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Two sides of the same coin: extinctions and originations across the Atlantic/Indian Ocean boundary as consequences of the same climate oscillation

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Abstract. Global climate change is correlated not only with variation in extinction rates, but also with speciation rates. However, few mechanisms have been proposed to explain how climate change may have driven the emergence of new evolutionary lineages that eventually became distinct species. Here, we discuss a model of range extension followed by divergence, in which the same climate oscillations that resulted in the extinction of coastal species across the Atlantic/Indian Ocean boundary in south-western Africa also sowed the seeds of new biodiversity. We present evidence for range extensions and evolutionary divergence from both fossil and genetic data, but also point out the many challenges to the model that need to be addressed before its validity can be accepted.

Keywords. adaptive divergence, global warming, phylogeography, range extension, sea surface temperature

Introduction

Past effects of climate change on biodiversity are of increasing interest because contemporary global warming may result in increased extinction rates (Mayhew et al. 2008). Although there is so far only weak evidence of extinctions linked to contemporary climate change, enhanced extinction rates are a logical probability and prediction (Thomas et al. 2004, Botkin et al. 2007). In contrast, our understanding of the mechanisms that have resulted in the originations of new evolutionary lineages and how these might be influenced by contemporary climate change is incomplete. Periglacial marine refugia, in which formerly widespread species survived glaciations and diverged in isolation, are commonly invoked as the main explanation for the emergence of new lineages at higher latitudes (Wares and Cunningham 2001, Maggs et al. 2008). Additionally, land bridges that formed or became disconnected as a result of climate oscillations are likely to have been important in shaping modern marine biodiversity (e.g., Jeffrey et al. 2007). In regions where there was no

glaciation and in which lowering of sea levels did not result in the formation of land bridges, it is more difficult to explain how climate change may have driven genetic divergence. Examples of such regions include the coastlines of Florida (Avice 1992), southern California (Dawson et al. 2001), central/northern Chile (Martin et al. 2007) and South Africa (Gersonde et al. 2003, Teske et al. 2011b).

Here, we discuss a model explaining how millennium-scale climate oscillations may have driven the evolution of new evolutionary lineages in coastal regions that lack absolute dispersal barriers, using the Atlantic/Indian-Ocean boundary in south-western Africa as an example. This mechanism was introduced in Teske et al. (2007a) and further elaborated (Teske et al. 2011a, 2011b). It involves range extension into formerly inhospitable habitat during a period of climate change (e.g., climatic warming), followed by isolation and adaptation of the new population when environmental conditions return to their original state (e.g., climatic cooling). Interglacial range extensions asso-

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ciated with geographic shifts of marine biogeographic disjunctions are well documented, particularly in the fossil record of south-west African molluscs (Kensley 1985), but subsequent isolation is harder to explain. Isolation must result from the establishment of barriers that reduce gene flow to the point where populations are effectively isolated, and/or from a selective sweep, after which the new populations are unable to re-establish themselves in the habitat of their sister population.

Present-day oceanography and biogeography

The Atlantic/Indian Ocean boundary in southern Africa is a biodiversity hotspot. Not only do biotic elements from the two oceans overlap in this region, but it also hosts large numbers of endemic species (e.g., Griffiths et al. 2010). The region is influenced by two major boundary currents, the warm Agulhas Current and the cold Benguela Current.

The Agulhas Current flows to the southwest along the eastern seaboard of South Africa, following the 200 m isobath of the continental shelf from southern Mozambique to the tip of the Agulhas Bank (the wide continental shelf south of Cape Agulhas, Figure 1). Further west, the current undergoes a retroflexion, turning back towards

the Indian Ocean as the Agulhas Return Current (Lutjeharms 2006). About once every two months, the retroflexion loop closes on itself, forming a retroflexion eddy (or Agulhas ring) about 320 km in diameter, which moves in a north-westward direction towards the South Atlantic (Lutjeharms 2006). In contrast, the coastal environment of western South Africa, Namibia and southern Angola is profoundly influenced by the Benguela Current, which transports cool water from the South Atlantic northwards to central Namibia, where the main flow is deflected away from the coast to the northwest (Wedepohl et al. 2000). These two currents each define a bioregion, the warm-temperate Agulhas province on the south coast and the cool-temperate Namaqua province on the west coast. An abrupt drop in mean sea surface temperature (SST) occurs west of Cape Agulhas (Figure 2), and the gradient in ocean temperatures between the provinces is steepest during summer upwelling on the west coast (Dufois and Rouault 2012).

Although the major mechanisms for exchange between the Indian and Atlantic Oceans are Agulhas rings and filaments that originate from the retroflexion of the Agulhas Current (Beal et al. 2011) these pockets of warm water drift into the South Atlantic and very rarely affect

Figure 1. Ocean currents off south-western Africa. Surface flow is shown as arrows: BC = Benguela Current; AC = Agulhas Current; AR = Agulhas Retroflexion; ARC = Agulhas Return Current; AL = Agulhas Leakage; STC = Subtropical Convergence. The broken line indicates the southernmost position of the coastline during the last glacial phase. The flow path of the Agulhas Current did not differ between glacial and interglacial phases (Franzese et al. 2006).

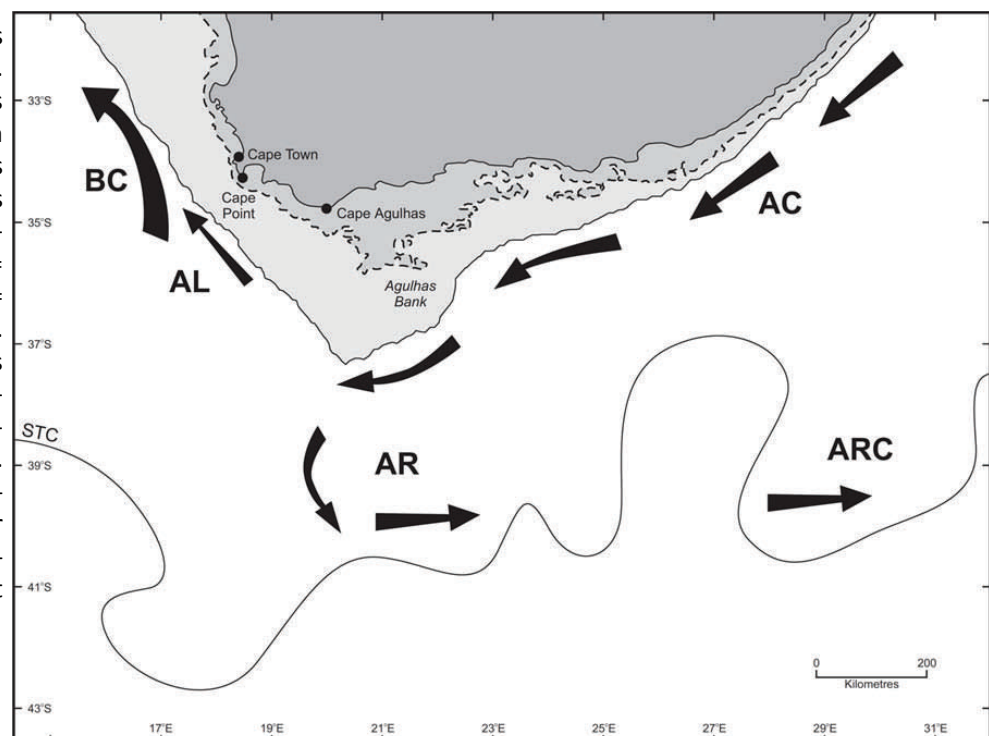
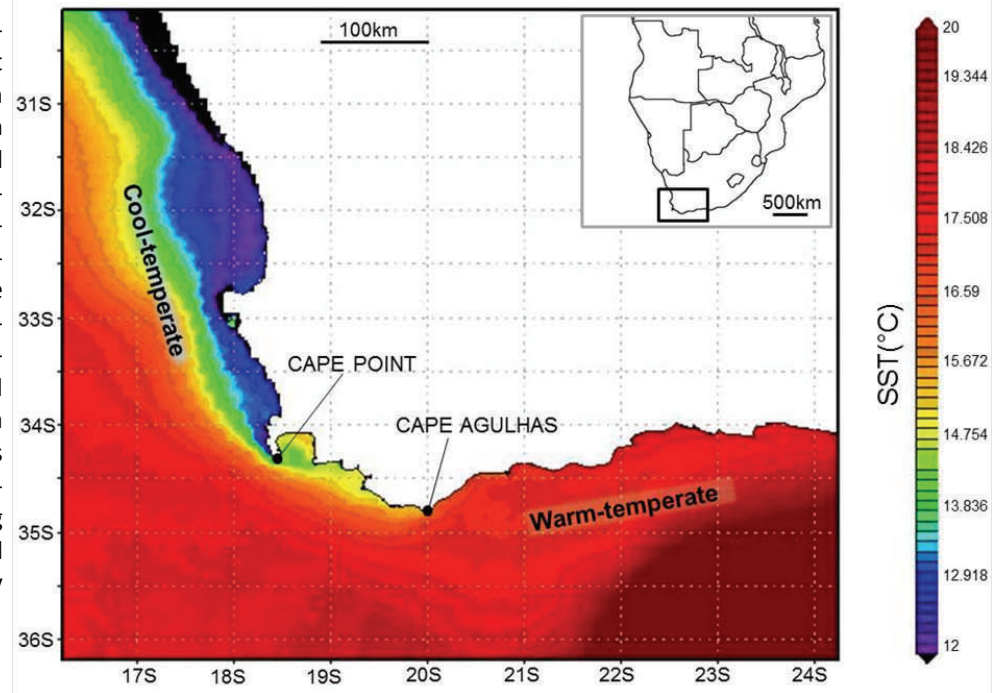


Figure 2. Monthly averaged (2009–2011) SSTs at the Atlantic/Indian Ocean boundary with a 4 km resolution and retrieved from the Moderate Resolution Imaging Spectroradiometer-Aqua (MODIS-Aqua) dataset, available from the National Aeronautics Space Administration (NASA) Goddard Earth Sciences (GES) Data and Information Services Center (DISC). Visualization was performed using Giovanni, a web-based application developed by the GES DISC.



the west coast of Africa (Rae et al. 1996). The dispersal of planktonic larvae between the regions probably occurs via surface water from the Agulhas Bank that drifts in a westward direction west of Cape Agulhas (Figure 1; Shannon and Chapman 1983, Zardi et al. 2011a, Jackson et al. 2012). The influx of warm water from east to west is highest during the summer months when south-easterly winds predominate. However, these same winds also result in maximum upwelling and offshore Ekman transport on the west coast (Lutjeharms and Meeuwis 1987) that reduces the chances of passively dispersing organisms from the Indian Ocean reaching the west coast.

Each south-west African marine province has its own assemblage of species, with the area between approximately Cape Point and Cape Agulhas (Figure 2) sometimes being considered a biogeographic transition zone (Bolton and Anderson 2009). Although a large number of species are present on both coasts, many comprise distinct evolutionary lineages associated with the two provinces (Teske et al. 2011b). The ranges of some of these sister lineages overlap in the transition zone (Teske et al. 2007b), but in other taxa, this region is inhabited by evolutionary lineages that are distinct from those on both the west and south coasts (Teske et al. 2007a, 2007b, Von der Heyden et al. 2011).

Contemporary oceanographic conditions in south-western Africa undoubtedly play a role in maintaining the intraspecific genetic structure and the distinctiveness of the species assemblages associated with the region's marine biogeographic provinces. However, as there are no absolute barriers to dispersal, contemporary oceanography cannot explain the origin of regional phylogeographic breaks. Previous studies have stressed the importance of historical events in driving genetic structure in south-western African marine broadcast spawners (Teske et al. 2007b, Von der Heyden et al. 2008), but the exact role of past geological and oceanographic changes has remained elusive. Below, we elaborate on a model of range extension followed by isolation and investigate how various historical factors could explain the split of ancestral populations into genetically distinct west and south coast populations.

The “range extension-divergence model”

Fossil data indicate that some marine organisms presently associated with the warm-temperate south coast and the subtropical east coast established themselves on the west coast during particularly warm phases, such as those prevalent during the previous (Eemian) interglacial (Kensley 1985) and at the beginning of the present interglacial (Clark et al. 2009). While most of the species

that are presently numerically dominant on the west coast not only persisted but even outnumbered the warm-water species, occasional extinctions of cool-temperate species have been reported. For example, the gastropod *Crepidula capensis praerugulosa*, a west coast endemic that is the most abundant shore-dwelling species in the Eemian fossil record, was no longer found at fossil sites postdating the last interglacial (Kensley 1985). Colonisation of the west coast by warm-temperate species would have been facilitated by input of Agulhas water, coupled with reduced upwelling and reduced offshore advection (Siegfried et al. 1990). Conditions favouring such large-scale gene flow from the south coast to the west coast have been reported during several recent warm temperature anomalies (Branch 1984, Roy et al. 2001, Dufois and Rouault 2012; Figure 3) and are strongly correlated with local wind speed anomalies and El Niño events (Dufois and Rouault 2012).

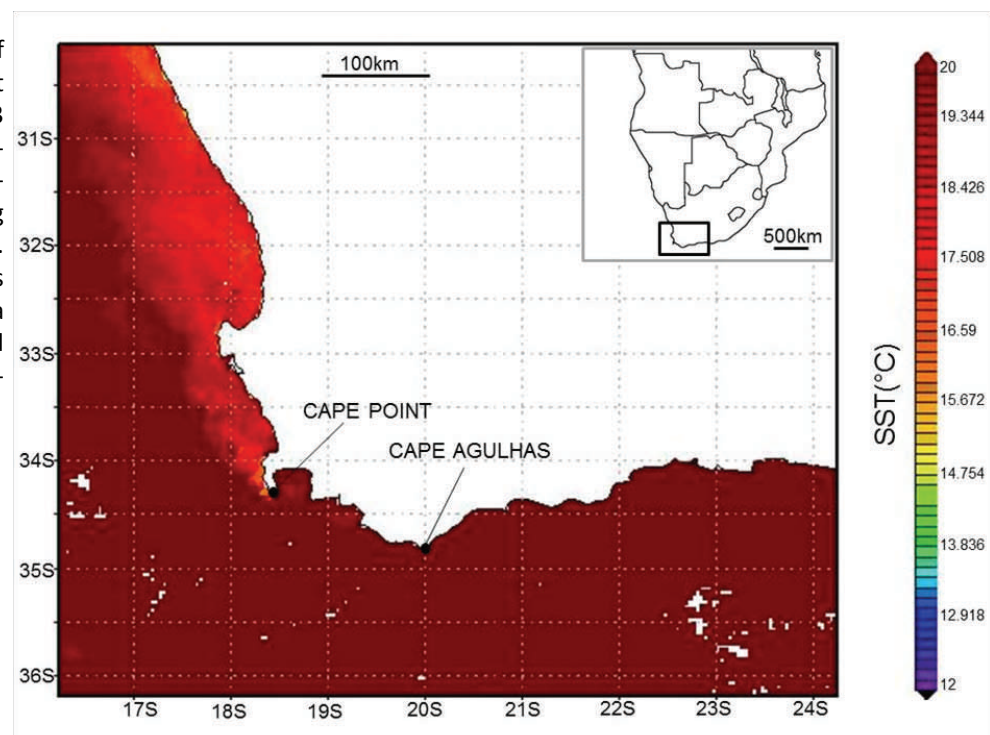
The range extension component of our model is relatively well explained by the fossil record and by present-day proxies, but explaining genetic divergence remains difficult. Below, we discuss the relative merits of the two main hypotheses explaining divergence among west and south coast populations. One assumes that populations were effectively isolated, and we explore a number of putative

physical or physiological barriers that could have contributed to this. The other assumes divergent selection in the face of ongoing gene flow.

1. Isolation hypothesis

Following the particularly warm deglaciations at the beginning of interglacial phases, the amount of gene flow between populations on the west and south coasts of South Africa is likely to have decreased and for several thousand years may have resembled present-day conditions. Although the direct influence of warm Agulhas water on the west coast was reduced and environmental conditions became less favourable for warm water fauna, genetic data (Von der Heyden et al. 2008, Bester-van der Merwe et al. 2011) and recruitment data (Branch 1984) from various marine organisms support the idea that there remains some contemporary gene flow. As conditions during interglacials were probably similar to those observed today and thus unlikely to drive genetic divergence by isolating the regional populations, it seems most appropriate to consider environmental conditions that were prevalent during glacial phases, in particular during glacial maxima. We explore the merits of the following interlinked historical factors in explaining divergence: a) the formation of a physical barrier, as much of the

Figure 3. Examples of warm SST anomalies that occurred in February 2003 (austral summer) as putative proxies of oceanographic conditions during historical warm phases. Period selection was based on monthly data reported in Dufois and Rouault (2012) and assessed as in Figure 2.



continental shelf south of the present-day coastline was exposed during glaciation; b) reduction in the intensity of the Agulhas Current and c) lower water temperatures and intensified upwelling in south-western Africa, which would have reduced the survival of the larvae of warm-temperate species, and further increased larval loss through off-shore advection.

a) Exposure of the continental shelf

During the Last Glacial Maximum (LGM; ~20.0–26.5 thousand years ago (kya); Clark et al. 2009), the sea level was approximately 120–140 m lower than it is today (Ramsay and Cooper 2002) and much of the continental shelf to the south of the African continent (today's Agulhas Bank, see Figure 1) was exposed. Von der Heyden et al. (2011) proposed that this resulted in a replacement of much of the region's rocky shore habitat by sandy beaches, thus driving divergence of populations inhabiting the remaining isolated rocky shores. We can find no published evidence of this, but if it is indeed the case, it would be particularly relevant to low-dispersal species in which genetic structure follows a pattern of isolation by distance, as geographically isolated populations of planktonic dispersers can maintain high levels of gene flow (Teske et al. 2011a).

An alternative explanation is that the poleward extension of the southern tip of the African continent as far south as 36°S (Figure 1) brought it in close geographic proximity to the Subtropical Convergence (STC), which shifts equatorwards during glacial phases, and that this created a geological-physiological dispersal barrier. However, while the northward shift of the STC resulted in the replacement of temperate taxa with cold-water taxa elsewhere in the southern hemisphere (e.g., Tasmania; Barrows and Juggins 2005), gene flow should still have been possible south of the African continent. The position of the STC remained south of 36°S, and Agulhas rings and filaments continued to pass through the gap between the two putative barriers (Rau et al. 2002).

b) Reduction in Agulhas Current intensity

During glacial phases, the Agulhas Current was

weaker and cooler in summer, and it may have been completely replaced by subtropical water in the south-western Indian Ocean during winter (Hutson 1980). As a consequence, Agulhas Leakage into the South Atlantic was significantly reduced (Franzese et al. 2006). However, weakening of the current during glacial periods may have been of little consequence in terms of reducing the amount of gene flow between the regions, because even under contemporary conditions, the Agulhas Current rarely affects the west coast (Rae et al. 1996, Demarcq et al. 2003).

c) Reduced sea surface temperatures and intensified upwelling

Low water temperatures can decrease the amount of gene flow between regions because they can reduce the survival of planktonic larvae, either because temperatures are below a threshold beyond which larvae cannot complete development, or because the slower larval development increases the chances of predation or starvation (e.g., Anger 2001). Interestingly, there is no compelling evidence for drastic cooling in south-western Africa during the LGM, but instead substantial ocean warming occurred from 41–18 kya (Sachs et al. 2001). Data from the northern Benguela upwelling region confirm that conditions were comparatively warm during the LGM and that the easterly winds that were prevalent during this time were not conducive to upwelling (Summerhayes et al. 1995). However, sea surface temperatures in this region were coldest and upwelling most intense just before 41 kya. Seasonality of upwelling presently differs for the northern and southern portions of the cool-temperate west coast, but increases in the strength and zonality of the trade wind system result in intensified upwelling along the entire region (Little et al. 1997). This suggests that climatic conditions prior to the LGM could have created a significant dispersal barrier to passively dispersing organisms originating from the warm-temperate south coast.

2. Diversifying selection hypothesis

Diversifying selection may represent an alternative explanation for genetic divergence in the ab-

sence of absolute dispersal barriers. Theory predicts that adaptive divergence between populations within a species will often reflect a balance between the diversifying effects of local selection and the homogenizing effects of gene flow (Lenormand 2002, Garante et al. 2007). Gene flow generally retards speciation by reducing genetic divergence among populations (Kawecki and Ebert 2004, Garante et al. 2007), although intermediate levels of gene flow may increase genetic variation and therefore adaptive divergence (Kirkpatrick 2001, Swindell and Bouzat 2006).

Strong selection across steep environmental gradients acting on a well-defined adaptive trait can maintain distinct genetic and morphological taxa in the face of substantial gene flow (e.g., Slatkin 1987, Postma and van Noordwijk 2005, Zardi et al. 2011b). Under such conditions, gene flow is restricted between populations locally adapted to one environment and maladapted to contrasting environments, as admixed individuals may experience reduced fitness and consequent elimination by selection (Garante et al. 2007).

Unlike the disjunctions among marine biogeographic provinces in other regions (Teske et al. 2008, Pelc et al. 2009, Teske et al. 2011a), which are characterised by steep environmental gradients that persist throughout the year, the differences between the cool-temperate and warm-temperate provinces in South Africa undergo seasonal fluctuation, decreasing during winter when upwelling on the west coast is less intense or during summer anomalies (Demarcq et al. 2003; Figure 3).

It is possible that physiological stress associated with frequent upwelling events, perhaps during glacial phases, may have resulted in a selective sweep in the west coast populations of some species. Migrants from the south coast that settled on the west coast would then not only have experienced increased environmental stress, but would also have been competitively excluded from west coast habitats by better-adapted sister lineages. No physiological experiments have yet been conducted on evolutionary lineages of coastal invertebrates from the west coast vs. those from the south coast, but the fact that numerous south

coast species with high dispersal potential are absent from the west coast supports the idea that these lack the physiological adaptations required to tolerate periods of low water temperature and establish themselves there in the long term. Even if diversifying selection did not play a role in driving divergence between the evolutionary lineages from the two regions, it is likely that it is important in maintaining genetic structure.

Challenges to the model

While the “range extension-divergence model” seems to explain the existence of genetically distinct sister lineages across the Atlantic/Indian Ocean boundary, and the occurrence of range extensions are confirmed by fossil data, several points challenge the model.

Shortcomings of genetic data

To confirm the model convincingly, genetic data sets would ideally exhibit a distinct east-to-west pattern of range extension, but few of the data sets generated to date show this clearly. West coast lineages that are nested within south coast lineages in phylogenetic trees (Figure 4a; Teske et al. 2007b, 2009), or west coast clusters that are in derived positions in haplotype networks (Teske et al. 2007a) represent particularly strong support for the idea that westward range extensions resulted in the formation of new evolutionary lineages. In these species, the new west coast population was likely initially small, carrying only a fraction of the genetic diversity of its source population, and for that reason their establishment on the west coast can be more adequately described as a colonisation event rather than a range extension.

In the majority of cases, however, so much time has passed since the divergence event that lineage sorting is complete and phylogeographic breaks are deep. In these cases, the two regional populations are represented as completely distinct lineages that form a dichotomy (e.g., Teske et al. 2009, Figure 4b). In other cases, species’ dispersal potential is so high that the westward range extension may have resulted in the formation of a large population that not only main-

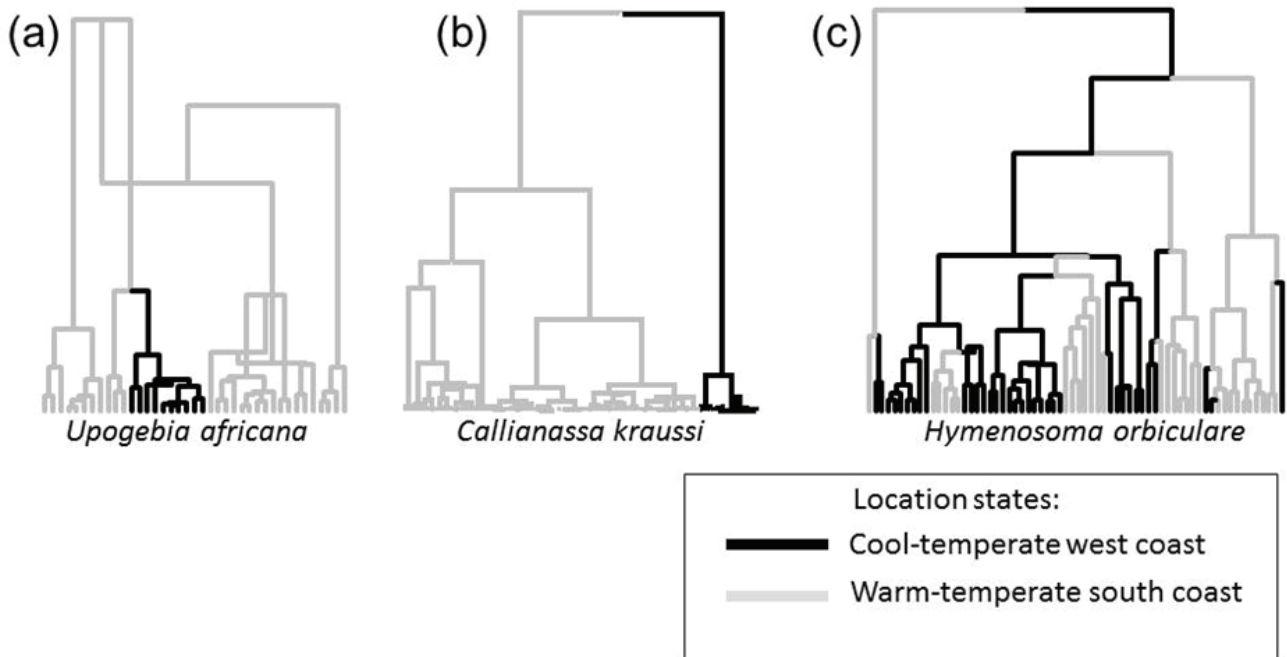


Figure 4. Maximum clade credibility (MCC) trees with location states (the most probable geographic location of each branch in the tree) based on COI sequence data (third character positions only) from three southern African coastal decapod crustaceans: (a) a west coast lineage is nested within a south coast lineage, (b) the two lineages form a dichotomy, (c) panmixia, but as lineage sorting proceeds, a dichotomy as in (b) may evolve. Trees were reconstructed in BEAST 1.6.1 (Drummond and Rambaut 2007) using the spatial diffusion method (Lemey et al. 2009) with default settings, and are not drawn to scale.

tained most of the genetic diversity of its source population (e.g., Banks et al. 2010), but also maintained high levels of gene flow with it. In the early stages of divergence, this would be indistinguishable from a pattern of panmixia (Figure 4c), but as lineage sorting proceeds, it may eventually resemble a dichotomy in which neither lineage can be clearly identified as being younger or older (as in Figure 4b).

Another challenge to the model is the fact that none of the molecular estimates of divergence times calculated from the data sets generated to date can be clearly linked to the time following interglacial periods because they are based on a small number of loci and are thus highly inaccurate (Felsenstein 2006), a problem that is exacerbated by uncertain calibration rates. In the examples in Table 1, divergence times estimated from mtDNA COI data predate, coincide with, or postdate, the previous interglacial, approximately 116–127 kya (Kaspar et al. 2005), and confidence intervals span several glacial and interglacial phases. The lower estimates for data sets based on the most variable third character positions

(calibration methods c and d) further indicate that published mutation rates are likely affected by saturation (see also Marko 2002). The generation of multilocus data is thus required to improve the accuracy of estimates, but for the many non-model organisms studied to date, this has been a major challenge because primers are available for very few loci (Teske and Beheregaray 2009).

Shortcomings of fossil data

At deeper phylogenetic levels, fossil data and genetic data tend to complement each other, but in lineages that diverged during the Holocene or Pleistocene, morphological differentiation tends to lag behind genetic divergence. In the southern African marine realm, the species examined that are present in more than one marine biogeographic province are subdivided into evolutionary lineages of varying depth (Teske et al. 2011b), but morphological differences have been identified in very few of these (Ridgway et al. 1998, Teske et al. 2008). Therefore, it is not possible to distinguish the fossils of a distinct west coast lineage from those of a warm-water lineage

COI character positions	Dating method	Species		
		<i>Upogebia africana</i>	<i>Palaemon peringueyi</i>	<i>Callinassa kraussi</i>
1-3	a	593 (295–1 023)	302 (189 – ?)	384 (61 – 951)
1-3	b	492 (245 – 853)	363 (156 – ?)	324 (52 – 801)
3	c	301 (132 – 602)	220 (91 – ?)	56 (10 – 287)
3	d	320 (140 – 642)	229 (92 – ?)	59 (11 – 305)

Table 1. Divergence times (in thousand years) among west coast and south coast populations of three southern African decapod crustaceans. Results are reported as means and 95% highest posterior density intervals (in brackets) using mutation rates estimated from published sequence data.

Divergence times were estimated in IMA2 (Hey 2010) using a generation time of one year and mutation rates for COI sequences based HKY distances among geminate sister species that were assumed to have diverged as a result of the closure of the Central American Seaway ~ 3.1 million years ago (Coates et al. 1992); (a) 0.8% per million years; *Sesarma* spp. (Schubart et al. 1998); (b) 1.0% per million years, *Alpheus* spp. (Knowlton and Weigt 1998); (c) 3.9% per million years (third character positions of *Sesarma* spp.); (d) 3.7% per million years (third character positions of *Alpheus* spp.). Question marks indicate that likelihood curves did not return to zero after having reached a peak.

that did not establish itself in the long term, or from those of a now-extinct older west coast lineage. In addition, many of the species that established themselves on the west coast during warm climatic phases are presently represented in multiple warm-water marine provinces and are likely to represent multiple cryptic species, so that the exact origin of thermally anomalous fossils is uncertain (Kensley 1985). Future research aimed at reconstructing the evolutionary history of coastal biotas would benefit greatly from identifying morphological characters useful for distinguishing between the evolutionary lineages identified by means of genetic data. Particularly an increased focus on taxa that are well represented in the fossil record (e.g., molluscs) can be expected to improve the integration of genetic and fossil data. Another shortcoming of the fossil data is that, while the fossil record of coastal species from interglacial phases (in particular from the previous interglacial and the period of deglaciation at the beginning of the present interglacial) is fairly informative (Tankard 1975, Kensley 1977, 1985, Compton 2001), almost nothing is known about species' distributions during glacial phases (Henshilwood et al. 2004). Most fossil sites from these periods are very difficult to access because they are located on the continental shelf.

Discrepancies between historical and contemporary consequences of climate change

Recent environmental changes are intensifying the warm-to-cold SST transition between the Indian and Atlantic Oceans (Figure 5) rather than eroding it, as documented for historical deglaciations. While Rouault et al. (2010) reported a cooling trend on the south coast, including Cape Agulhas, over the last three decades, this was based on analysis of satellite data with low spatial resolution. Using finer resolution, we identified significant warming trends in coastal waters between 20° 07' E and 21° 22' E, while flanking shores did not experience significant changes in SST (Figure 5). Thus environmental trends indicate that the cline in SST from the warm-temperate south coast to the cool-temperate west coast will become more pronounced, possibly enhancing local adaptation and divergence of populations inhabiting these contrasting shores.

Conclusions and future issues

The model discussed in this review suggests that historical increases in SST on the Atlantic coast of southern Africa have not only resulted in the extinction of some species, but that they may also have facilitated the colonisation of this region by warm water species originating from the Indian Ocean. During subsequent climatic cooling, the new populations established in this way would have been subjected to a combination of direc-

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