

Collision, mantle convection and Tethyan closure in the Eastern Mediterranean

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Abstract

The Tethys Seaway once linked the Atlantic and Indo-Pacific oceans. Its gradual shallowing and closure impacted global ocean circulation, faunal diversification and climatic changes. In this Review, we evaluate the tectonic causes and the topographic changes across the Eastern Mediterranean over the past 66 Ma and explore the consequences of Tethys Seaway closure. Mantle convection led to collisional tectonic processes, mountain building and crustal thickening along the Tethyan realm. The Ethiopian flood basalts mark the arrival of the Afar plume at ~30 Ma, followed by northward-trending volcanic activity indicating that plume material had moved to northwest Arabia by ~20 Ma. Plume-induced mantle flow generated kilometre-scale uplift across East Africa, at ~8° N at ~35 Ma, and along Arabia and led to the formation of the *Gomphotherium* land bridge at 30° N, ~20 Ma. Afro-Arabian uplift contributed to the development of modern-like Asian monsoons, and the land bridge between Africa and Asia enabled one of the greatest faunal interchanges of the Cenozoic. The gradual shoaling and final closure of the Tethys Seaway likely facilitated the transition towards a stronger overturning circulation in the North Atlantic, contributing to the Cenozoic cooling trend. Future research should incorporate more detailed spatial and temporal uplift models into paleogeography and paleoclimate models to better simulate consequences for ocean circulation, climate and biogeographic dispersals.

Sections

Introduction

Africa–Arabia tectonic evolution

Mantle convection and the Afar plume

Implications of land bridge formation

Summary and future perspectives

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Introduction

The Arabia–Eurasia continental collision closed the Neotethys Ocean, ending the oceanic transport between the Indian and Atlantic Oceans through the Tethys Seaway. The collision was governed by plate tectonics and mantle convection and had profound impacts on ocean circulation, biogeography and the climate system beyond the Eastern Mediterranean–Tethyan realm.

The Tethyan Belt (also known as the Alpine–Himalaya belt) is an area of orogenic activity encompassing the mountain ranges from the western Mediterranean to the Himalayas in the east (Fig. 1 and Box 1), driven by subduction and continental collision. Since the Late Cretaceous, at ~100 Ma, subduction of the Tethys Ocean has caused the African Plate to slowly approach Eurasia, and it has also been uplifted and thinned by mantle plumes, contributing to its fragmentation into continental blocks. The continental blocks consist of Adria (Alpine Mediterranean orogeny), Arabia (Bitlis–Zagros–Caucasus–Alborz) and India (Karakoram–Himalayan–Tibet). These continental blocks drifted apart from Africa at different times and moved northward towards the Tethyan subduction zone, colliding and ending up amalgamated with Eurasia^{1–4}. Adria rifted apart from Africa in the Late Jurassic but remained kinematically linked to Africa as a promontory until at least the past million years. India separated from Africa in the Late Cretaceous (~90 Ma), and Arabia lastly starting in the Late Oligocene (~25 Ma)^{2,5,6}. The process leading to the separation of those blocks from Africa involves mantle upwellings, at least in the case of Arabia and India, as indicated by likely associated large igneous provinces, the Afar and Deccan flood basalts, respectively^{7,8}.

The tectonic, geodynamic and climatic history of this region is now becoming better constrained^{9–13}, as is the regional paleogeographic importance of these interconnected processes in influencing large-scale biogeographic dispersals¹⁴ and even impacting human evolution by providing migration routes for early anthropoid primates¹⁵.

In this Review, we explore the tectonic and geodynamic processes that caused the closure of the Tethys Seaway and discuss the implications for ocean circulation, faunal diversification and climate. We focus on the formation of the Tethys collisional belt, particularly in Arabia and the Middle East, as the separation of Arabia from Africa is relatively recent (~25 Ma)^{16,17}, and collision is ongoing. We begin by evaluating the tectonic and geodynamic evolution of the Mediterranean–Tethyan realm, followed by the relative role of tectonics, volcanism and mantle convection in the closure of the Tethys Seaway. Finally, we explore the impact on biogeography and Cenozoic climate evolution.

Africa–Arabia tectonic evolution

Africa and Arabia were connected in the early Cenozoic, until rifting in the Red Sea and Gulf of Aden led to separation by the Miocene. Concurrently, Arabia's northward motion and collision with Eurasia caused major crustal deformation, volcanism and plateau uplift. These tectonic processes ultimately closed the deep oceanic part of the Tethys Seaway.

Africa–Arabia separation

To understand the history of Arabian plate motion, we need to reconstruct its evolution in the early Cenozoic, before continental collision, around ~50 Ma to 40 Ma. At that time, Arabia was still part of Africa and separated from Eurasia by the Neotethys Ocean, with the oceanic lithosphere subducting northward along the Bitlis–Zagros, Aegean and Cyprean trenches^{1,2,5,13}. Africa–Arabia was progressing at a speed of about ~2–3 cm yr⁻¹ relative to Eurasia in a north-northeasterly direction¹⁸.

The separation of Arabia from Africa started with the formation of the Gulf of Aden and Red Sea rift systems at the beginning of the Oligocene^{16,19,20}. However, full separation at a mid-ocean ridge did not start until the Miocene, at ~17 Ma in the Gulf of Aden¹⁶ and at ~13–12 Ma in the Red Sea¹⁷. The northward movement of Arabia as a single plate was accommodated by the development of two transform plate boundaries: the Dead Sea Fault to the west²¹ and the Owen Fracture Zone to the east²².

Along the margins of the Red Sea, dykes and basaltic floods were emplaced during the Oligocene^{19,20}, and syn-rift deposits accumulated from the Oligocene–Miocene (~30–25 Ma) to Miocene (14 Ma)^{18,23}. Thermochronology shows that uplift of the Red Sea rift shoulders commenced at ~29–26 Ma and peaked at ~20 Ma (ref. 20). Continental rifting at the Gulf of Aden is likely older, between 38 Ma and 33 Ma (refs. 24–26), concurrently with, or slightly earlier than, the onset of the Arabia–Eurasia collision.

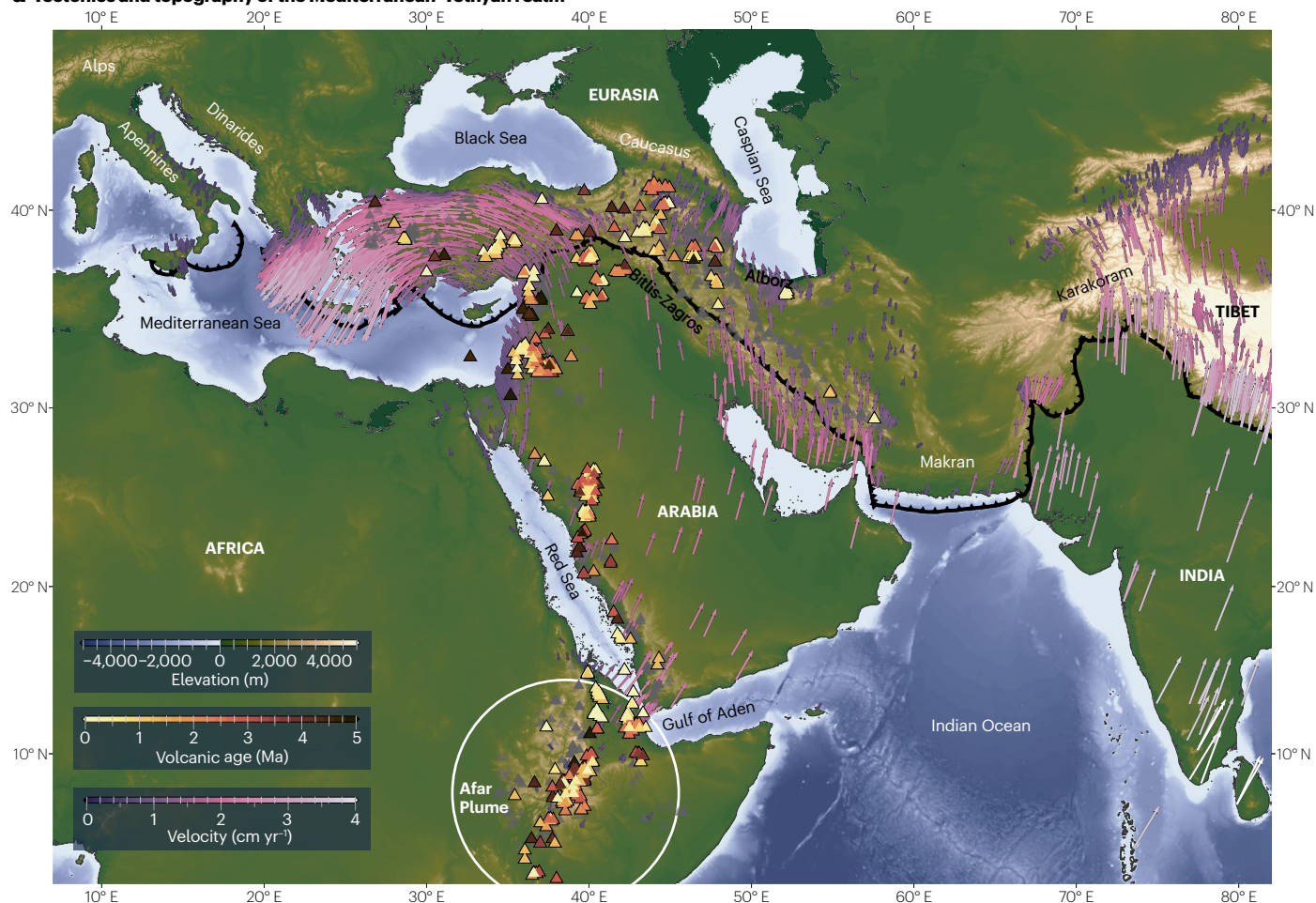
Volcanism in Ethiopia slightly predates extension, starting at ~40–45 Ma (ref. 27), but with a climax during the Oligocene formation of the Ethiopian flood basalts²⁸, which covered parts of Ethiopia, Eritrea, southern Sudan and western Yemen (Fig. 1) with the emplacement of 1 million cubic kilometres of lava by 31–29 Ma (ref. 29). The emplacement of this large igneous province was accompanied by the development of a regional truncation surface extending from the northern Red Sea to the southern Levant region related to the formation of a crustal dome, ~3,000–1500 km in radius, above the Afar plume^{30–33}.

Intraplate volcanism is also present in Arabia with large basaltic effusions and within the collisional zone (Eastern Anatolia), with an overall progressive northward-younging trend^{34–37} (Figs. 1 and 2 and Box 1). Volcanism in Arabia at Harrat Ash Shamah and in northwestern Syria began ~25 Ma (refs. 34,35) and has continued intermittently since then. The change in geochemical signature in eastern Anatolia ~10 Ma has been also connected with the arrival of a new source of hot mantle material within the collisional zone^{36–38}.

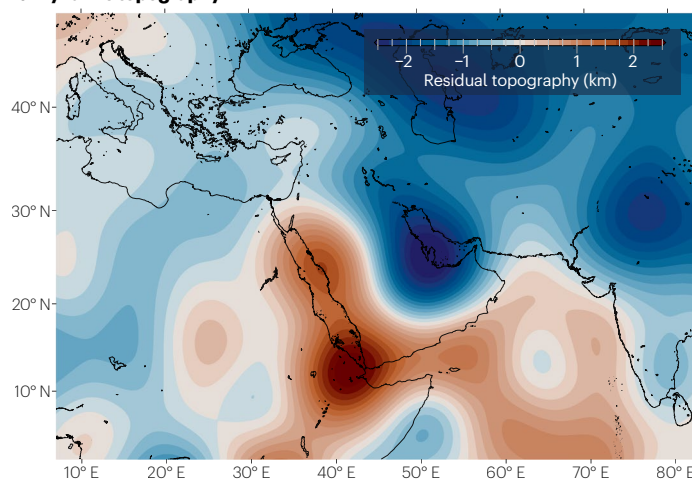
Arabia–Eurasia collision

The onset of the Arabia–Eurasia collision is controversial and probably includes an initial phase of 'soft' collision, which is characterized by a transition from subduction of oceanic lithosphere to thinned continental margin, followed by a 'hard' one, with the arrival of thick continental crust. Collision is likely to be diachronous, with an overall eastward-younging trend³⁹. It is considered to have occurred sometime between the late Eocene^{39–43} and the early Miocene^{3,44,45}, although newer studies indicate that by the middle Oligocene (~28–26 Ma), the Neotethys oceanic lithosphere had been subducted, placing the Arabia passive margin and its cover of abducted Late Cretaceous ophiolites in the foreland position^{46–48}. Between 30–35 Ma and ~20 Ma, collisional deformation was very limited and mostly localized in proximity of the plate suture⁴² and along the northern edge of the collision zone, around the southern Caspian Sea rigid block³⁹. Meanwhile, the subduction velocity decreased progressively from ~3 cm yr⁻¹ to 1.5–2.0 cm yr⁻¹ because the trench stopped retreating and started advancing⁴⁹. Regardless, shortening increased across the entire collision zone by 20 Ma, leading to the accretion of the Arabian passive margin to the upper plate with the formation of the high Zagros, the Zagros fold and thrust belt, and the Bitlis mountains^{3,40,42,50}. The shortening was accompanied by the gradual thickening of the crust with maximum values of up to 70 km beneath the suture zone^{51,52} and by the extensive upper plate deformation with the inversion of Meso–Cenozoic extensional basins along the

a Tectonics and topography of the Mediterranean–Tethyan realm



b Dynamic topography



c Mantle heterogeneities

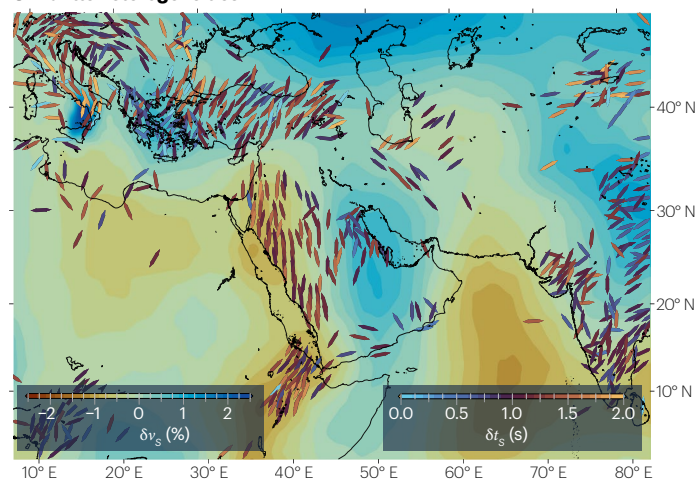


Fig. 1 | Topography, kinematics and dynamics of the Mediterranean–Tethyan realm. a, Elevation of the Alpine–Himalaya region, marked with active collisional plate boundaries (bold black line with triangles). The estimated location of the Afar plume is marked with a white circle. Recent volcanics (0–5 Ma; coloured triangles) are obtained by joining together the data sets from refs. [38](#),[132](#), volcanics older than 5 Ma are coloured transparent grey. Global Positioning System (GPS) velocities show the tectonic motion

relative to Eurasia (purple arrows; data from the compilation of ref. [212](#)). **b**, Residual topography (data from ref. [148](#)). **c**, Seismic tomography at 250 km depth (data from TX2019 (ref. [213](#))). Coloured arrows show SKS splitting (shear-wave splitting of SKS waves, updated compilation of ref. [214](#)). There are correlations among elevation, volcanism, residual topography and seismic tomography.

northern sectors of the collision zone from the Central Pontides in Turkey to the Koppeh Dag in eastern Iran^{39,53–55}.

The collision was also associated with large-scale surface uplift, leading to the formation of the second largest collisional plateau on Earth after Tibet: the Anatolian–Iranian Plateau that extends from central Anatolia to southeast Iran⁵⁶. Overall, upper plate shortening is expected to be on the order of ~300 km (ref. 49), although a substantial fraction of plate convergence could have been locally accommodated by intraplate subduction processes beneath the Caucasus⁵⁷ and along its eastern continuation in the central Caspian Sea Apsheron Balkhan Sill⁵⁸. Additional mechanisms that accommodated collisional deformation are oroclinal bending across different rigid crustal blocks forming the northern margin of the collision zone^{59,60} and the lateral extrusion of Anatolia along the North and the East Anatolian faults from the late Miocene^{61–63}. Finally, during the early collision stages in the Oligocene, a pronounced phase of back-arc extension initiated in the Aegean due to trench retreat, which is slab rollback in an absolute, lower mantle reference frame^{1,64,65}.

Those constraints indicate that the separation of Arabia from Africa and the origin of new oceanic lithosphere occurred during an

ongoing collisional process to the north. In addition, the northward velocity of Arabia motion surprisingly remained roughly constant, regardless of the ongoing collision which probably produced an increase in resisting forces, and lacks slab pull forces^{66,67}. Its present-day motion, as derived from GPS (Fig. 1 and Box 1), does not differ from the plate tectonic estimate of motion since the early Miocene¹⁸.

Closing the deep gateway

The arrival of the stretched continental passive margin of Arabia at the Eurasian trench instigated the closure of the deep oceanic gateway, perhaps as early as the late Eocene^{1,68}. Marine conditions just south of the plate boundary could have persisted until the Early Miocene^{45,69}, although there was likely no continuous deep marine gateway after this time (Fig. 3). However, an intermediate-shallow seaway crossed the Arabian continent during the Oligocene and early Miocene, connecting the Indo-Pacific and proto-Mediterranean oceans. This seaway is sometimes referred to as the Mesopotamian Trough and allowed shallow water throughflow between the nascent Mediterranean Sea and the Indian Ocean. This epicontinental seaway acted as an efficient biogeographic barrier hindering mammal exchange between Afro-Arabia and Eurasia⁷⁰. That seaway eventually closed in the late early Miocene (~19 Ma) with the emergence of the *Gomphotherium* land bridge, named after the iconic proboscideans that reached Asia from Africa at that time^{70,71}. Although the major land bridge is thought to have remained in place, there are geological indicators for a re-opening of a shallow seaway in the mid Miocene (~16–12 Ma) across Arabia^{9,72–74}. A similar marine connection might have existed across the upper plate in periods from the Oligocene to the early Miocene. This epicontinental sea, known in Iran as the Qom Sea, marks an episode of regional subsidence that occurred across the entire collision zone, possibly due to dynamic subsidence induced by slab and/or deep mantle dynamics⁴⁹.

The separation of Africa and Arabia and the subsequent collision with Eurasia altered regional geography and closed the deeper part of the Tethys Seaway. However, regional topographic evolution, Arabia plate motion and closure of the epicontinental seaway across Arabia were ultimately driven by mantle convection and corresponding dynamic topography (discussed subsequently), which fundamentally impacted the geography of the Middle East and beyond.

Mantle convection and the Afar plume

Mantle convection has driven and modified surface processes in the Tethys region. We explore both the theoretical underpinnings of mantle convection and the numerical modelling methods that could unravel its impact on regional uplift, volcanism and tectonic reconfiguration.

Mantle convection-surface tectonic links

The Mediterranean–Middle East Horn of Africa is a promising area to explore the connections between mantle convection and surface tectonics. Here, subduction and collision are flanked by a large-scale upwelling and large igneous province emplacement, which has influenced the evolution of the region. Previous efforts illustrate that the mantle has a dominant role for tectonics in this scenario^{38,75–80}.

The general dynamics of plate tectonics as part of mantle convection can be explored, for example, by capturing Earth's complexities such as temperature-dependent viscosity and the role of phase transitions in generic numerical models. Such computations can provide general insights into heat and mass transport rates and typical convective scenarios, such as the controls on slab avalanching and subduction triggering plumes at the core–mantle boundary (CMB)^{81–83}.

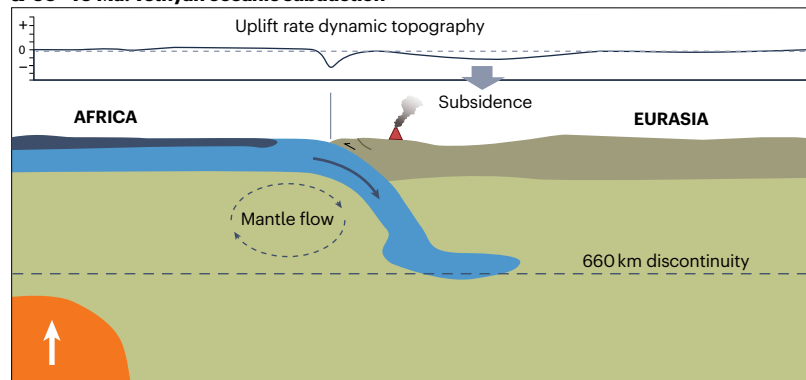
Box 1 | Present-day kinematics and dynamics of the Mediterranean–Tethyan realm

Space geodetic techniques provide a detailed picture of the Africa–Arabia–Eurasia system^{119,216,217} (Fig. 1a), showing Arabia moving northward at a rate of ~1.5 cm yr⁻¹ relative to Eurasia, much faster than Africa. This movement causes the opening of the Red Sea to the south and colliding to the north. Anatolia moves westward at ~2 cm yr⁻¹ (ref. 217), and the Aegean region moves even faster at ~3.3 cm yr⁻¹ south towards the retreating Hellenic trench^{216,217}. This pattern generates a large, anticlockwise circuit with a pole of rotation around the Nile Delta¹¹⁹ (Fig. 1a).

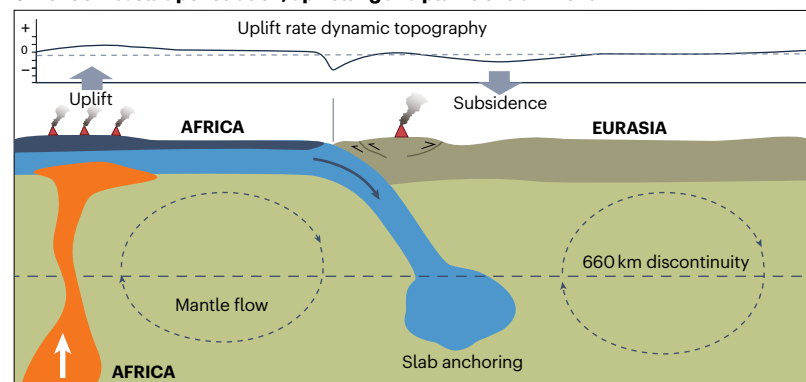
Residual topography estimates show elongated positive anomalies, with a large bulge over the Ethiopian plateau, following the eastern shoulder of the Red Sea and extending northward towards northwest Arabia^{37,107,152,153} (Fig. 1b). By construction, these topographic anomalies are not isostatically supported and can be compared with seismic tomography (Fig. 1c). Both positive and negative residual topography anomalies correspond to low and high seismic velocity anomalies in the upper mantle, respectively. This correlation suggests that the thermal structure of the mantle and the associated radial convection patterns, with hot upwellings and cold downwellings, are influencing surface topography^{37,78,89,106,107,152,218}.

Horizontal mantle flow can be deduced from SKS splitting inferences of seismic anisotropy, sensitive to the orientation of deformation in upper mantle flow^{37,80,219}. The SKS 'fast axes' align with shear to first order and thus indicate a northerly flow trend in the region, following the positive residual topography and then turn to a northeasterly direction below Anatolia and Iran (Fig. 1c). Mantle flow, therefore, likely contributes to higher elevations from Afar towards northwest Arabia at present, and past convective effects were also likely relevant, including for the Arabia–Eurasia collision and closure of the Tethys Seaway.

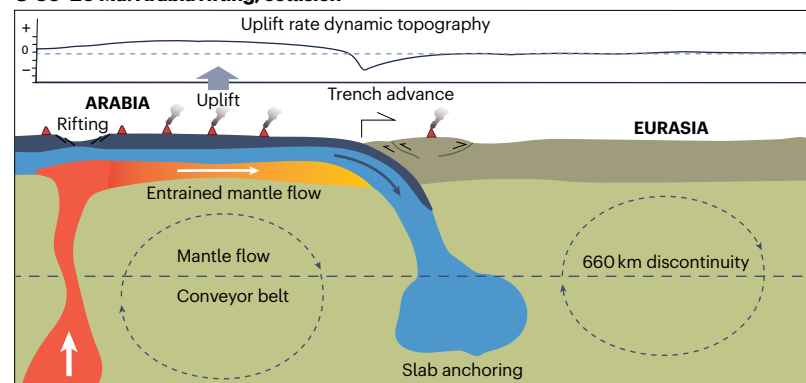
a 50–40 Ma: Tethyan oceanic subduction



b 40–30 Ma: slab penetration, upwelling and plume entrainment



c 30–20 Ma: Arabia rifting, collision



d 20–10 Ma: Arabia break-up, collision and slab break off

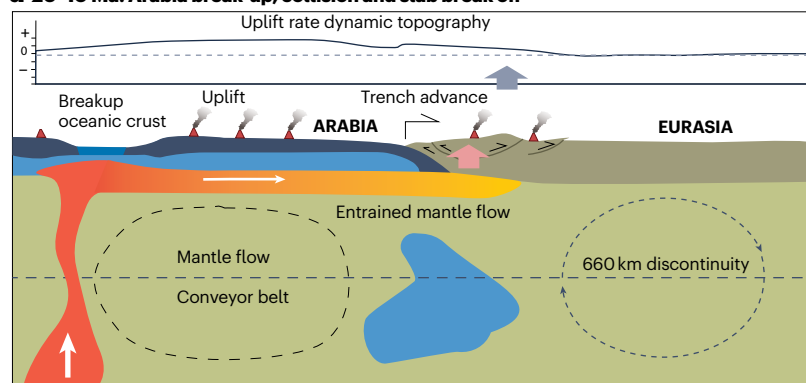


Fig. 2 | Tectonic and geodynamic evolution of the collisional system. **a**, Subduction causes subsidence in the overriding Eurasian plate above the slab (blue region). **b**, The plume (orange region) arrives below the African lithosphere and causes uplift and volcanism above. Subducted material penetrates into the lower mantle (slab anchoring), and subsidence in the upper plate continues as the amount of subducted material increases. **c**, The plume-induced uplift could migrate laterally if the plume material is entrained by large-scale convection towards the collisional zone. Continental crust arrives in the subduction zone and the trench begins to advance. **d**, Uplift eventually also occurs in the overriding plate, as the plume material further migrates laterally, the trench advances further and the slab breaks off. This figure shows the stepwise Cenozoic evolution of the Eastern Mediterranean–Tethyan realm.

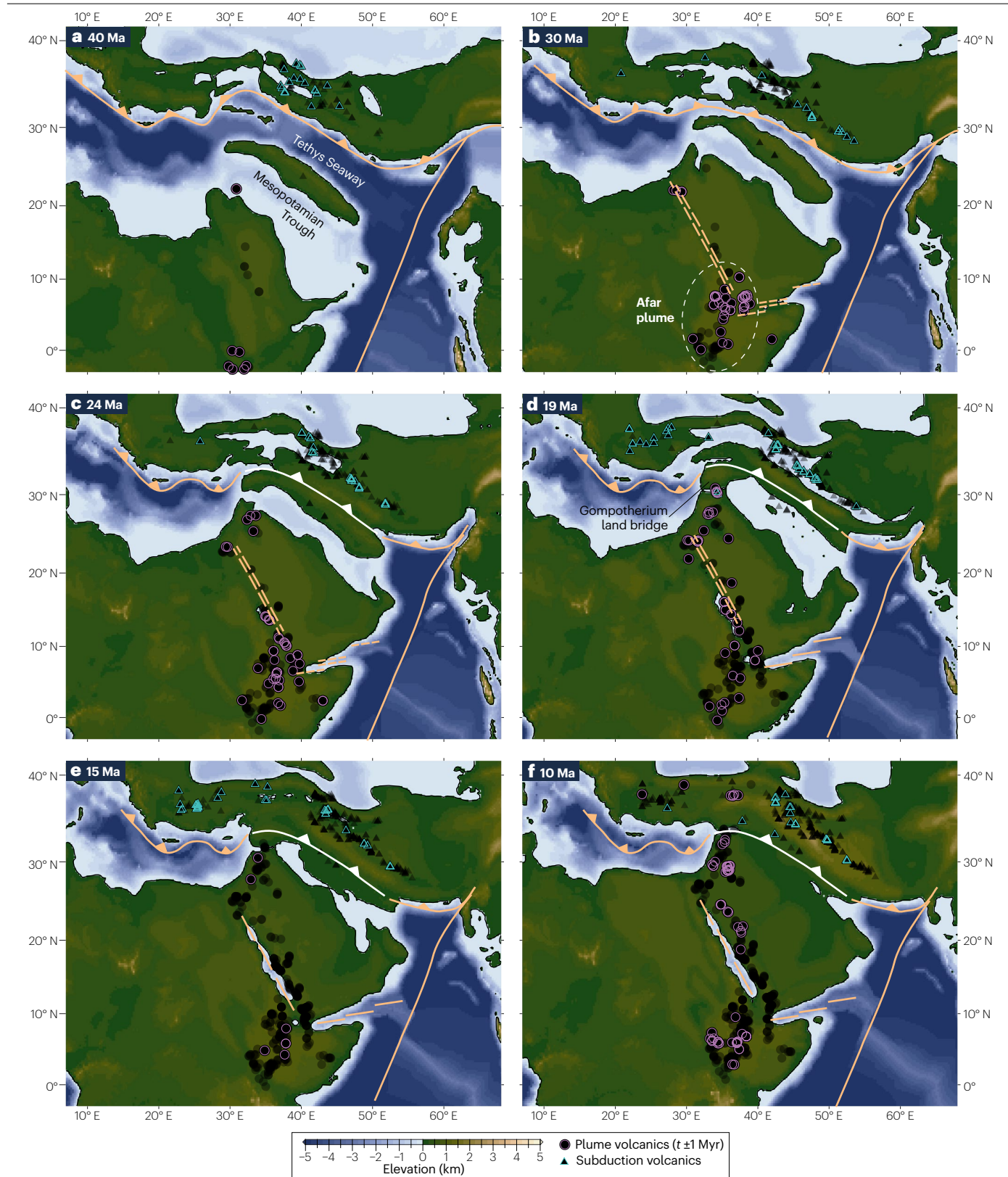


Fig. 3 | Paleogeography and volcanic activity during the Arabia–Eurasia collision. **a**, Triangles indicate subduction-related volcanism, whereas the circles indicate mantle-related or plume-related volcanism. The purple outlined circles and cyan outlined triangles show volcanics dated within ± 1 Myr from the specific time. Orange lines show plate boundaries. Data on volcanism were derived from

published studies realized between 1976 and 2023 within the study area (see Supplementary Dataset 1 for the complete list) and by joining together the data sets from refs. 38,132. The volcanism migrated northward from East Africa in the Late Eocene, across Arabia and moving further northward until the present.

However, when exploring the details of tectonics or specific contributions to surface topography in settings such as the Eastern Mediterranean, then global mantle circulation computations that incorporate seismological and other constraints are advantageous.

Mantle circulation models solve the equations of conservation of mass and momentum and predict velocities and stresses for any type of plate boundary configurations and internal density and viscosity distributions^{84–86}. Density anomalies can be inferred from Wadati–Benioff zone delineated slabs, or throughout the mantle from scaled seismic velocity anomalies in mantle tomography^{85–89}. Although compositional anomalies and imaging issues complicate such interpretation, away from the cratonic lithosphere at the surface or the lowermost mantle’s thermochemical anomalies, shear wave tomography of the mantle is, to first order, dominated by temperature anomalies. Mantle rheology is complex but absolute, average upper mantle viscosities can be inferred from global isostatic adjustment and laboratory constraints, for example, and lateral and depth variations of viscosity can be inferred from the given temperature anomalies and matching geophysical constraints such as the geoid^{90–92}. The assumptions inherent in constructing such mantle circulation can then be tested further using several independent constraints, including plate velocities, total heat transport and the match to seismic anisotropy^{84,93–98}.

There are trade-offs in such modelling. For example, the sinking (Stokes) velocity of an anomalously dense slab within the mantle, or the velocity of the plate it is being connected to, is given by the ratio of density anomaly and viscosity, and both properties are only known within uncertainties. However, combination of a range of constraints allows building consistent models. For example, the stress-related quantities of the geoid or dynamic topography will, to first order, not change if mantle viscosity changes by a constant factor everywhere, which provides an opportunity for joint inversion^{88,99,100}. The current generation of mantle circulation models can fit both the geoid and plate velocities well for simple mineral physics motivated scalings of tomography, as long as an increase of viscosity from the upper to the lower mantle, and a relatively strong lithosphere is included^{101–105}.

With the background of having confidence in such large-scale geodynamic background, or ‘reference’, models, one can then move to explore regional mobile belts, for example, the Afar–Arabia–Anatolia system presented below, and test the role of different contributions such as active upwellings compared with regional slab pull for driving plate and microplate motions, generating dynamic topography or explaining the seismic anisotropy signal seen in SKS splitting (Fig. 1c) from mantle shear^{37,78,89,106,107}.

One can also attempt to quantitatively reconstruct the internal density distribution of the mantle for the relatively recent geological past during the evolution of the plate–mantle system. This reconstruction can be done by utilizing or assimilating geological information on past plate geometries and motions, for example, by prescribing those kinematics and then turning back the clock by reversing the flow in the mantle^{108–113}. Such backward mantle convection methods are limited in their reliability to the past ~60 Ma and to those anomalies that are not advected into or out of thermal boundary layers and are

subject to a range of uncertainties^{109,114}, but are possible because heat transport in vigorous thermal convection in the interior of the mantle is dominated by advection. However, diffusion becomes relevant over longer times and in the thermal boundary layers, that is, within the lithosphere and near the CMB. At the surface, paleo-age grids can be used¹¹⁵ as a constraint for past lithosphere thermal and density structure¹¹⁰. At depth, one must make other choices as diffusion is not time reversible.

However, such convection reconstructions can provide good first-order estimates, for example, of the time-evolving dynamic topography as associated with the transport of density anomalies towards the state at present as seen by seismic tomography^{107,116–118}.

Collision dynamics

On largest scales, the motion of Arabia is part of the closure of the Tethyan ocean, which is at present reflected in broadly comparable patterns of collision and extrusion in the Anatolia–Arabia system in the west and the India–South East Asia system in the East⁵². Within this system, previous models suggested that Arabia’s northward movement relative to Africa is driven by the pull of the active subduction system in the Hellenic. The westward acceleration of the geodetic field supports this mechanism as the primary driving force^{37,119}.

The motion of Arabia has also been related to slab pull^{120,121}. However, there is evidence that the slab has been broken beneath the Bitlis suture, most likely since the middle Miocene^{61,66,67,122}, so that the only active subduction zone is confined to the Makran, where the subduction of oceanic lithosphere is still occurring¹²³. This configuration, however, is likely too narrow to account for the motion of the entire Arabian plate. Another possible explanation is that the Afar plume is pushing Arabia northward, even though the constant velocity attained by Arabia during the past ~30 Ma (ref. 121) contrasts with the expected progressive decrease in velocity from a main upwelling plume phase at ~32 Ma (ref. 124). Another possible model proposes that mantle drag related to a large-scale convection cell could efficiently pull continental plates towards collisional zones (Fig. 2), thus favouring indentation^{37,78,125}. This conceptual model is supported by several arguments discussed in the following sections.

The development of a large-scale convection cell for mantle drag, however, requires the establishment of an efficient asthenospheric-scale circulation system involving both upwelling and downwelling. For such scenarios of links between the deep mantle and surface tectonics, seismic tomography anomalies can be helpful, either from direct interpretation or from mantle circulation modelling, including going backward in time. Although evidence of upwelling comes from the Afar Plume, the downwelling must be located beneath the collision zone.

One way to illustrate the links between tectonic evolution and tomography is by means of associating past subduction with convergent plate boundaries⁹². One such research effort is the ‘Atlas of the Underworld’¹²⁶, which illustrates connections between a range of seismic tomography anomalies and tectonics and their uncertainties. In the Tethys region, the Atlas identifies a number of separate slabs, associated with individual subduction zones that occurred in the

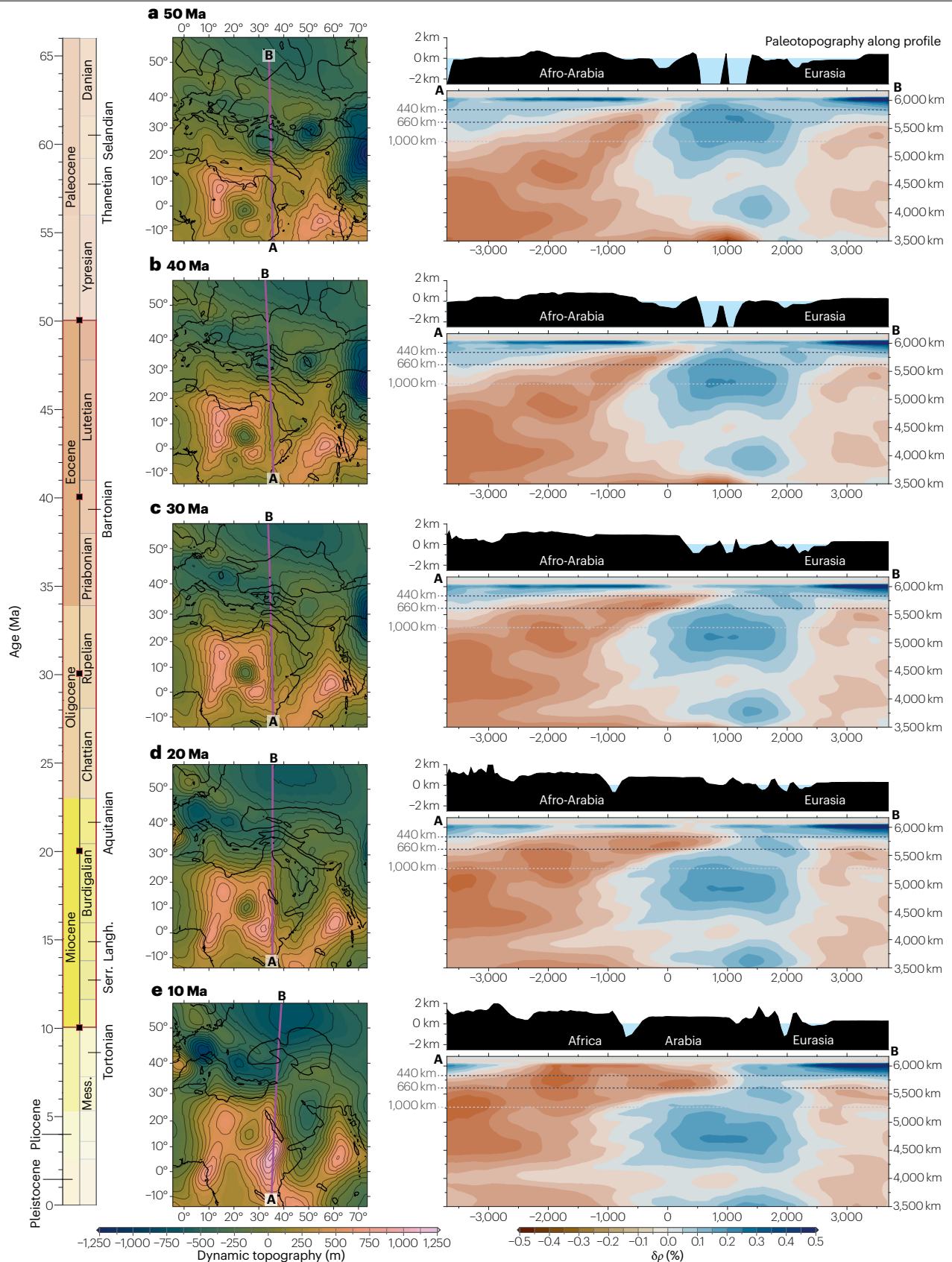


Fig. 4 | Evolution of paleodynamic topography, paleotopography and mantle cross-sections. a, 50 Ma. b, 40 Ma. c, 30 Ma. d, 20 Ma. e, 10 Ma. The maps on the left of each panel show paleodynamic topography from the results of ref. 9 using TX2019 (ref. 213), seismic tomography. The right panels show the paleotopography and mantle density structure along the profiles coloured pink

collision zone. For example, along the cross-section shown in Fig. 4, and conceptualized schematically in Fig. 2, ref. 126 identifies the Arabia slab at depth 1,100–2,200 km with top age 75–65 Ma and the Mesopotamia slab at depth 1,250–2,200 km with top age 70–60 Ma. However, these two slabs are not clearly distinguishable in the tomography models, with exception for Model SEMUCB-WM1 (Supplementary Fig. 5), which are the basis of the numerical model shown in Fig. 4 and Supplementary Figs. 1–5 and thus also of our schematic in Fig. 2.

The backward-advection procedure seeks to explore links between convective paths over the past tens of million years to what has been imaged in tomography. This approach is most appropriate for high seismic velocity structures in the mid-mantle, interpreted as regions of high density. Backward-advection reconstructions work to bring the tops of those high seismic velocity regions back close to the surface at 50 Ma. The results of this approach match well with the top ages of those slabs¹²⁶. At that time, their bases are computed to be in the lower mantle. Hence, we estimate that those slabs entered the lower mantle somewhat earlier than 50 Ma. Further west, the entrance of the Aegean slab into the lower mantle has been estimated to have occurred at 50–40 Ma (refs. 37,127–129). This slab can also be identified in the right-side upper part of the left most (top row) cross-sections of Supplementary Figs. 1–5.

Such backward-advection modelling indicates that the Aegean slab entered the lower mantle somewhat earlier than 50–40 Ma, related to its present-day extent somewhat deeper than 1,400 km, according to the tomography models shown (Supplementary Figs. 1–5). Further east below Iran and Afghanistan, ref. 126 identified the Zagros and Sistan slabs. These slabs can also be identified in the cross-sections of the tomography models displayed in Supplementary Figs. 1–5: the Zagros slab can be seen – although somewhat smeared out – in the upper parts of the third row, whereas the Sistan slab is in the middle parts of the fourth row. These global models do not distinguish so clearly between individual slabs and both horizontally and vertically, images are more like a continuous, although somewhat blobby, slab curtain.

Estimates of the age of tomographic anomalies critically depend on assumed or modelled slab sinking rate, and those are somewhat uncertain. For example, global correlation analysis based on mantle circulation modelling leads to sinking rates that are faster than those of refs. 126,130,131. The entrance of the Tethyan slab into the lower mantle below Iran is less clear. However, there are two important episodes of regional upper plate subsidence that could have marked this event⁴⁹. One occurred in the late Eocene and was associated with a widespread magmatic flare-up, whereas the other took place in the early Miocene and was linked to volcanism localized in proximity to the suture zone¹³². In terms of the establishment of a mantle convection cell, slabs do not need to reach the CMB to trigger plumes there. Rather, as soon as they have reached the high-viscosity lower mantle, they start pushing material ahead of them that could trigger plumes at the CMB. In regions of large-scale upwelling flow, the plume heads might take less than 30 Myr to reach the surface¹³³. Hence, slabs entering the lower mantle at ~60–50 Myr could have triggered the Afar plume reaching the surface at ~30 Ma.

in the maps on the left. The latter is computed by backward-adverting present-day density structure inferred from tomography. Profiles are moving with the mantle in the paleomagnetic reference frame of ref. 215. The modelled dynamic topography anomaly moves northward, corresponding to northward mantle flow seen in the cross-section of the mantle density anomalies.

In conclusion, the entrance of the slab into the lower mantle and Afar plume upwelling may be considered as connected, generating a convection cell and a conveyor belt, whose expression on the surface should be manifested by two main processes: topography and volcanism (Fig. 2). Although here we reconstruct past mantle structure by backward-adverting density anomalies inferred from tomography, an alternative approach uses subduction history to forward model mantle density and adjust the model to obtain a good fit with seismic tomography^{134–136}. A slab sinking speed of $2 \pm 0.8 \text{ cm yr}^{-1}$ was determined by matching features that occur in both geodynamic and tomography models¹³⁰, a value substantiated by the analysis of ref. 131. Subducted slabs in such models will trigger plumes at the CMB, particularly along margins of thermochemical piles^{137–139}, the locations of which can be compared with actual large igneous provinces¹⁴⁰. Instead of imposing subduction zones, it is also possible to let them develop self-consistently. Also in this case, they will trigger plumes forming at the CMB¹⁴¹.

Plume arrival, mantle flow and volcanism

The development of the topography connecting Africa and Eurasia (the Middle East) began in the late Eocene. Around 40–35 Ma, the Tethyan Ocean continued subducting beneath the Hellenic-Cyprus Arcs, whereas the Arabian continent moved towards the trench to the east, initiating an early incipient collision stage. Meanwhile, hundreds of kilometres south of this convergent margin, a large-scale uplift and doming process commenced (Fig. 3) in East Africa (specifically the Ethiopian Plateau) and Yemen, gradually extending to northern Arabia^{11,30,31,33,142–145} (Fig. 1a). This uplift was likely linked to the arrival of the Afar plume and associated mantle flow, accompanied by volcanic activity that culminated in the massive eruption of the Ethiopian large igneous province around 35–30 Ma (refs. 27–29).

Beginning in the late Eocene and continuing through the Oligocene and early Miocene, volcanic activity, associated with mantle flow and subduction, deposited numerous volcanic rocks throughout the Tethys region and the region stretching from East Africa towards the Tethys (Fig. 3). This volcanic activity, related to mantle flow, appears to have migrated northward from present-day northeast Africa, eventually extending to northwest Arabia^{11,38,132} (Figs. 1 and 3). By the early Miocene, the main zone of increased volcanism had reached what is northern Arabia, coinciding with the formation of the *Gomphotherium* land bridge and the closure of the Tethys Seaway (Fig. 3). Volcanic records, mantle flow models and topographic reconstructions suggest a connection between mantle upwelling and surface uplift, which contributed to the formation of this land bridge.

If the Afar plume arrived below the lithosphere around 35 Ma at approximately 8°N ¹⁴⁶ and the land bridge occurred at ~20 Ma at 30°N , this would imply a mantle flow speed of $20\text{--}15 \text{ cm yr}^{-1}$ – substantially faster than typical northward flow estimates of $5\text{--}10 \text{ cm yr}^{-1}$ (for example, ref. 147). Mantle flow velocities could indeed be higher with lower asthenospheric viscosities, and northward flow may have been channelled between regions of thicker lithosphere, which are marked by

faster seismic velocities in the uppermost mantle^{37,38,148}. For example, assuming a channel width of 500 km, a depth of 100 km and a density anomaly of 25 kg m^{-3} (equivalent to a temperature anomaly about 250 K), a mean flow speed of 20 cm yr^{-1} would correspond to a buoyancy flux of approximately $8 \times 10^3 \text{ kg m}^{-3}$. This buoyancy flux is notably higher than present-day estimates based on swell size, but buoyancy flux could have been much higher than today's flux shortly after the eruption of the plume head.

Similar flow speeds can also be estimated for other plumes. For example, in Iceland, radial viscous fingering of hot asthenosphere¹⁴⁹ (5 fingers, each 500 km wide and 100 km deep with 3% velocity anomaly corresponding to $\sim 25 \text{ kg m}^{-3}$ or 250 K; 28 Mg s^{-1} buoyancy flux) would result in an average flow speed of $\sim 14 \text{ cm yr}^{-1}$ (ref. 147). However, 28 Mg s^{-1} is 20 times higher than an estimate based on swell size¹⁵⁰.

For the Canary plume, mantle plume material is thought to flow through a subcontinental lithospheric corridor beneath Africa to the Mediterranean¹⁴⁶. With a channel width of 250 km and depth 100 km and the same density anomaly 25 kg m^{-3} , a flow speed of 10 cm yr^{-1} (1,500 km in 15 Myr) would correspond to a buoyancy flux of about 2 Mg s^{-1} . This buoyancy flux is already twice the total plume flux estimated based on swell size¹⁵⁰, but tomography yields a much higher total plume flux estimate of about 10 Mg s^{-1} (ref. 151), in which case the flux through the corridor would be 20% of the total plume flux. Part of such discrepancies might be caused by complicating effects of compositional buoyancy during fractionation, as well as the effects of nonlinear rheology, which allows for local viscosity reduction and enhanced flow speeds compared with Newtonian approximations.

The Afar plume could have arrived beneath the lithosphere earlier, probably $\sim 40 \text{ Ma}$ (ref. 27), which would imply that the flow speeds necessary to align the timing and relative positions of the plume and the uplift could be lower than 20 cm yr^{-1} . On the basis of several estimates^{9,144}, one can expect those dynamic topography contributions to be of kilometre scale (Fig. 4).

A land bridge supported by mantle flow

Backward circulation modelling can also help explore the role of time-variable convection on the topographic evolution of the Eastern Mediterranean⁹. Modelled mantle density anomalies capture the arrival of the Afar plume and show the progression of a slow-seismic and low-density anomaly extending northward below Arabia (Fig. 4). In Supplementary Figs. 1–5, this can be seen in the second-row cross-sections, but not the other cross-sections to the left and right, consistent with the concept of a columnar plume upwelling that feeds into a sublithospheric channel towards the north. Comparison between geodynamic estimates based on different tomography models, a crude measure of 'uncertainty' shows that this convective scenario is a robust result found from most tomographic models. This geometry contrasts with the subducted slabs, which are also consistently imaged, but with subduction occurring on a broad front, although a careful analysis of high-resolution tomography¹²⁶ can identify separate individual slabs as part of this front. The surface expression of this northward progression can be seen from the timing and composition of regional volcanic centres^{36–38,132} (Fig. 3).

Mantle dynamics in the region thus seems to be associated with a convection cell where the deep upwelling beneath the Horn of Africa is connected to a downwelling in the Tethyan region, forming a whole mantle convection cell or a 'conveyor belt'^{37,78} (Fig. 2). The Afar plume could be dragged by mantle flow and advance in the upper mantle below the plate at a velocity that is faster than the surface speed of

the plate owing to Poiseuille (pressure-driven) flow effects in the lower viscosity asthenosphere, as shown in the numerical models of ref. 9. Such regional 'mantle leading the plate' flow agrees well with the northward progression of volcanism^{36,38}, and the positive dynamic topography anomaly likewise migrates northward, supporting prior numerical models^{89,106,107,118,152,153}. The time-dependent convective scenario of Fig. 4 shows how mantle convection could have influenced the topographic evolution of Arabia. Mantle flow from the Afar plume causes northwardly progressing uplift and volcanism, which had a role in the seaway closure and the formation of the Arabian–Eurasian land bridge. A regional-scale geodynamic model based on tomography supports this finding, showing the presence of mantle flow from the Arabian Plateau towards the East Anatolian Plateau¹⁰.

The mantle flow and associated volcanism likely controlled the nature and timing of the Tethys Seaway final closure and the establishment of the land bridge. Although the deep oceanic part of the gateway closed owing to plate tectonic subduction, convergence and collision, the Mesopotamian Trough remained open until the Miocene (20–19 Ma) when the plume material advected by northward mantle flow reached today's Middle East causing uplift. Regional volcanism^{38,132} and paleogeographic reconstructions⁹ show that mantle flow-induced volcanism and uplift reached the location of the seaway in the early Miocene (Fig. 3), which likely impacted the topography, closed the Mesopotamian Trough and caused the land bridge to emerge much earlier than it would have without the plume influence (Figs. 3 and 4).

The interplay between deep mantle flow and surface processes highlights how internal Earth processes can control the surface morphology in the Tethys region. The next sections explore how these tectonic and geodynamic processes induced ocean circulation, climate and biogeographic changes by closing the Neotethys and controlling the formation of the *Gomphotherium* land bridge.

Implications of land bridge formation

Paleogeographic changes in the Tethyan region influenced ocean circulation and climate far beyond the Mediterranean–Tethyan realm and resulted in massive faunal migrations between Africa and Eurasia peaking in the middle Miocene. Here, we examine the consequences of seaway closure and land bridge formation, which likely had an important role in developing the modern ocean circulation and climate system, as well as influencing faunal migrations and likely also human evolution.

Consequences for marine circulation

The isolation of the eastern and western parts of the Neotethys had major consequences in the marine domain and occurred in two steps: first with the closure of the Neotethys deep oceanic gateway between 40 Ma and 30 Ma (ref. 9), following the complete disappearance of the Neotethyan slab through subduction in the collision zone; second, with the drying of the shallow Mesopotamian Trough, occurring first in the early Miocene (20–19 Ma), re-flooded in the early middle Miocene, but fully achieved by the middle Miocene ($\sim 14 \text{ Ma}$)^{9,72–74}. The long-term fall of the sea level since the late Eocene, in response to reduced mid-oceanic spreading and the growth of the polar ice caps^{154,155}, likely contributed to the retreat and later closure of the Mesopotamian Trough. Temporary re-flooding(s) of the seaway (~ 16 – 14 Ma) could have been triggered by averagely higher middle Miocene eustatic levels¹⁵⁶, and the final closure of the Mesopotamian Trough coincided with the sea-level drop caused by Antarctica ice-sheet expansion at $\sim 13.8 \text{ Ma}$ (ref. 72). However, the paleobathymetric changes required to close the seaway from depths of $>500 \text{ m}$ in the middle Oligocene to subaerial in the

middle Miocene^{9,157} (Fig. 3) are much greater than the most extreme paleo-sea-level changes proposed during that period (with maximum of -120 m)^{158–160}. Topographic changes related to post-collisional tectonics and/or mantle plume dynamics are thus needed to explain the evolution of the Mesopotamian Trough⁹.

The main consequence of this protracted closure is a gradual and irreversible decrease in water throughflow, resulting in an overall increase in sea surface salinity and water temperatures in the western Neotethys. Several climate sensitivity experiments closing Neotethyan and Paratethyan connections with the Atlantic also promote higher salinities in the North Atlantic^{161–163}. This high salinity is an important condition for deep water formation in the North Atlantic and a critical step for the onset of the Atlantic Meridional Overturning Circulation (AMOC)^{164,165}.

The impact of the first closure step of the Neotethyan seaway on the proto-AMOC during the Eocene and Early Oligocene remains yet to be clearly drawn (Fig. 5). Coupled global earth system model experiments of ref. 163 show that shallowing the seaway in the Late Eocene to 150 m, while keeping it relatively wide (~500 km), increases the surface salinity of the North Atlantic (by >5 psu) and triggers a spike in North Atlantic Deep Water (NADW) formation and the proto-AMOC (to -10 Sv). However, the increase in overturning disappears when their simulation stabilizes. Fully closing the seaway with Eocene boundary conditions, as in ref. 161, triggers a more permanent increase in the NADW and the proto-AMOC (to -12 Sv). Closing other nearby seaways, such as the Danish–Polish Trough (the proto-Paratethys–North Sea connection further North), show a similar effect on Eocene sea surface salinities¹⁶², but whether this triggers a proto-AMOC depends on the configuration of the Atlantic–Arctic oceanic gateways. It is thus difficult to quantitatively assess the impact of the sole protracted Neotethyan oceanic gateway closure on the proto-AMOC as it depends on several factors such as nearby oceanic gateways (for example, the Atlantic–Arctic gateways and Polish Trough), the global paleogeography and background climate state^{161–164,166}.

Isotopic tracers for marine currents indicate the persistence of a significant water throughflow even after the disappearance of the deep oceanic gateway, until the second step of Neotethyan closure associated with the drying of the Mesopotamian Trough in the early Miocene⁷². However, the impact of the second closure step on the AMOC and global oceanic circulation is also controversial. The climate sensitivity study by ref. 167 shows that the closure of the Mesopotamian Trough strengthens the AMOC (by 3–6 Sv) and the Tethyan Indian Saline Water (discussed subsequently) when the seaway depth goes from 1,000 m to 250 m, whereas ref. 166 finds little impact on the North Atlantic surface salinity and AMOC when the seaway depth changes from 120 m to closure. Recent paleogeographic reconstructions show that the latter is likely more realistic for the middle Miocene, as the Mesopotamian Trough was very shallow^{9,157}, whereas the effects modelled by ref. 167 are more relevant for the shoaling from late Oligocene to the early Miocene.

The ocean circulation changes from the closure of the Neotethys Mesopotamian Trough in the Miocene are also not fully understood. When the seaway is open, most modelling studies show a surface flow oriented from the Indo-Pacific towards the Mediterranean and Atlantic Ocean^{161,163,164,168} (Fig. 5). However, there may have been a flow of intermediate and deep saline waters flowing in the other direction, towards the Indian Ocean^{167,169,170}. This eastward flow could have induced a warm and saline water mass in the Indian Ocean¹⁶⁷ corresponding to the Tethyan Indian Saline Water¹⁶⁹. The closure of the Neotethys could

then have freshened and cooled the Indian Ocean^{167,170}, impacting the latitudinal density gradient and resulting in an intensification of the Antarctic Circumpolar Current¹⁶⁷. More recently, the climate modelling study of ref. 171 suggests that the final closure of the Mesopotamian Trough triggered the emplacement of marine upwelling along the Arabian coast, favouring marine productivity blooms and setting up the modern large-scale oceanic circulation in the Indian Ocean.

There is thus no clear consensus among climate modelling studies on the relative impact of the disappearance of the deep oceanic gateway versus the later drying of the Mesopotamian Trough on the AMOC and establishment of the modern-day global ocean circulation^{161,167}. The closure of the Neotethys has to be considered in combination with other paleogeographic changes surrounding the Atlantic, including variations in the Atlantic–Arctic Oceanic gateways^{163–165,172}, closure of the Central American Seaway^{173,174} and the opening of the Southern Ocean gateways^{175–178}, and future ocean and climate modelling studies should include a realistic two-step closure model to determine the relative role of the Neotethys through time. However, on the basis of the previous climate simulations, it does seem that the closure of the Neotethys was a necessary domino to fall for the transition from a global circulation mode dominated by Southern Ocean Deep Water to one dominated by North Atlantic Deep Water¹⁶¹.

Consequences for the oceanic carbon cycle

The closure of the Neotethys had also an indirect impact on the oceanic carbon cycle. Following the onset of the soft collision stage, crustal shortening and thickening resulted in the gradual emergence of the Anatolian and Iranian segments of the Eurasian Neotethyan subduction zone^{39,179,180}. This emergence caused the drying of the last latitudinal seaways connecting the Neotethys and Paratethys, in times as early as the middle-late Eocene (~45–35 Ma; Fig. 5), around the time when atmospheric CO₂ dropped from ~1,000 ppm to ~500 ppm (ref. 181) (Fig. 6). The increased isolation of Paratethys waters resulted in the development of widespread anoxic conditions starting episodically in the late-middle Eocene and fully achieved in the earliest Oligocene¹⁸². These changes in the global oceanic circulation have been proposed to enhance organic carbon sequestration and favour the late Paleogene global cooling trend⁶⁸, by reducing atmospheric pCO₂, although no quantification has been published yet. Exhumation, river integration and sediment transport associated with the closure and subsequent mantle plume dynamics could also have played a minor role in the late Paleogene CO₂ drop. Their impact has not been modelled nor fully quantified yet. Exhumation rates increased during the middle-late Eocene onwards from central Anatolia to Iran¹⁸³ (Fig. 6), where easily weatherable, mafic and ultramafic rocks are widespread. Further south, the integration of the Nile River drainage, possibly starting as early as the Oligocene in response to nascent uplift in eastern Africa, was associated with the erosion of rather mature basement rocks¹⁸⁴. However, the paleo-position of these two areas during the late Paleogene, outside the tropical domain, suggests a poor weatherability of the whole region¹⁸⁵. Sediment fluxes from the Nile River start to have a noticeable impact only much later, during the middle-late Miocene. Since then, their variations drive ocean productivity and water stratification in the Eastern Mediterranean, resulting in the deposition of organic-rich sapropels with an extraordinary orbital regularity¹⁸⁶.

A contrasted hydroclimate response on land

Climate sensitivity modelling studies show that the gradual emergence and uplift associated with the Neotethyan closure have dramatic and

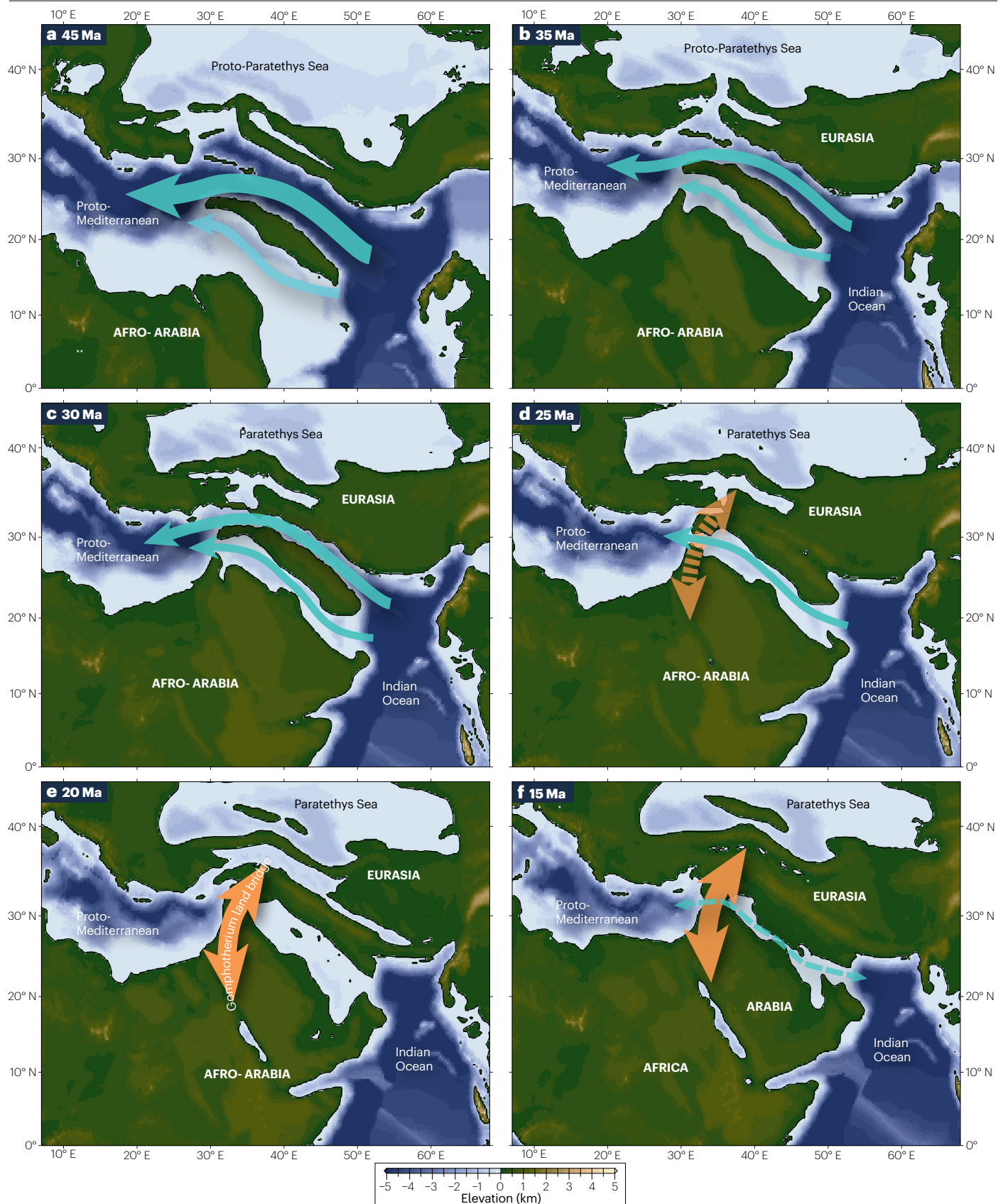


Fig. 5 | Ocean circulation and mammal migration during closure of the Tethys Seaway. Paleogeography from ref. 9. Orange arrows indicate mammal migration across the *Gomphotherium* land bridge. Blue arrows show ocean surface flow transport through the Tethys Seaway inspired by modelled paleo-ocean circulation of refs. 161,163. The two-step closure of the Tethys Seaway resulted in the establishment of the *Gomphotherium* land bridge. **a**, At 45 Ma the Mesopotamian Trough and the oceanic part of the Tethys seaway were open

and deep allowing for a surface flow from the Indo-Pacific Ocean towards the Atlantic Ocean. **b**, At 35 Ma the deeper oceanic part is narrowing and shallowing. **c**, At 30 Ma both seaways were relatively shallow and narrow. **d**, At 25 Ma the land bridge starts to emerge. **e**, At 20 Ma the *Gomphotherium* land bridge was in place and the seaways closed. **f**, At 15 Ma there was a possible re-opening of a shallow epicontinental seaway.

different impacts on the hydroclimate of both the African and Eurasian sides of the collision zone. The emergence of the Arabian Peninsula locally altered sea-surface temperatures in nearby oceanic basins and resulted in strengthened seasonal temperature gradients and increased regional aridity in a wide belt from north Africa to central Asia^{187,188}. It notably reduced northeastward heat transport from the Atlantic to Africa and dampened the African monsoon¹⁸⁹. This process is already observed in Oligocene climate simulations¹⁸⁷ and likely reached its climax during the Miocene. This aridity trend was likely enhanced by Miocene uplift in eastern Africa related to mantle plume dynamics, which further reduced the northeastward penetration of African monsoonal moisture¹⁹⁰. The chronology of eastern Africa uplift remains poorly documented, and it is unclear when this effect started to kick in. The final drying of the Mesopotamian Trough has been proposed as a final trigger for Saharan desertification in the late-middle Miocene¹⁸⁹. This event predates the age of the oldest dated Saharan dunes ~7 Ma (ref. 191) (Fig. 6).

By contrast, the same emergence and topographic uplift enhanced the Somali jet offshore the Arabian coast and increased monsoonal moisture transport inland South Asia¹⁷¹. The onset of high productivity offshore the Arabian coast, which is commonly associated with a strong Somali Jet, appears synchronous with the last drying of the Mesopotamian Trough^{171,192}. The later (Mio-Pliocene) uplift of the Zagros, Iranian Plateau and Anatolian Plateau⁵⁶ reduced the penetration of westerlies into South Asia, further enhancing monsoonal transport via the Gangetic Jet in India and Pakistan^{12,193}. Overall, the topographic changes associated with the plume migration enhanced Asian monsoonal rainfall and wettened South Asia.

The end of island Africa

The formation of the *Gomphotherium* land bridge ended 75 Myr of African biogeographic isolation¹⁹⁴. Cretaceous and Paleogene terrestrial faunas of Africa were highly endemic, poorly diversified and renewed by discrete pulses of sweepstakes dispersal from Laurasia. But in the early Miocene, the creation of the *Gomphotherium* land bridge generated a wave of massive dispersal known as the Great Old World Biotic Interchange (GOWBI)¹⁴. The GOWBI, similar to the earlier Grande Coupure¹⁸⁰ and later GABI (Great American Biotic Interchange)¹⁹⁵, is a classic example of large-scale geodispersal and highlights the fate of endemic taxa when they are put into contact with a wider, more diverse population.

As seen for the *Grande Coupure* and the GABI, mammalian exchanges between the two continental masses were asymmetric: most of the species involved in the geodispersal were Asian taxa reaching Africa, including rodents (members of muridae, scuiridae, spalacidae families), artiodactyls (bovidae, anthracotheriidae, giraffidae, suidae), carnivora (mustelidae, ursidae, felidae, viverridae) and perissodactyls (rhinocerotidae, chalicotheriidae)¹⁴. Their arrival into Africa resulted in the extinction of multiple endemic clades, such as embrithopods, many hyracoids and other Afrotherian mammals, as well as several

lineages of endemic rodents. Nonetheless, several African endemic taxa successfully made it to Asia, including hyaenodonts and multiple species of proboscideans (and the iconic *Gomphotherium*)¹⁹⁶.

The perhaps most interesting dispersal event related to the closure of the Neotethys involves crown anthropoid primates. The first anthropoid primates are known from Asia in the middle Eocene, and they are one of the few clades that dispersed to Africa before the GOWBI during the late-middle Eocene¹⁵. This dispersal might have been favoured by the incipient closure of the Neotethys and the use of Balkan Anatolian islands as steppingstones^{180,197}. Although anthropoid primates got extinct in Asia during the Oligocene, their African lineages diversified on Island Africa¹⁹⁸ and re-colonized Asia during the GOWBI¹⁴.

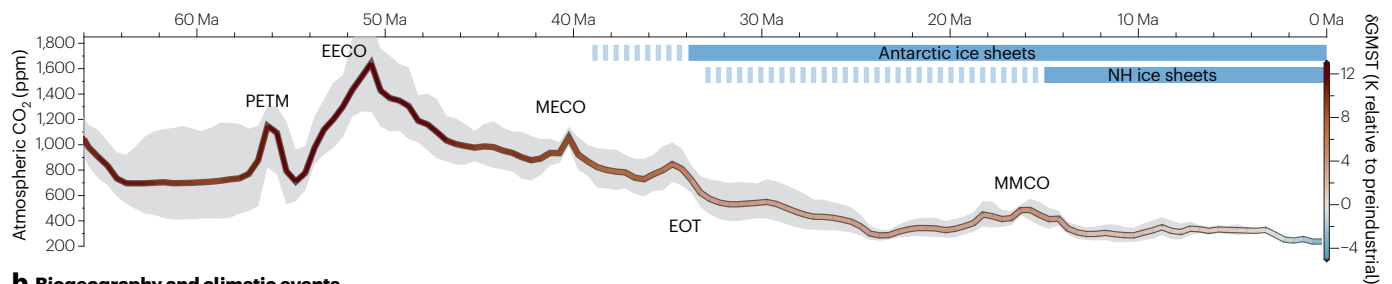
The magnitude of the GOWBI, both in the distance covered by some taxa and the amount of involved species, is particularly surprising considering that the emergence of the peninsula promoted aridification and must have reduced and partitioned arboreal habitats at continental scale¹⁸⁹. The presence of a wide desert over the Middle East, as predicted by some climate models¹², should have significantly limited biotic interchanges. Paleoenvironmental data on the dispersal pathway are unfortunately scarce before the late Miocene¹⁹⁹. Early Miocene Eastern African ecosystems displayed a high heterogeneity with forested and grassland habitats, hosting some of the first C4 plants²⁰⁰. In Central Asia, early Miocene ecosystems were dominated by steppe-desert taxa, where grasses only played a minor role²⁰¹. South Asia has yielded multiple early Miocene fossil wood taxa, indicating the presence of seasonally wet, monsoonal tropical forests²⁰². The ecosystems of the buffer zone between these three areas, across the Arabian Peninsula, the Levant and modern Iran, remain virtually undocumented for the early Miocene. This paradox remains to be explained by further data, as well as with ecological niche modelling studies associated with detailed paleogeographic reconstructions.

The gradual isolation of the western Neotethys from the soon-to-be Indian Ocean also led to the development of the endemic Mediterranean aquatic fauna. Fossil taxa and molecular clocks date back to the divergence of several western Neotethyan marine clades up to the late-middle Eocene, such as for killifishes or estuarine gastropods^{203,204}. Most western Neotethyan taxa yield divergence estimates around the Oligocene and early Miocene times, indicating that the creation of the *Gomphotherium* land bridge irreversibly isolated Mediterranean aquatic taxa^{70,205}. This isolation is associated with a shift of marine biodiversity from the western Neotethys to the Indo-West Pacific, and only few species including echinoderms⁷⁰ dispersed between both biogeographic provinces during the ephemeral middle Miocene re-opening of the Mesopotamian Trough.

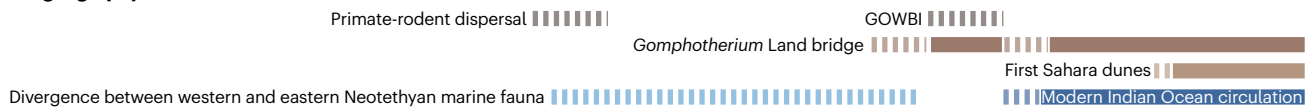
In summary, the two-step closure of the Neotethys created cascading effects on oceanic heat and salinity distribution, regional aridification and monsoon patterns and faunal dispersal routes. These interconnected changes underscore the role of tectonic and deep Earth processes in driving Earth's climatic transitions and shaping biodiversity over geological timescales.

Review article

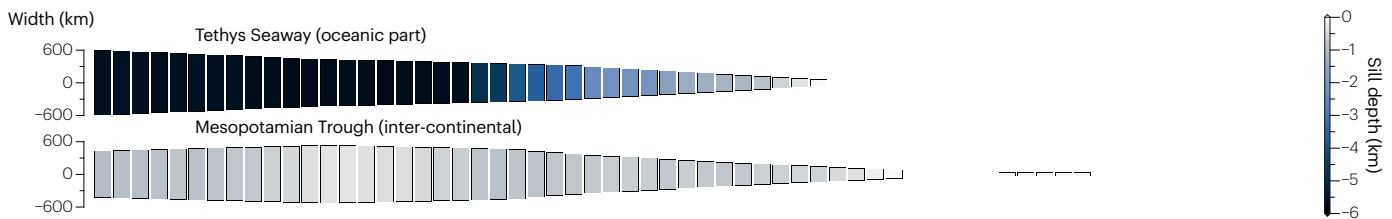
a Atmospheric CO₂ and estimated global mean surface temperature



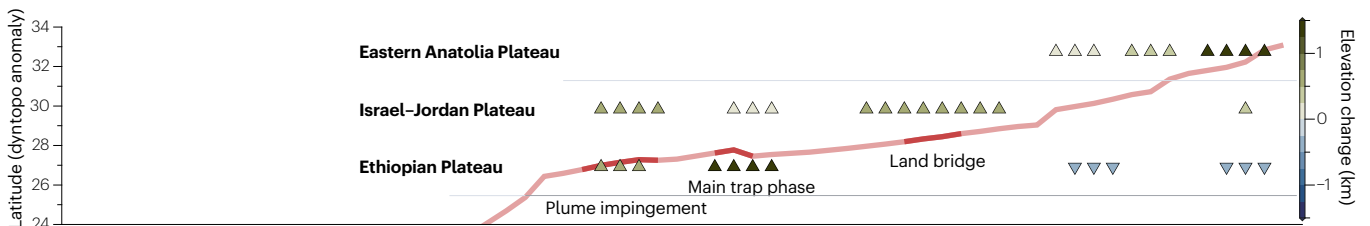
b Biogeography and climatic events



c Width and depth of oceanic gateways



d Uplift and northward progressing positive dynamic topography



e Paleotopography and geodynamic evolution

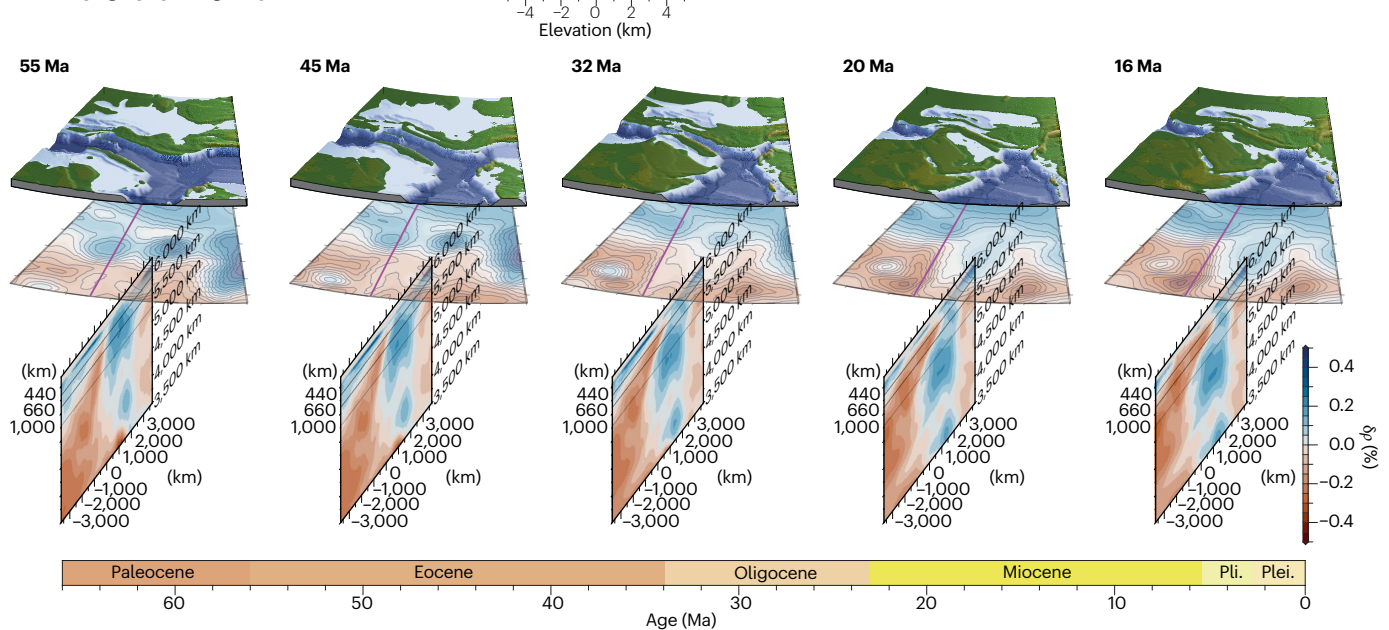


Fig. 6 | Geodynamic, topographic, climatological and biogeographical evolution of the Tethys system. **a**, Cenozoic atmospheric CO₂ and estimated global mean surface temperature (GMST) from ref. 181. Major climate intervals are marked for reference: Paleocene–Eocene Thermal Maximum (PETM), Early Eocene Climatic Optimum (EECO), Middle Eocene Climatic Optimum (MECO), Eocene–Oligocene Transition (EOT), Mid Miocene Climatic Optimum (MMCO) and establishment of Antarctic and Northern Hemisphere (NH) ice sheets. **b**, The timing of biogeographic and climatic events. **c**, The width and depth of the oceanic Tethys Seaway and Mesopotamian Trough, from the digital elevation models of ref. 9 **d**, The northward progression of the positive dynamic

topography anomaly (orange line). This anomaly is calculated by extracting the northernmost positive anomaly along the profiles shown in panel **e**. Recorded uplift or subsidence from the Ethiopian, Israel–Jordan and Anatolia Plateau are shown with triangles, based on data from refs. 33, 56, 118, compiled by ref. 11. The triangle colour indicates the amount of elevation change. **e**, Regional paleogeographic evolution from 55 Ma to 16 Ma, with profiles showing mantle density anomalies from ref. 9. Overall, there is a clear correlation among the northward progressing dynamic topography anomaly, the recorded uplift of the Ethiopian, Israel–Jordan and Anatolia Plateaus, the shallowing and closure of the Seaway and mammal migrations. GOWBI, Great Old World Biotic Interchange.

Summary and future perspectives

The geology of the Eastern Mediterranean region has recorded complex interactions among subduction, continental collision, mantle dynamics and topography. The deeper parts of the Tethys Seaway closed owing to tectonic convergence and collision, but ultimately the shallower portions closed with the formation of the *Gomphotherium* land bridge owing to mantle convection and volcanism. On the basis of the age of the Ethiopian flood basalts²⁹, the Afar plume is estimated to have arrived below the lithosphere in the early Oligocene, at ~35 Ma, then further north reaching Sinai northwest Arabia by ~20 Ma in the early Miocene, which correlates with volcanic activity trending younger towards the north. Mantle flow generated kilometre-scale uplift from East Africa, at ~8° N ~31 Ma (ref. 146), along Arabia and generated the *Gomphotherium* land bridge at 30° N ~20 Ma. The emergence of the land bridge marks the end of the marine gateway among the Atlantic, proto-Mediterranean and Indo-Pacific Oceans, which impacted marine and terrestrial diversification and migration patterns, as well as ocean circulation and climate.

In the classical ‘Wilson-type’²⁰⁶ plate tectonic scenario, the arrival of a continental block in a subduction zone causes the onset of large-scale crustal thickening and shutdown of subduction. When viewed with a mantle convection context, however, the push of the continental block could be sustained if driven by large-scale convection cells including active mantle upwellings and slab pull from the downgoing attached oceanic part of the plate²⁰⁷ (Fig. 2). Ultimately, the collisional processes leading to extreme crustal thickening, such as the one observed along the Tethyan realm in the Himalaya–Tibet or in the Turkish–Iranian Plateau, could only occur under the protracted and vigorous action of mantle convection. The time-dependent signatures of this process on the surface included volcanism and dynamic topography^{9,38,132}. Generating large-scale mountain belts through the collision of continents following subduction represents a specific mechanism and it requires prolonged kinematic convergence leading to an increase in gravitational potential energy. Drivers for this mechanism require either a distinctive tectonic organization or contributions from the mantle. Such reorganizations could, however, have happened several times during the co-evolution of continental dynamics and mantle convection and hence represent a generally relevant process. The efforts to fully understand such processes, and in particular how they are expressed in the geological record, including their consequences on the topography evolution and on ocean circulation, climate and biogeography, are still in their infancy stages.

Although substantial progress has been made, mantle dynamics and tectonics in the Mediterranean–Tethyan region remain a complex puzzle, and there are several critical aspects that need further exploration. For example, the role of the Afar plume could be important not only for generating regional uplift but also for affecting plate

motions by means of modifying the asthenospheric viscosity. A better understanding of the dynamics in the region should be the subject of future research efforts; for example, by studying the interaction of the Afar plume with large-scale mantle flow and a lithosphere of variable thickness. This interaction could be both ways in that plume material is being channelled towards regions of already thinned lithosphere in the direction where it is pushed by the mantle wind, but in these regions the material further erodes and thins the lithosphere from underneath.

Furthermore, more geological data constraining the uplift history of the collisional system and the environmental changes associated with the formation of the *Gomphotherium* land bridge are needed to better constrain the surface and atmospheric expression of these dynamics. For example, more detailed spatial and temporal uplift models should be incorporated into paleogeography and paleoclimate models to more realistically simulate consequences for regional and global ocean circulation and climate.

An important aspect of future work should be the exploration of the relative role of paleogeography and climatic changes on the biogeographic dispersal of terrestrial species, which has become more accessible with paleoclimate simulations^{161,163,167,171,187} and realistic paleogeographic reconstructions^{9,208–211}. Dispersal occurrences not only depend on available pathways provided by paleogeography but also depend on the environment and climatic conditions.

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E.O.S. contributed with conceptualization, writing/editing, formal analysis, data curation and visualizations. C.F. contributed with conceptualization, writing/editing and visualization. T.W.B. and B.S. contributed with conceptualization as well as writing/editing. A.S. contributed with writing/editing and data curation. Z.G., A.L. and P.B. contributed with writing and editing.

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