eocene western Tethys.	The key elements of modern IAA biodiversity should have functional/ecological similarity to those of the Eocene western Tethys.
Did Caribbean senescence cause hopping?	Taxa that went extinct during the Plio-Pleistocene Caribbean extinction event should have been pumped out to the west and east to some degree.	NA

(Harzhauser et al. 2007). The biodiversity centre moved eastwards, with a diversity decrease in the western Tethys and a diversity increase in the Arabian region (i.e. Arabian hotspot) during the late Eocene–early Miocene, coinciding with the collision of the Arabian and Eurasian plates. The Arabian hotspot ceased during the middle Miocene as the continental collision proceeded, and the vast shallow-marine carbonate platforms on the Arabian Shelf and the central Iranian basins became increasingly restricted and finally subaerially exposed (i.e. the final closure of the Tethyan Seaway at ~19 Ma, Renema et al. 2008, 2009, Bellwood et al. 2012). Indo-Pacific biodiversity started to increase during the Miocene at ~23 Ma (i.e. IAA hotspot) when the collision of Australia with the Pacific arcs and the south-east Asian margin formed a complex archipelago (Renema et al. 2008, Bellwood et al. 2012), connecting shallow-marine habitats. With eastern shifts in peak biodiversity from the Arabian to IAA region, IAA biodiversity has remained persistently high from the Miocene to today. By correlating the formation and senescence of each of the three replicate

hotspots with successive tectonic collisions along the Eurasian plate from west to east, the Hopping Hotspots model indicates strong abiotic control (i.e. plate tectonics) on evolutionary-scale biodiversity patterns (Renema et al. 2008).

However, the long-term impacts of plate tectonics must manifest through mechanisms that underpin the origination and accumulation of individual species to foster high biodiversity (Beaugrand et al. 2018). In the case of IAA, a complex mosaic of continental seas, island arcs and microcontinental fragments formed within the convergence zone between tectonic plates (Hall 2002, 2012). This geological complexity is of great ecological importance as it may disrupt population connectivity, increase the area and heterogeneity of shallow habitats, accumulate species from peripheral regions, and form an overlap zone of species-distribution ranges (Hoeksema 2007, Bellwood et al. 2012). All these processes may contribute to high biodiversity through speciation of marine taxa.

The Hopping Hotspots model is supported by fossil and molecular evidence. The fossil record of multiple shallow-marine taxa (e.g. large benthic foraminifera, reef corals, mangroves, bivalves, gastropods) consistently suggests eastern shifts of maximal alpha diversity following biodiversity hotspots from the Eocene Tethys to Arabia and eventually to the late Miocene–Recent IAA (Renema 2007, 2008). Larger benthic foraminiferan palaeobiogeographical data tend to show similar taxonomic composition among the hotspots, indicating spatial and temporal connectivity of component taxa from the Tethys through Arabia to the Indo-Pacific (Renema 2007, Renema et al. 2008). In addition, recent molecular and phylogenetic studies, together with first occurrence data in fossil records, demonstrate the early origination of many extant IAA taxa, ranging from the Eocene to late Miocene (Williams & Duda 2008, Bellwood et al. 2017). In some case studies of taxonomic groups with an exceptionally good fossil record (e.g. LBF), palaeobiogeographical distributions indicate that higher taxa (genera, families) originated in the western Tethys, radiated east following the Tethyan hotspot senescence and reached Indonesia as the IAA hotspot emerged (Renema 2007, Dornburg et al. 2015). As these taxa moved with the Hopping Hotspots to the IAA region, many species seem to have arisen from them thereafter (Bellwood et al. 2012). With growing recognition of the importance of historical processes in shaping modern biodiversity, the Hopping Hotspots model emphasises the spatiotemporal shifts of particular shallow-marine taxa ('Tethyan elements') to tectonically active (or continental collision) regions to form new biodiversity hotspots. We now understand the IAA hotspot as the latest manifestation of a biodiversity pattern analogous to that of the Eocene western Tethys (Renema et al. 2008).

However, the degree to which biodiversity hotspots really 'hopped' sideways or arose and fell independently through time has not been tested quantitatively. Shifts in geographic ranges from the Eocene western Tethys to the Miocene IAA have been elucidated for only a few key taxa (Bellwood et al. 2012). Limited fossil evidence in the literature is often not sufficient or robust to validate the palaeobiogeographical affinities between historical hotspots. Older literature often needs taxonomic updates and lacks stratigraphic and palaeoecological information. Palaeontological databases, while useful, often adopt the data without further critical evaluation. These factors are limiting for comparison of fossil assemblages from different chronostratigraphic stages and regions. In addition to abiotic controls (i.e. tectonic events and climate changes) over large-scale biodiversity patterns, the Hopping Hotspots model implies that biotic controls (i.e. shifts of higher taxa/Tethyan elements) are also important by proposing a correlation between palaeobiogeographical similarities and biodiversity dynamics among the hotspots (Renema et al. 2008). However, it remains unclear if the shifts of Tethyan taxa are causally linked to development of high biodiversity given that major tectonic collisions control the area and variability of suitable shallow-marine habitats. Testing the validity of the causal link between biogeography and biodiversity, and consequently the Hopping Hotspots model, may increase our understanding of the interplay between biotic and abiotic factors in shaping regional to global biodiversity patterns over evolutionary timescales. If a causal link is detected (e.g. high biodiversity is characterised by certain higher taxa, instead of miscellaneous rare species, Table 2), it may be feasible to identify a representative range of taxa that are indicative of

high biodiversity. These indicator taxa will be useful to monitor biodiversity for conservation and management purposes and to reconstruct past biodiversity hotspots, without full biodiversity census data that is time-consuming to obtain.

As discussed above, the Hopping Hotspots model suggests that biogeographic shifts of certain taxa fostered biodiversity through biotic interactions in suitable habitats set by plate tectonic movements. On the other hand, Cenozoic tropical biodiversity dynamics may also be explained simply by a rise and fall of diversity in each region, regardless of biogeographic shifts of certain taxa between hotspots (=hopping). We call this null hypothesis 'Whack-A-Mole', in which moles (=biodiversity hotspots) rise and fall individually, without moving from hole to hole (Table 2). This hypothesis suggests that abiotic factors such as plate tectonics, climate and oceanography control the 'capacity' for number of species in an area (Benton 2009, Tittensor et al. 2010) regardless of 'Tethyan elements'. Shifts of taxa in this case, if occurring at all, may be regarded as random dispersal events out of the senescing hotspot where tectonic subsidence and collision caused habitat loss. As coral phylogeny indicates, a hotspot may provide suitable habitats for many species and may have nothing to do with macroevolutionary mechanisms (Pandolfi 1992). Noticeably, there is not a dichotomy between the Hopping and Whack-A-Mole hypotheses, and we need to understand their relative importance (i.e. more biotic or abiotic controls over biodiversity?) by testing the putative effects of palaeobiogeographical shifts on biodiversification (Table 2).

Global Hopping Hotspots model: Caribbean–Tethys relationship

While the original Hopping Hotspots hypothesis does not include the Americas, the tropical Americas were a part of the Tethys during the Mesozoic–Paleogene greenhouse world when the Atlantic Ocean was narrower. For example, there are ostracod species in common between the Caribbean and the western Tethys in the Eocene (McKenzie 1967, 1987, Yasuhara et al. 2019a). Even in the Miocene, some 'westward' dispersal is known in certain groups of bivalves and gastropods (Harzhauser et al. 2007) and bryozoans (Cheetham 1968). Thus, the Caribbean hotspot can be incorporated into the global Hopping Hotspots model (Figure 7, Table 2). Hotspots could hop not only to the east, but also to the west, with the Eocene–Miocene connection between the Caribbean and western Tethys and the subsequent Miocene–Pliocene diversification in the complex shallow-marine habitats created by tectonics/collision in the Caribbean. This global Hopping Hotspots process is clearly depicted in the LBF data as well as coral and other taxonomic group data (Figures 5 and 6).

'Centre-of' hypotheses and geographical barriers

A set of 'Centre-of' hypotheses have been proposed to explain the diversity centre in the IAA, focused on the centre of speciation (species originate in the centre and successively disperse to surrounding areas), centre of accumulation (species arise in the peripheral locations and subsequently move to the centre), centre of survival (species originate anywhere and better survive in the centre), centre of overlap (species geographical ranges overlap in the centre) and/or other varieties of these hypotheses (see review by Bellwood et al. 2012) (also see Pandolfi 1992, Bellwood et al. 2005, Briggs 2005, Cowman & Bellwood 2013a, Cowman 2014, Huang et al. 2018). These 'Centre-of' hypotheses can be applied to all Cenozoic diversity hotspots. The 'Centre-of' mechanisms can operate only when a tropical hotspot is situated in 'the centre' with connection to adjacent regions both to the east and west. In this regard, the death of a hotspot has occurred when a barrier is formed to block out its eastern or western connection. For instance, the closures of the Tethyan Seaway and Central American Seaway changed the Paleogene western Tethys and Miocene–Pliocene Caribbean hotspots to enclosed marginal seas, respectively. This east-west connection may be an important condition for the existence of a biodiversity hotspot (Figure 7). Although little consensus has been reached regarding the patterns and modes of macroevolution, most of these 'Centre-of' hypotheses

invoke tectonic, eustatic, climatic, oceanographic and geomorphological processes (TECOG) as the underpinning mechanisms of the bullseye pattern of IAA diversity (Rosen 1984, Bellwood et al. 2012, Cowman & Bellwood 2013a) that might have also operated in the extinct western Tethys and Caribbean hotspots.

Role of shallow-marine habitat size and complexity

Habitat area and complexity are considered the main diversity drivers in the Hopping Hotspots model (Renema et al. 2008) and Phanerozoic global marine diversity (Valentine & Moores 1970, Zaffos et al. 2017), and some of drivers of the present-day coastal diversity (Tittensor et al. 2010). For example, see the similarity between coastal species richness and coral reef distributions in Figure 1. We tried to quantify habitat size and complexity by using palaeogeographical reconstructions of palaeo-coastlines and flooded continental shelf distributions for the last 50 Myr (Kocsis & Scotese 2021). Habitat size was expressed for every hotspot area in every 5 Myr bin using the total shelf area between the reconstructed maximum transgression coastline and the continental margin (–1400 m isobath, Kocsis & Scotese 2021, Figures 5, 6 and 10). We approximated habitat complexity in the coastlines by calculating the lengths of the coastlines in the same areas. These coastline length calculations were executed using the 'yardstick' method (O'Sullivan & Unwin 2010), with a yardstick length of 100 km. Hotspot sizes were inferred to be almost constant, but latitudinal and longitudinal extents changed over time along with changing palaeogeography (Figures 6 and 10). Thus, we operationally defined the hotspot areas as follows: The IAA ranged between 70°E–160°E and 10°S–25°N in 50–0 Ma. The Tethys (note that this is in a broad sense, including both the western Tethys and Arabian hotspots, because it is difficult to define the western Tethys and Arabian regions separately on maps) was expressed as the union of a spherical rectangle covering the Mediterranean (10°W–20°E and 19°N–45°N) and another covering the western basin of the Indian Ocean (20°E–60°E and 0°N–50°N in 50–35 Ma, 20°E–60°E and 10°S–40°N in 35–0 Ma). The Caribbean ranged between 90°W–60°W and 0°N–40°N in 50–45 Ma, 95°W–65°W and 0°N–40°N in 40 Ma, 95°W–60°W and 0°N–35°N in 35–25 Ma, 100°W–65°W and 0°N–35°N in 20–10 Ma, 100°W–62°W and 0°N–32°N in 5–0 Ma. Both habitat size and coastline length were calculated using a similar method with penta-hexagonal grids (Kocsis 2020) with a mean grid cell edge length of 6.66° (Figure 5).

Shallow-marine habitat area and complexity trend show substantial similarity to those of regional diversities (Figures 1, 5 and 6). IAA diversity increased with an increase in shelf area and coast line length, and Tethyan diversity decreased with a decrease in shelf area and coast line length, respectively. Larger habitat areas and hotspot locations are well matched on present day and palaeo maps (Figures 1, 5 and 6). This quantitative evidence supports the view that suitable habitat (size and complexity) created by active tectonics is important for the development and maintenance of biodiversity hotspots, and, thus, both the Hopping Hotspots and Whack-A-Mole models.

Role of temperature

There is increasing consensus that present-day and Quaternary large-scale marine biodiversity patterns are mainly temperature-driven, and that higher temperature areas (e.g. tropics) or times (e.g. interglacials) retain more species (Yasuhara et al. 2009, Tittensor et al. 2010, Yasuhara et al. 2012b, Beaugrand et al. 2013, Costello & Chaudhary 2017, Reygondeau 2019, Gagné et al. 2020, Rogers et al. 2020, Yasuhara et al. 2020b). In addition, global Cenozoic diversity curves tend to bear considerable similarity with temperature trends (Condamine et al. 2019, Yasuhara et al. 2020b). Indeed, the IAA is now sitting in the warmest spot in the world (Figure 5). However, the IAA has been the warmest region throughout the Cenozoic, even in the Eocene when peak biodiversity was situated
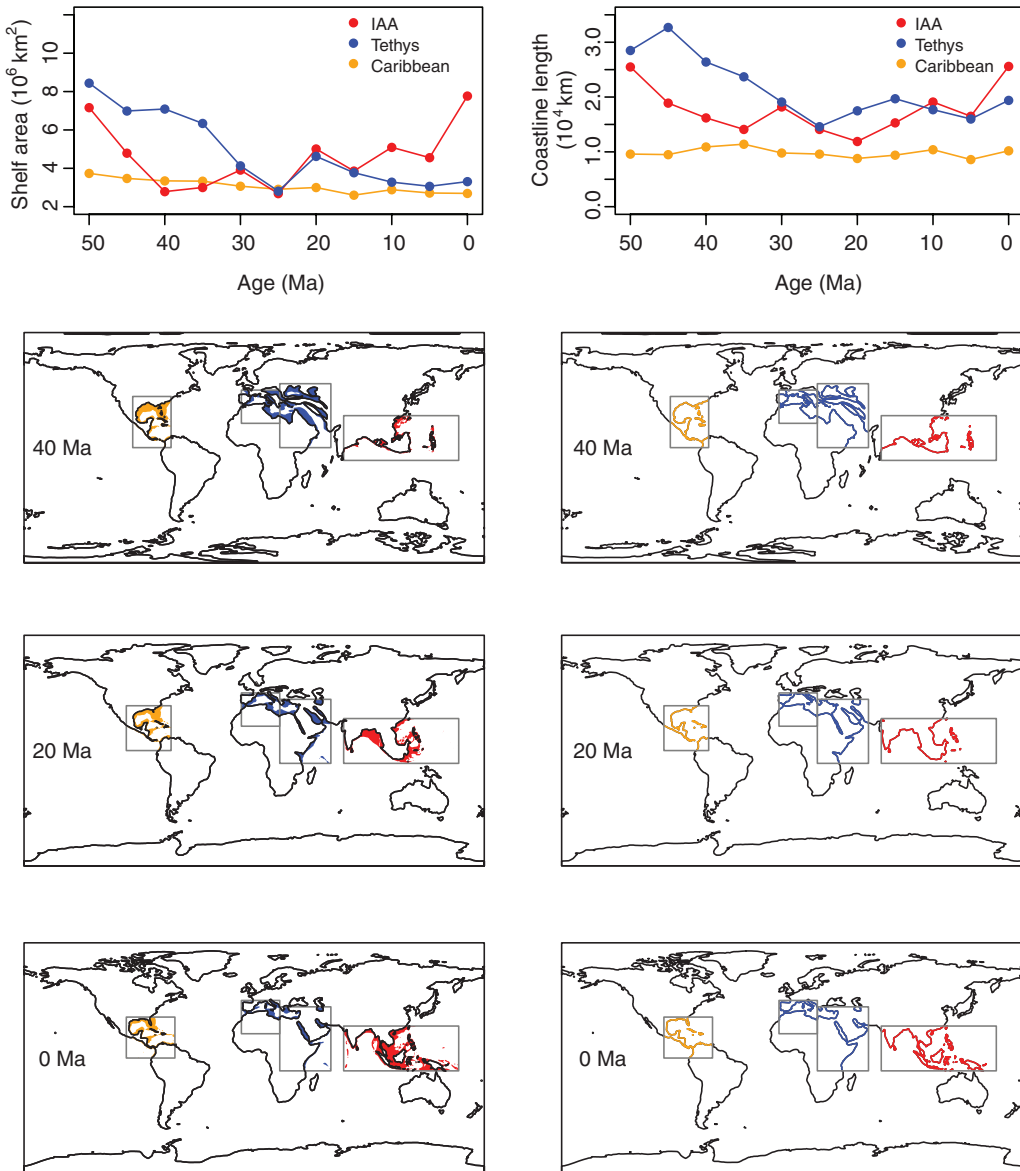
Figure 10 Shelf areas (left column) and coastline lengths (right column) in the IAA, Tethys (western Tethys+ Arabian) and Caribbean areas. The top panels show values every 5 million years from 50 to 0 Ma (see Figure 6 and Section 'Role of shallow-marine habitat size and complexity'). The maps in the second to fourth rows illustrate the calculations in the 40, 20 and 0 Ma time slices, respectively.

in the western Tethys (Figure 5). The western Tethys was not the warmest region in the Eocene, yet hosted the highest diversity at that time (Figure 5). From a temperature perspective, this inconsistency may mean that Eocene equatorial regions might have been too hot to host high levels of biodiversity.

We now know that equatorial temperatures can be too hot for marine organisms. Latitudinal diversity gradients become bimodal with an equatorial dip in both the past and present in concert

with warming oceans (Kiessling & Simpson 2011, Chaudhary et al. 2016, 2017, Yasuhara et al. 2020b, Yasuhara & Deutsch 2022). Many pelagic and benthic marine species have shifted their distribution away from the equator into mid-latitudes since the 1950s as predicted by climate change models (Chaudhary et al. 2021). Major marine taxonomic groups show decreases in species richness above 20°C–25°C (Chaudhary et al. 2021). This pattern points to a role for temperature in the past development of tropical biodiversity hotspots. Hopping Hotspots from the western Tethys to IAA ranged from moderately low latitude to equatorial through time. Other than tectonics, this latitudinal shift may, in part, be due to cooling, and most equatorial oceans, including the IAA, may have been too hot in the greenhouse Paleogene (Worm & Tittensor 2018).

For the Eocene super-greenhouse world, little is known with respect to the distribution, structure and biodiversity of coral reefs in low latitudes, except for framework reefs being rather uncommon and small (Perrin 2002). In this respect, we draw a parallel with the last interglacial where coral diversity seemed to have been low near the equator and many coral taxa displayed poleward range shifts (Kiessling et al. 2012). These same shifts are occurring now in planktonic foraminifera (Yasuhara et al. 2012b, 2020) and many other groups (Poloczanska et al. 2013, Pecl et al. 2017). Tropical sea surface temperatures during the Eocene were ~5°C higher than present (Evans et al. 2018, Hollis et al. 2019, Lunt et al. 2021) (Figure 5) and therefore likely to have caused a zone depauperate in coral reefs within the equatorial warm pools, e.g. Southeast Asia (Wilson & Rosen 1998, Scheibner & Speijer 2008). In addition to temperature stress to reef corals, ocean acidification also contributed to the reef crisis during the Paleocene–Eocene thermal maximum (PETM) (Kiessling & Simpson 2011) and a possible reef gap during the early Eocene Climate Optimum (Perrin & Kiessling 2011, Norris et al. 2013). Notably, a recent molluscan study showed that the early Eocene latitudinal diversity gradient was U-shaped with minimum diversity at the tropics (Boag et al. 2021). But note that Eocene planktonic foraminifera do not show a strong equatorial dip in diversity (Fenton et al. 2016). LBF also experience a turnover event around the Paleocene–Eocene transition, but an increase in diversity through the early Eocene (Whidden & Jones 2012). Scheibner and Speijer (2008) also show a global shift across the PETM from coral-dominated to LBF-dominated platform systems. So, although corals and LBF show similar patterns of diversity relating to tectonics, perhaps temperature/ocean chemistry events differentiate between their responses. Yasuhara et al. (2012b) further showed the extinction of warm-adapted tropical planktonic foraminifera species via global cooling since the Pliocene. There may have been some taxa adapted to super high temperature in the equatorial Paleogene before the Neogene cooling caused their extinction.

During the early Eocene, sea surface temperature was >34°C at the tropics where the IAA and Caribbean regions were situated, whereas the western Tethys hotspot temperature was ~28°C, similar to the present-day IAA temperature (Figure 5). At this temperature of >34°C, oxygen will be less than 6 mg/L when fully saturated, and thus low latitude ocean habitat would have been significantly oxygen limited (Shi et al. 2021). In the middle Miocene, the equatorial IAA and Caribbean remained >30°C, when biodiversity in these hotspots was only moderately high (Figures 5 and 7). By the mid-Pliocene, the Mediterranean Sea (western Tethys region) became too cold to house a tropical fauna (Figure 5). Recent studies indicate that temperatures >25°C are too hot for many organisms and may result in diminished diversity (Yasuhara et al. 2020b, Boag et al. 2021, Chaudhary et al. 2021). Thus, Eocene and perhaps Miocene equatorial temperature was too high to generate and maintain high levels of biodiversity comparable to the present-day IAA. Even the present-day IAA temperature of ~28°C is too hot, as we see equatorial diversity declines (Yasuhara et al. 2020, Chaudhary et al. 2021). Thus, the higher present-day temperature in the IAA compared to the Caribbean probably does not explain higher diversity in the IAA. In sum, temperature may be an important constraint (i.e. hotspots cannot be fully developed in places that are too cold or too hot), but does not explain the entire history of tropical biodiversity hotspots.

Human impacts on biodiversity hotspots

A major question is how the biodiversity that we see today has been degraded by humans, decreasing diversity levels from a 'pre-anthropogenic disturbance' baseline. A substantial diversity decline from the Pleistocene to the present is known from ostracods in the IAA (Yasuhara et al. 2017a), potentially due to human-induced ecosystem degradation. Although extant tropical biodiversity of both the IAA hotspot and the Caribbean is often described with human activities evidenced by coral bleaching, IUCN endangered species and outbreaks of harmful taxa such as crown-of-thorns starfish (De'ath et al. 2012), these constitute only a few aspects of human-induced ecosystem degradation. Our understanding of the true human impact on the local (alpha) and regional (gamma) biodiversity of major taxonomic groups in these areas remains qualitative or insufficient (Rogers et al. 2020).

Caribbean Sea

In the Caribbean region, exhaustively compiled observational data have shown that coral cover declined from >30% in the 1970s to less than 20% in the 2000s, while macroalgal cover increased from ~10% to 25% in the same time period (Jackson et al. 2014). This dramatic shift in benthic dominance represents the alteration of the regional ecosystem by human activities, primarily through increased development, water pollution, anthropogenic species invasion and overfishing, and by recent climatic warming via coral bleaching (Glynn 1993, Hughes 1994, Jackson et al. 2014, Hughes et al. 2018). However, it is known that degradation began well before the start of biological observations around the 1970s (Hughes 1994, Gardner et al. 2003, Jackson et al. 2014) as it is well documented in historical and palaeontological archives (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003, Pandolfi & Jackson 2006, Cramer et al. 2012, 2017, Cramer et al. 2020a,b).

Human perturbations likely began to permanently alter the composition of Caribbean ecosystems with the arrival of European settlers and colonisation (Jackson 1997). One of the most notable documented degradations is the complete collapse of the branching *Acropora* forests that characterised Caribbean reefs since the early Pleistocene (Jackson 1992, Pandolfi & Jackson 2006). This collapse was caused by rapid human population growth and likely agricultural impacts (Cramer et al. 2020b), white-band disease (Aronson & Precht 2001, Knowlton 2001, Jackson 2008) and bleaching (Aronson et al. 2000). It has caused a 'flattening of the Caribbean reefs', or a decrease in reef complexity, leading to further biodiversity loss and altering ecosystem function (Alvarez-Filip et al. 2009, O'Dea et al. 2020). Similar human-induced collapse of *Acropora*, the dominant reef builder for the last 1.8 Myrs, is known regionally and globally (Renema et al. 2016, Cybulski et al. 2020). Comprehensive palaeoecological works have been conducted in the Bocas del Toro region of Panama where bivalve, gastropod and foraminiferal assemblages suffered a deterioration of reef ecosystem conditions by land-based agricultural activities and resulting eutrophication in the mid-twentieth century or earlier (Cramer et al. 2015, 2020b, Figuerola et al. 2021). Declines in the accretion rates of Panamanian coral reefs were linked to the historical overfishing and decrease in parrotfish since the mid-eighteenth–mid-nineteenth century (Cramer et al. 2017). Fossil echinoid spines showed that the lack of recovery of the sea urchin *Diadema antillarum* after its mass mortality event in the 1980s (Hay 1984, Hughes 1994, Jackson 1997, 2008, Cramer et al. 2018) may have been due to the long-term overfishing of piscivorous fishes that released damselfishes, an effective competitor of *Diadema*, from predation pressure (Cramer et al. 2017, 2018). This imbalance of *Diadema* in the reef ecosystem is particularly striking when palaeorecords indicate that they were the most abundant sea urchin on reefs for the last 125,000 years (Gordon & Donovan 1992, Jackson 1997). Parrotfish and *Diadema* are both important herbivores (Hay 1984), and the loss of these populations in the region has contributed to a phase shift in the reefs from coral- to algal-dominated ecosystems (Jackson 1997). Recent invasion of predatory lionfish (*Pterois volitans*) may have also

been a factor, because their prey includes juvenile parrotfishes and other small herbivorous fishes (Johnston & Purkis 2011, Albins & Hixon 2013, Côté & Smith 2018).

Historical resource overexploitation, poaching, habitat alteration, environmental pollution, European trade, and other human activities in the Caribbean has permanently changed marine faunal composition through the removal of large sharks and large trophy fish, and reduced populations of manatees, sea turtles and humpback whales (Mignucci-Giannoni et al. 2000, Reeves et al. 2001, Romero et al. 2002, Smith & Reeves 2003, McClenachan 2009, McClenachan et al. 2010, Ward-Paige et al. 2010, Lotze & McClenachan 2014, Dillon et al. 2021). It also led to the complete extinction of the Caribbean Monk Seal due to intensive human hunting (McClenachan & Cooper 2008). Perhaps the best proxy for larger animal and higher trophic level decimation in the Caribbean is seen with the collapse of sea turtle populations. Before colonial hunting, it is estimated that green and hawksbill turtle populations numbered over 6.5 million and are now reduced to around 300,000, a 95% decline (McClenachan et al. 2006). By using these larger taxa as a proxy for other marine life needed to support the food chain, it can be calculated that Caribbean fish and invertebrate biomass has seen as much as an 80% reduction since historical times (McClenachan & Cooper 2008).

IAA

Although it is the type example of a modern-day marine biodiversity hotspot that harbours much higher biodiversity than the Caribbean, much less is known for the IAA despite recent increased scientific interest. Top ranked areas for global marine biodiversity, the Philippines and Sunda Islands, are associated with very high 'threat score' from human impacts (Roberts et al. 2002). The IAA is also a region with some of the highest levels of intrinsic risk globally – or risk of extinction for modern taxa based on palaeontological data – mainly due to climate and human stressors (Finnegan et al. 2015).

Very little research has been done on the extent of human impacts on IAA ecosystems. In Papua New Guinea, a comparison of fossil and modern assemblages showed greater coral biodiversity in the past and decreased modern reef variation due to anthropogenic degradation (Edinger et al. 2001). In general, the limited historical ecology research in Papua New Guinea agrees with general biodiversity degradation due to anthropogenic forces, showing that numerous taxa (herbivores, carnivores, suspension-feeders and corals) have all been exploited by human populations since indigenous times and are being pushed closer to ecological extinction (Berzunza-Sanchez et al. 2013). Microfossils (foraminifera and ostracods) in surface sediments show ecosystem degradation in the IAA region (Delinom et al. 2009, Renema 2010, Fauzielly et al. 2013a, Nurruhwati et al. 2020). However, there are no palaeoecological studies investigating long-term changes, except an ostracod study in Jakarta Bay showing a faunal shift at ~1950 related to the increased population of Jakarta City and resulting eutrophication (Fauzielly et al. 2013b).

Nearby areas to the IAA can be used to draw general biodiversity conclusions for the western Pacific, such as in the Great Barrier Reef and the South China Sea. The Great Barrier Reef, south of the IAA, is one example of a marine region with documented biodiversity changes over the Anthropocene. Although some low diversity reefs have remained unaffected for the last 1,200 years despite high sedimentation and nutrient loads due to European colonisation (Perry et al. 2008), other turbid reefs experienced similar collapses of previously dominant *Acropora* in the 1920s–1960s from water quality degradation after European settlement and again in the 1980s–1990s due to cyclones, thermal stress and flood events (Roff et al. 2013, Clark et al. 2017).

The South China Sea, adjacent to the IAA and similar in terms of high marine biodiversity, though classified as a high-latitude marginal reef system, has become an area where recent palaeobiological reconstructions have built a strong understanding of biodiversity change through the Anthropocene. Hong Kong represents a case study for extreme levels of human development juxtaposed with high marine biodiversity that could be applied to much of the South China Sea region

(Duprey et al. 2017, Ng et al. 2017). Cybulski et al. (2020) investigated the previously unknown history of fossil coral communities in sediment cores there. Similar to the Caribbean (Cramer et al. 2020a), Hong Kong has experienced a 40% range decline in important reef building *Acropora*, which has led to a decrease in reef habitat complexity and functionality for the area (Cybulski et al. 2020). The modern assemblages in areas that are located closest to sources of poor water quality show lower genus diversities compared to those of the natural-baseline fossil assemblages. They concluded that increased nutrients and perhaps sedimentation, associated with extreme development in the region, is the leading stressor impacting modern coral communities – a threat common to most marine life throughout Southeast Asia and the IAA (Todd et al. 2010). Overall degradation of reef ecosystems and a decline in biodiversity resulting from modern Anthropogenic impacts characterise many marine communities within the South China Sea (Chen et al. 2009, Zhao et al. 2012, Li et al. 2013, Clark et al. 2019, Yan et al. 2019, Cybulski et al. 2020).

In summary, multiple lines of observational, historical and palaeobiological evidence reveal that coastal development associated with post-European settlement and overexploitation has degraded Caribbean reef ecosystems for over two centuries (Jackson 1997, Pandolfi et al. 2003, Cramer et al. 2020a). Similar threats are obvious in the IAA as seen in fossil data from adjacent areas such as the Great Barrier Reef and the South China Sea, discussed above, but much less long-term evidence is available for the IAA itself. The similarity between the degradation that occurred in the Caribbean and the degradation we are currently seeing in a region of maximum biodiversity is alarming, particularly as we do not currently have an understanding of the scale or temporal origins of these impacts. In addition, even for the better studied Caribbean region, it remains challenging to quantify how much biodiversity has been lost since the natural Pleistocene baseline estimated by fossil records (Figure 7), especially given the fact that ecosystem compositional change does not directly mean extinction.

There is increasing evidence that anthropogenic-induced climate changes leading to ocean warming, acidification and deoxygenation are degrading the world's marine tropical ecosystems (Yasuhara et al. 2012a, Anthony 2016, Altieri et al. 2017, Breitburg et al. 2018, Yasuhara et al. 2019c, 2020b, Yasuhara & Deutsch 2022). As predicted by some palaeoecological studies, the tropics may become less habitable in the near future (Kiessling et al. 2012, Yasuhara et al. 2020b, Yasuhara & Deutsch 2022). The negative impact of exceedingly high temperatures on tropical diversity is increasingly better recognised, as seen by the equatorial diversity dip for various marine organisms (Chaudhary et al. 2016, Saeedi et al. 2017, Rivadeneira & Poore 2020, Yasuhara et al. 2020b, Boag et al. 2021, Chaudhary et al. 2021, Yasuhara & Deutsch 2022). However, the detrimental impact of warming on tropical alpha diversity was not exclusively anthropogenic, because the start of tropical diversity decline predates the Anthropocene and industrialisation and did not involve any extinction but rather distributional shifts (Yasuhara et al. 2020b). Direct human impacts such as overpopulation, overexploitation, habitat degradation and loss, and pollution, have been, up until recently, more damaging (Jackson et al. 2001, Pandolfi et al. 2005, Lotze & McClenachan 2014) than those as a result of anthropogenic greenhouse gas emission.

Future directions: leading questions and testable hypotheses

Our review of all major hotspots simultaneously allowed us to identify data deficiency and areas of future research, as listed below:

1. The western Tethys and Arabian hotspots have more detailed palaeobiogeographical information, but tend to lack diversity syntheses. The IAA has better syntheses of the history of bio diversity from both palaeontological and molecular data, but palaeobiogeographical distributions are poorly known and palaeontological data remain limited compared to the

western Tethys. Although Caribbean food web and functional groups are well studied in regard to productivity and other oceanic conditions, such information is virtually absent in other hotspots. Complementary studies that focus on these missing pieces will bring a more holistic understanding of diversity dynamics across the global tropics. In general, synthetic and quantitative palaeontological biodiversity data are extremely scarce. This is the major next step.

2. Similarly, comparisons of historical patterns from palaeontological data among different hotspots are needed. The Caribbean hotspot has, for example, seldom been compared with other hotspots. Consequently, the following important questions remain unresolved.

   Is extinction in the Caribbean the primary reason for the differences in IAA and Caribbean biodiversity today? If so, was Caribbean biodiversity as high as that of the IAA in the Miocene before the Pliocene–Pleistocene Caribbean extinction event? Caribbean diversity dropped in the Pliocene–Pleistocene, while IAA fauna avoided similar levels of extinction (as far as we know), with diversity continuing to increase towards the Recent. Indeed, bryozoan data indicate that the Caribbean extinction event was a major reason for lower present-day Caribbean diversity compared to the IAA, and that Miocene Caribbean diversity was at a similar level to Miocene IAA diversity (Di Martino et al. 2018) (Figure 7). However, these patterns have been evaluated only for one well-sampled group, bryozoans, and their universality has yet to be established. This leads to the questions: Was origination, extinction or immigration more important to explain present-day tropical diversity and its heterogeneity than the others? Was diversification in the Miocene–Pliocene (i.e. pre-Caribbean extinction) in both the IAA and Caribbean driven by the same mechanism? Origination, immigration and/or extinction rates may well have been different for the two regions, e.g., based upon their relative connectivity to other regions. To resolve these questions, comparisons of diversity patterns in well-sampled geological sections need to be made, ideally with an understanding of the relative importance of in situ diversification vs immigration as well as estimates of the rates of extinction and origination across different ecological groups.

3. Although the Hopping Hotspots and Whack-A-Mole models explain high diversity as the result of habitat area and complexity provided by tectonic collision, this has neither been tested rigorously nor quantitatively. Our first preliminary attempt (Figures 5 and 6) reveals the importance of quantifying habitat size and complexity in the Cenozoic, which supports both the Hopping Hotspots and Whack-A-Mole models. Alternative drivers, such as temperature, are also important to consider, preferably through the use of regression models and a model selection framework (e.g. see Yasuhara et al. 2009, 2014, 2017b). In addition, the relationship between diversity and environmental factors may not be linear. Therefore, non-linear causality analyses, such as convergent cross mapping, could be more appropriate when attempting to identify drivers of diversity patterns (e.g. Doi et al. 2021).

4. Did the Hopping Hotspots mechanism operate in deeper times? This is a reasonable question, because continental configuration and fragmentation are argued as the main controlling factor of global Phanerozoic marine biodiversity (Valentine & Moores 1970, Zaffos et al. 2017), which is a similar argument to the Hopping Hotspots model with emphasis on habitat size and complexity (nearly equal to continental configuration and fragmentation). Thus, the global hypothesis (Valentine & Moores 1970) may be reasonably scaled down to the regional hypothesis of the Hopping Hotspots (Renema et al. 2008). For example, the Mesozoic (especially Triassic and Jurassic) is a time known for lower continental fragmentation compared to the Cenozoic (Zaffos et al. 2017). Given this, do we expect not to see a biodiversity hotspots in the Triassic and Jurassic? Or, did the Hopping Hotspots mechanism still operate in the Triassic and Jurassic in some other way?

Even in the Cenozoic, we do not have sufficient diversity data to include the Paleocene and early Eocene in our review. Shallow-marine biotic responses to the PETM are known to be complicated (McInerney & Wing 2011, Speijer et al. 2012, Self-Trail et al. 2017, Tian et al. 2021). The Cretaceous–Paleogene (K-Pg) extinction is known to have wiped out the majority of marine species (D'Hondt 2005). However, it is not certain if these events affected the distribution of tropical diversity hotspots. Mannion (2020) suggested similar flat latitudinal diversity gradients both in the Late Cretaceous and the early Eocene. However, Boag et al. (2021) showed substantially different latitudinal diversity patterns between the Late Cretaceous and late Paleocene. Thus, important questions remain: Were tropical hotspot distributions in the Paleocene and early Eocene similar to those of the middle Eocene (in other words, did western Tethys diversity remain highest at that time)? Did the PETM and K-Pg events affect biodiversity hotspots, and if so, how and how much? Did the Hopping Hotspots mechanism operate in the Mesozoic before the K-Pg extinction?

5. The western Tethys, Arabian, Caribbean and IAA regions were once a single pan-tropical Tethyan realm before the Oligocene–Miocene transition, which, then, separated into different biogeographic realms with distinct faunal elements and compositions (e.g. McKenzie 1991b, Harzhauser et al. 2007, Perrin & Bosellini 2012, Yasuhara et al. 2019a). This view may be too simplistic, since a taxonomic group that has a better fossil record than most other groups, the LBF, shows substantial provincialism already in the Eocene (Renema 2007). Accordingly, modern syntheses and updates quantifying and delineating global Eocene tropical biogeography are needed to better understand cosmopolitanism and provincialism in the Cenozoic, and the tectonic contribution to global beta and gamma diversity.

Similarly, did the western Tethys hotspot have disproportionately high biodiversity compared to adjacent regions in the middle Eocene? In our new LBF compilation of late middle Eocene diversity (Figure 5), western Tethys diversity appears higher regionally on average, but there are a few higher diversity sites found in the Arabian and Caribbean regions (red dots in Figure 5). Thus, the important questions are: Was the western Tethys the single hotspot in the middle Eocene before the Arabian hotspot achieved higher diversity in the late Eocene? Otherwise, did the pan-tropical Tethyan realm (at least western Tethys, Arabian and Caribbean regions) have similarly high diversity during the middle Eocene and before it?

6. Did the closure of the Tethyan Seaway at ~19 Ma cause global biotic change? Oligocene–Miocene Caribbean biotic turnover may be associated with this closure as discussed in Section 'Early Cenozoic Tropical America'. A recent study discovered a global shark extinction event at ~19 Ma (Sibert & Rubin 2021a), although the validity of this event has been actively debated (Feichtinger et al. 2021, Naylor et al. 2021, Sibert & Rubin 2021b, c) and a global analysis using a comprehensive fossil dataset found a Cenozoic shark extinction event at the Eocene–Oligocene transition (~34 Ma) instead of at ~19 Ma (Condamine et al. 2019). Thus, the possibility that the Tethyan Seaway closure may have affected not only adjacent regions of the western Tethys, Arabian and IAA, but also the Caribbean and even globally requires further investigation. The breakdown of the vast and single pan-tropical ocean may have affected marine biodiversity substantially and globally.

In addition, unidentified extinction events merit investigations. For example, the Eocene–Oligocene extinction is known in the Caribbean (Hansen 1987, Hansen et al. 2004), western Tethys (Renema 2007) and IAA regions (Renema 2007), but not in the Arabian hotspot (Figure 7). An extinction event is documented in the Oligocene–Miocene transition at ~23 Ma in the Caribbean (Johnson et al. 2008, 2009) and western Tethys regions (Renema 2007), but not in the Arabian and IAA (Figure 7). The LBF record indicates a middle–late

Miocene extinction event just after their diversity peak in the middle Miocene in the IAA (Renema 2007) (Figure 7). So far, this extinction event has not been identified in any other regions and organisms. Further efforts to obtain more original data and harmonise data from other regions and organisms may allow us to understand the nature of these extinctions (region- and/or taxon-specific or global) and, more generally speaking, to identify still unknown regional and global extinction events in different groups.

7. Quantifying the Anthropocene defaunation. Human-induced degradation of tropical biodiversity hotspots is obvious, as we reviewed here. However, accurate quantification of local (alpha) and regional (gamma) diversity loss is more difficult. Study of recent fossil records (Kidwell 2015) can help to quantify what has been lost and when. Down-core analyses of microfossils in short cores covering the Anthropocene or a few hundred years are a powerful tool to reconstruct past human-induced impacts on marine biodiversity (e.g. Yasuhara et al. 2007, Tsujimoto et al. 2008, Yasuhara et al. 2012a, Roff et al. 2013, Narayan et al. 2015), but this is seldom applied in tropical hotspot regions. The other approach is live-dead assemblage comparison (Kidwell 2007). Death assemblages can provide quantification of natural, pre-industrial baseline biodiversity (Clark et al. 2014, Tomašových & Kidwell 2017, Yasuhara et al. 2020b). Conservation palaeoecology using young (Holocene) fossils is increasingly important to understand pre-historical baselines and anthropogenic impacts on biodiversity in decadal and centennial scales beyond the time of biological monitoring (Kidwell 2015) that remains seldom applied in tropical regions (but see Pandolfi & Minchin 1996, Greenstein & Pandolfi 1997, Pandolfi & Greenstein 1997, Greenstein et al. 1998, Roff et al. 2013, Hong et al. 2021, 2022). These approaches are also applicable to investigate how invasive species have changed or affected regional biodiversity (Yasuhara et al. 2012a, Albano et al. 2018), which can be substantial as seen in the Lessepsian migration (Por 1978, Rilov & Galil 2009, Albano et al. 2021, Costello et al. 2021) and Caribbean lionfish (Johnston & Purkis 2011, Albins & Hixon 2013, Johnston & Purkis 2015, Côté & Smith 2018).

8. Some studies use alpha diversity (local diversity: number of species per sample) (e.g. Renema et al. 2008, Yasuhara et al. 2017a) and others use gamma diversity (regional diversity: total number of species in an entire hotspot region in a time bin) (e.g. Jackson & Johnson 2000, Renema 2007). Few studies quantify beta diversity (differences in faunal composition between samples/sites). It is important to understand alpha, beta and gamma diversity to fully characterise macroevolutionary (origination and extinction) and macroecological processes (coexistence and dispersal) that operate(d) on biodiversity. In addition, consistent use of a standard diversity measure will maximise the comparability of biodiversity across studies. Recently, there has been increasing consensus in ecology that Hill numbers (Hill 1973) should be the species diversity measure of choice (Ellison 2010, Chao et al. 2014, 2020). The use of Hill numbers has recently become more common in palaeontology (Yasuhara et al. 2016, Allen et al. 2020, Trubovitz et al. 2020, Yasuhara et al. 2020b, Strotz & Lieberman 2021) and is recommended.

Conclusions

The analysis of biodiversity hotspots through time provides a synthetic view on the Cenozoic history of tropical marine biodiversity (Figures 4 and 7, Tables 1 and 2). All of the biodiversity hotspots of the Eocene Tethys, Eocene–Miocene Arabian, Miocene–Pliocene Caribbean and Miocene–Modern IAA developed in a similar tectonic setting that is an ocean with connections both to the east and to the west and with complex coastlines and numerous islands derived from the collision of continental plates (Harzhauser et al. 2002, 2007, Renema et al. 2008, Coates & Stallard 2013, O'Dea et al. 2016, Hou & Li 2018, Jaramillo 2018). This common ground strongly supports the

roles of Hopping Hotspots and 'Centre-of' mechanisms in generating species diversity. The global Hopping Hotspots model likely explains the Cenozoic diversity among hotspots (Figure 7, Table 2): (1) After the Eocene biodiversity peak, the western Tethys hotspot began declining from the Oligocene to the Miocene due to the narrowing connection to the Indian Ocean and cooling. (2) Related to the decrease in suitable habitats in the western Tethys at that time, Tethyan taxa pumped out to the east towards the Arabian hotspot and then to the IAA and west towards the Caribbean. (3) In the Miocene, tectonics created suitable habitats and preconditioned the IAA and Caribbean hotspots. (4) Thus, the IAA and Caribbean hotspots commenced from the Miocene (the Caribbean hotspot may have commenced a bit earlier, in the Oligocene). In contrast, the 'Centre-of' hypotheses may better explain diversity dynamics within a hotspot. Indeed, the IAA hotspot with connection to adjacent regions both to the east and to the west further diversified into the present day, aided by a Pliocene–Pleistocene biological pump with TECOG processes. The Caribbean hotspot collapsed due to a Pliocene–Pleistocene extinction event caused by the closure of its western connection (but note that the Caribbean showed substantial diversification again after the extinction and seaway closure).

Temperature may have been an important precondition in the western Tethys becoming an Eocene biodiversity hotspot, i.e., the temperature was not too hot but still sufficiently high to sustain high biodiversity compared to 'too hot' equatorial regions at that time. Human activities have subsequently degraded the IAA and Caribbean hotspots, yet a quantitative estimate and timeline of biodiversity loss (either locally with reduced coexistence in an area or regionally with extinctions) since the natural Pleistocene baseline is lacking. Aside from the iconic extinction and collapse of charismatic megafauna such as the Caribbean monk seal and sea turtles, little is known about Anthropocene marine extinctions of fishes and invertebrates.

Our review highlights recent progress in understanding Cenozoic tropical biodiversity hotspots. However, many aspects of past tropical biodiversity remain unknown. By tackling the above-mentioned questions in the last section, we will advance the understanding of tropical biodiversity in the past, present and future. Quantitative deep-time synthesis of global marine tropical biodiversity will require substantial effort.

Acknowledgements

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