Original Article:

Sub-orbital climatic variability and centres of biological diversity in the Cape region of southern Africa

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Running heading: Sub-orbital climatic variability and centres of diversity

Word counts: 299 (Abstract); 5478 (Introduction to Discussion); 82 (Acknowledgements);
8070 (Abstract to References inclusive); 139 (Biosketch);
74 references; 1 table; 5 figures; 10 keywords.

Abstract

Aim: To explore the magnitude and spatial patterns of last glacial stage orbitally-forced climatic changes and sub-orbital climatic fluctuations in southern Africa, and to evaluate their potential roles in determining present biodiversity patterns.

Location: Africa south of 15° S.

Methods: Palaeoclimate scenarios for southern Africa were derived for 17 time slices using outputs from HadCM3 atmosphere–ocean general circulation model experiments, including five designed to mimic Heinrich Events. Species' distribution models for birds of Karoo (45) or Fynbos (31) were used to simulate species' potential past distributions. Species-richness patterns were assessed for each time slice, and minimum species-richness for regional endemics of each biome determined for each grid cell. Areas of greatest 'stability' for endemics of each biome were identified using grid cells with greatest minimum richness.

Results: Simulated sub-orbital climatic fluctuations were of greater magnitude than orbitally-forced changes and had anomalies of opposite sign in many areas. The principal local driver of sub-orbital fluctuations was marked contrasts in South Atlantic circulation and temperature between experiments mimicking Heinrich Events and those with only slow forcings. These contrasts in ocean circulation and temperature were consistent with marine sediment core evidence of changes in the South Atlantic coincident with Heinrich Events in the North Atlantic. Whereas orbitally-forced last glacial climates generally resulted in range expansions and increased species richness in many grid cells compared to present, the contrasting conditions of Heinrich Events resulted in much reduced ranges and species richness, especially for Karoo species. Very few grid cells remained suitable for larger numbers of endemic species of either biome under all palaeoclimate scenarios examined, but this minority of 'stable' grid cells correspond to present diversity centres.

Main Conclusions: Sub-orbital climatic fluctuations during the last glacial stage were likely of considerable magnitude in southern Africa. This may account for apparent inconsistencies between regional palaeoclimate records, as well as being key to determining present biodiversity patterns.

Keywords:

birds;

Cape Floristic Province;

endemics;

Fynbos;

Heinrich Events;

hosing experiments;

last glacial stage;

South Atlantic;

species distribution models;

Succulent Karoo.

Introduction

The Cape Floristic Province has long been recognised as an area of extreme diversity of vascular plants, with high levels of endemism (Good, 1964; Goldblatt & Manning, 2002); it is also a centre of diversity and endemism for various animal groups (e.g. Stuckenberg, 1962; Branch *et al.*, 1995; Skelton *et al.*, 1995; Picker & Samways, 1996; Proches & Cowling, 2006). Two biomes, Fynbos and Succulent Karoo, defined by dominance of distinct plant functional types (Mucina & Rutherford, 2006), characterise the region (Midgley *et al.*, 2005). Each biome has a high overall species diversity and high level of endemism; both also have well-recognised centres of diversity. They are also currently under threat from various forms of human land-use; as a result they have been identified as priority areas for conservation (Myers *et al.*, 2000; Mittermeier *et al.*, 2004). Developing effective strategies to achieve the conservation of such important centres of biological diversity (Cowling & Pressey, 2003), however, requires an understanding of the factors determining their locations (Cowling & Lombard, 2002). This becomes especially important in a world with rapidly increasing atmospheric carbon dioxide concentrations and human land-use pressures, as well as changing climates.

Understanding the origin and persistence of such centres of biological diversity provides insights into their potential vulnerabilities and is crucial to formulating biodiversity conservation strategies. A wide range of hypotheses has been advanced to account for global biodiversity patterns (Gaston, 2000), and especially for the location of centres of biodiversity. Broadly, these hypotheses fall into two categories, those that focus upon the present environment and those that invoke historical factors. Although patterns of global productivity, present climatic patterns and topographic diversity all have been shown to correlate with biodiversity patterns to some extent and in at least some regions (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Thuiller *et al.*, 2006), such determinants alone cannot generally account fully for present patterns (Jetz *et al.*, 2004). When historical factors have been considered, these have often been shown to provide a more complete explanation of the observed patterns (Huntley, 1993; Araújo *et al.*, 2008; Voelker *et al.*, 2010). Some such studies invoke processes operating over geological time scales of millions to tens of millions of years, often with an emphasis upon tectonic processes, or focus upon substantial long-term climatic or other environmental changes that occurred millions of years ago, especially during the Tertiary Period (e.g. Linder & Hardy, 2004) or at the transition from the Tertiary to Quaternary Periods (e.g. Voelker *et al.*, 2010). Others focus upon the Quaternary Period (the last *ca*. 2·6 Ma), mainly considering the large magnitude changes in global climates associated especially with the alternating glacial and interglacial stages that characterise the last million years or so of that Period (e.g. Huntley, 1993; Dynesius & Jansson, 2000). These and other multi-millennial Quaternary climatic changes result from predictable periodic variations in the Earth's orbital characteristics with frequencies of 10^1 – 10^2 ka (Hays *et al.*, 1976). The impacts of these orbital changes upon the global climate have been studied using both geological evidence and general circulation models (GCMs) of the climate system (COHMAP Members, 1988; Wright *et al.*, 1993), and a mechanism has been advanced to explain how the differing relative impacts of these changes in different regions can account for global biodiversity patterns (Dynesius & Jansson, 2000).

The diversity of the Cape Floristic Province, and of the Fynbos and Succulent Karoo biomes in particular, cannot readily be explained solely by factors relating to the present environment (Cowling & Lombard, 2002; Tolley *et al.*, 2006), and it has been argued that it may reflect climatic changes between glacial and interglacial stages of the Quaternary, and consequent repeated and reciprocal expansions and contractions of the two biomes (Midgley & Roberts, 2001). However, the general circulation model (GCM) simulations used to simulate the shifting extents and distributions of the two biomes in the latter study were perpetual January and July simulations made using CCM0 (Kutzbach & Guetter, 1986), an early GCM that simulated only the atmospheric general circulation, sea surface temperatures for the simulations being prescribed following CLIMAP (CLIMAP Members, 1976). Advances in GCMs since those early simulations not only enable full seasonal cycles to be simulated, but, more importantly, especially given the role that it is now clear is played by the ocean thermohaline circulation (THC) in rapid climatic changes, provide coupled simulations of both ocean and atmosphere dynamics. Palaeoclimate experiments made using such coupled atmosphere–ocean models, and designed to explore how the climate system responds to orbital forcing, have indicated that southern Africa experienced relatively modest climatic changes on orbital time scales (Dynesius & Jansson, 2000). However, this appears inconsistent with evidence from terrestrial palaeoclimatic records that has been interpreted as indicating a mean cooling of 5 – 6°C during the Last Glacial Maximum (LGM), with winter temperatures as much as 8 – 10°C cooler than present, and conditions generally moister in the west and drier in the east of the region (Chase & Meadows, 2007).

Although, given the limitations of available terrestrial records from southern Africa that are "*rarely of sufficient length or resolution to justify correlation with anything beyond the broadest cycles of climate* *variability*" (Chase & Meadows, 2007, p. 133), such a generalised interpretation is all that currently can be achieved with confidence, the evidence synthesised by Chase and Meadows (2007), as well as by earlier authors (Deacon & Lancaster, 1988; Meadows & Baxter, 1999), contains some apparent inconsistencies. Notable amongst these, as Chase and Meadows (2007) discuss, are conflicts between ages ascribed to phases of dune activity in the Kalahari, interpreted as arid phases, and the often similar ages ascribed to evidence of increased regional moisture availability. Furthermore, as Chase and Meadows (2007, p. 116) observe, "*There is … marked variability within the LGM, highlighting the possibility that the homogenisation inherent in the interpretation of the lower resolution records from the region is likely to mask potentially important shifts in climate systems during this period*". This observation becomes especially relevant in the context of the increasing volume of evidence that rapid climatic shifts of large magnitude occurred at sub-orbital (i.e. millennial) time scales during the Pleistocene. Evidence of such millennial climatic fluctuations during the last glacial stage has been reported from a variety of palaeoclimatic records, including ice cores (e.g. GRIP Members, 1993; Blunier & Brook, 2001; Andersen *et al.*, 2004; Wolff *et al.*, 2010), corals (e.g. Yokoyama *et al.*, 2000), cave deposits (e.g. Wang *et al.*, 2008) and palaeovegetation records from lake sediment cores (e.g. Grimm *et al.*, 1993; Allen *et al.*, 1999; Allen *et al.*, 2000). Evidence from ice cores taken in Greenland and Antarctica clearly establishes that such large climatic changes occurred at millennial time scales not only throughout the last glacial (Wolff *et al.*, 2010) but during at least the last eight glacial stages (Loulergue *et al.*, 2008). It has also become clear that variation in the strength of the THC, and the Atlantic meridional overturning circulation (AMOC) in particular, plays a key role both as a mechanism for rapid climatic changes and in linking changes in distant regions of the globe (Broecker, 1992). Notably, the bi-polar see-saw of alternating stadials and interstadials in the northern and southern hemispheres (Blunier & Brook, 2001) is linked to alternations between different patterns of the THC (Vidal *et al.*, 1999). Despite the wealth of evidence now available relating to the ubiquity, rapidity and magnitude of sub-orbital climatic variations, during Pleistocene glacial stages in particular, the potential relevance of these variations to the origins of present biodiversity patterns has not generally been considered. Furthermore, their potential impacts in southern Africa, that may help explain apparent inconsistencies in the palaeoclimatic record, also have not been explored to-date. However, recent experiments using fully-coupled models of the general circulations of the atmosphere and oceans (AOGCMs), and designed to explore millennial-scale variability of glacial climates (Kageyama *et al.*, 2010; Singarayer & Valdes, 2010), have shown that the area is likely to have been extremely sensitive to such sub-orbital climatic fluctuations.

We have used a recent internally-consistent series of AOGCM experiments spanning the last glacial–interglacial cycle made using HadCM3, and including so-called ‘hosing’ experiments (in which large a large volume of fresh water is added to the North Atlantic to mimic the melting of ice-berg armadas) designed to mimic Heinrich Events (Singarayer & Valdes, 2010), to explore the potential sensitivity of southern African palaeoclimates to orbital and other slow forcings, as well as to changes in the THC during Heinrich Events, comparing the simulated palaeoclimatic changes to various records of the regional palaeoclimate. We have also used the AOGCM experiment results to re-examine the hypothesised role of Pleistocene climatic changes in accounting for present patterns of diversity and endemism in the Fynbos and Succulent Karoo, taking into account not just orbitally-forced climatic changes but also sub-orbital climatic fluctuations. To do this we first fitted species’ distribution models, relating species’ recorded present distributions to a small number of bioclimatic variables, for a series of bird species associated with either Fynbos or Karoo, including many species endemic to southern Africa. We then used these models to simulate species’ potential distributions for 17 palaeoclimate scenarios. We chose to model birds because their southern African distributions have been mapped more completely and systematically than have those of any other taxonomic group in the region (Harrison *et al.*, 1997). They also have a substantial rate of endemism in southern Africa, show greater diversity in the Cape Floristic Province then in adjacent areas to the north (Jetz *et al.*, 2004), and include species strongly associated with the Karoo and Fynbos biomes.

Methods

Observed climatic data for 1961–90 ('present') were obtained from a global compilation of mean monthly data at 0·5° longitude x latitude resolution (New *et al.*, 1999). Seventeen palaeoclimate scenarios, for 6, 9, 12, 15, 18, 21, 24, 30, 36, 42, 48 and 120 ka BP, and for Heinrich Events H1 (17 ka BP), H2 (24 ka BP), H3 (32 ka BP), H4 (38 ka BP) and H5 (46 ka BP), were derived from the series of experiments performed by Singarayer and Valdes (2010) using the HadCM3 AOGCM. These 17 experiments were selected because together they span the range of conditions simulated during the last interglacial–glacial cycle. Anomalies for monthly mean temperature, precipitation and cloudiness values, relative to a pre-industrial experiment, were calculated for each palaeoclimate experiment for each GCM grid cell. Using thin-plate spline surfaces fitted to the GCM anomalies for each of the 36 variables (Hutchinson, 1989), the anomalies for each palaeoclimate experiment were then interpolated from the GCM resolution to the 0·5° grid for which the 1961–90 observed climatic data were available, this grid being extended to shelf areas exposed by the lowered sea level of glacial times as described by Huntley *et al*. (2013). Interpolated anomalies were then applied to the 1961–90 data, and the resulting monthly mean values of temperature, precipitation and cloudiness used to calculate, for the cells of the 0·5° grid, the bioclimatic variables used to model bird species' distributions. Monthly mean values of temperature, precipitation and cloudiness for the 0·25° cells used to record bird distributions were obtained by bilinear interpolation from the surrounding cells of the 0·5° grid and used to calculate the bioclimatic variable values for the 0·25° cells.

Bird species' data used were from the first Southern African Bird Atlas Project (SABAP, 1987–91) (Harrison *et al.*, 1997) that mapped each species' reporting rate, a proxy for abundance (Huntley *et al.*, 2012), for 0·25° longitude x latitude grid cells in South Africa, Lesotho, Swaziland, Namibia and Zimbabwe, and for 0·5° grid cells in Botswana. Response surface models (Huntley *et al.*, 2006; Huntley *et al.*, 2007; Huntley *et al.*, 2012) were fitted, using locally-weighted regression (Cleveland & Devlin, 1988), to relate species' reporting rates for the SABAP grid cells to a series of bioclimatic variables for those grid cells. Each model used four bioclimatic variables. All models used the mean temperatures of the coldest and warmest months and an annual integral of the ratio of actual to potential evapotranspiration (Hole *et al.*, 2009). The fourth variable used was whichever of two measures, one the intensity of the wet season and the other the intensity of the dry season (Huntley *et al.*, 2006), gave the model with the better overall goodness-of-fit, the latter being assessed by considering the consensus of a series of 11 measures, as described by Huntley and Barnard (2012); these measures included Cohen's kappa (Cohen, 1960), area under the curve of a receiver operating characteristic plot (Metz, 1978) and the true skill statistic (Allouche *et al.*, 2006).

An initial selection of 48 Karoo and 32 Fynbos bird species was made by identifying those species listed by Hockey *et al*. (2005) as having Karoo or Fynbos as their main habitat. Of these, three Karoo and one Fynbos species were not mapped by SABAP because they were more recent taxonomic splits, only the previous unsplit taxon having been mapped. We were thus able to fit models for 45 Karoo species (19 endemic to southern Africa) and 31 Fynbos species (24 endemic to southern Africa); 10 species were common to both Karoo and Fynbos (Table 1). All species gave satisfactory models in terms of their goodness-of-fit measures when used to simulate species' present distributions for the cells of the SABAP grid (Table 1). All were hence used to make projections of species' potential present and past distributions for the cells of a 0·5° grid across the region, and the potential species' distributions used to assess potential changes in species richness.

Results from the simulations of species' potential distributions were summarised by counting and mapping the numbers of species for which each grid cell was potentially suitable under each palaeoclimate scenario. The potential extent and stability of areas of higher species richness was then assessed by counting the number of palaeoclimate scenarios for which each grid cell was potentially suitable for more than appropriate threshold numbers of Karoo (> 20, > 30) or Fynbos (> 10, > 15) species. Finally, the minimum number of Karoo or Fynbos species endemic to southern Africa for which each grid cell was suitable under the 1961–90 climate and all 17 palaeoclimate scenarios was determined.

Results

Figures 1 and 2 present maps of two of the four bioclimatic variables used to fit the species' models, those variables illustrated being two that are readily compared with palaeoclimatic reconstructions for the region, namely the mean temperature of the coldest month (MTCO) and the annual integral of the ratio of actual to potential evapotranspiration (APET), the latter a measure of overall moisture availability. In each case the first panel of the figure maps the observed present (i.e. 1961–90) values whilst the other 17 panels map anomalies between the values simulated by the AOGCM for a particular time slice and values simulated by the AOGCM in the pre-industrial ('control') experiment.

Focusing first upon the anomaly maps for the 'normal' AOGCM experiments, in which only the relatively 'slow' forcing factors (orbital configuration; atmospheric composition; ice sheet extent and topography; sea-level; and land–sea mask) are changed, a number of key results emerge. Firstly, the simulated palaeoclimatic changes are not spatially uniform across the region, instead showing marked and often temporally consistent spatial patterns, anomalies often being of opposite sign in different parts of the region. Notable in this context is the consistent area of cooler but markedly drier conditions in the Eastern Cape seen in the three simulations that span the LGM (18, 21 and 24 ka BP) that contrasts with the much less marked cooling and drying simulated for the Western Cape and with the generally marginally moister conditions simulated to the north. Secondly, although there is some consistency in the magnitude of the simulated changes in moisture availability (Figure 2) and their spatial patterning across the three simulations spanning the LGM, this consistency does not extend to other time slices of the last glacial stage, when the orbital forcing, in particular, differed from that around the LGM, nor is it seen overall in the simulated changes in winter temperature (Figure 1). Thirdly, the general magnitude of the simulated LGM cooling of winter temperatures at the LGM (21 ka BP) is relatively small, at 2 – 3°C across most of the region. Fourthly, most of the region is simulated to have been marginally moister at the LGM, although with drying in some areas and greater increases in moisture in others, notably in the extreme north-east of the region.

Turning to the Holocene and last interglacial time slices, these simulations show generally marginally drier conditions across the region, although with the south-west Cape a striking and consistent exception that is marginally moister in all cases. The strongest drying is seen in the last interglacial (120 ka BP) time slice and especially in the north-west of the region. Perhaps surprisingly, winter temperatures are simulated generally to have been consistently marginally cooler (anomalies of -1 – 0°C) in the southern part of the region at these times, but warmer, by up to 2°C, in central northern parts of the region. Strikingly, in the simulations for both 6 and 120 ka BP there is an area of cooling, by as much as 3°C, in the north-west of the region centred on the highlands of western Namibia. This is related to a simulated intensification of the Benguela upwelling at these times.

The most striking changes, however, and the anomalies of greatest magnitude, are seen in the results from the five simulations designed to mimic Heinrich Events H1 – H5. In all five simulations winter temperatures are simulated to show a strong spatial pattern of change, with positive anomalies of 2 – 3°C along the west coast and negative anomalies of -4 – -5°C in the north-east or north of the region. Moisture availability anomalies also show generally consistent, but much more complex, spatial patterning across the five experiments. The north-west, especially the area now occupied by the Namib Desert, is consistently simulated to be markedly moister, with APET anomalies > 0·4. Most of the rest of the region shows moist anomalies, although the increase in moisture availability is consistently less in the southern Kalahari. A striking and consistent area of simulated drier conditions coincides with parts of north-east Namibia, south-east Angola and north-west Botswana today occupied by an extensive stabilised linear dune field that has been shown to have had several phases of activity during the last glacial stage (Thomas *et al.*, 2000). The principal mechanism underlying these simulated changes in the terrestrial palaeoclimate is a simulated weakening and movement offshore of the Benguela Current, and a poleward shift of the Angola–Benguela front.

Figure 3 shows the spatial patterns of species-richness for Karoo and Fynbos bird species simulated for the climate of 1961–90, and for climates simulated for the 'Holocene thermal optimum' (HTO – 6 ka BP), LGM (21 ka BP) and a Heinrich Event (H2 – 24 ka BP). These time slices were selected because their species-richness patterns represent the variety of those seen across all 17 palaeoclimate scenarios. These maps lead to a number of conclusions about the potential impacts of late-Quaternary climatic changes on biodiversity patterns in southern Africa. Firstly, notwithstanding the relatively modest magnitude of the climatic changes simulated in response to the slow forcings, and especially to orbital changes, these climatic changes result in substantial changes in the potential distributions of species of both the Karoo and Fynbos, and consequent marked changes in their species-richness patterns. In particular, and in contrast to previous studies (Midgley & Roberts, 2001), the extent of the area of richness of Karoo species is considerably expanded northwards under LGM conditions (Fig. 3(c)); that of Fynbos species also expands, albeit to a lesser extent, but principally towards the east and north-east (Fig. 3(g)). Perhaps surprisingly, both species groups also show small increases in the extent of their areas of richness at the HTO. The potential impacts of sub-orbital climatic changes associated with shut-down of the AMOC during Heinrich Events, however, are much more substantial than those arising primarily from orbital forcing. The climate simulated for H2 leads to very much reduced potential distributions of species in both groups, and hence much reduced extents of their areas of richness, relative not only to those simulated for the LGM palaeoclimate but also for both the 6 ka BP and present climates. Two outlying areas of potential richness should be noted: Both species groups show an area of potential richness in north-western Namibia for the 1961–90, HTO and LGM climates, and both species groups show an area of potential richness for the H2 climate that coincides with the area of linear dunes mentioned earlier.

In order to summarise the results for all time slices in terms of the changing extent of the areas of species richness for the two species groups, the number of cells potentially suitable for more than appropriate threshold numbers of species in each group was counted for each time slice. These values are shown in Figure 4, plotted against the ages of the time slices. Also shown on the figure is summer (December 21st – January 20th) insolation at 30°S, calculated following Laskar *et al*. (2004), to illustrate the principal orbital forcing. Figure 4 reveals systematic temporal patterns in the potential numbers of species-rich grid cells. Firstly, the potential number of species-rich grid cells for Karoo species, especially those with >20 species, varies systematically at orbital time scales, to a large extent more or less paralleling summer insolation at 30°S that in turn is dominated by the *ca*. 21 thousand year precession cycle. Secondly, the potential number of species-rich grid cells for the Fynbos species, especially those with >10 species, also appears to vary systematically at orbital time scales, although in contrast to the Karoo species it reaches a maximum around the time of the obliquity minimum at *ca*. 30 ka BP, and shows a similar value to the present at 120 ka BP when obliquity was also close to the present value (Laskar *et al.*, 2004). Thirdly, the potential number of species-rich grid cells for Karoo species is markedly reduced under the climatic conditions simulated for Heinrich Events, with reductions of relatively greater magnitude when summer insolation at 30°S is higher. Fourthly, the potential number of species-rich grid cells for Fynbos species also is generally reduced for the Heinrich Event climates, although mostly to a much lesser extent than for the Karoo species; exceptions, however, are seen for H2 (24 ka BP), when the reduction is more marked than for other events, and especially for H3 (32 ka BP), when the potential number of species-rich grid cells is increased compared to both 30 and 36 ka BP. These results suggest that, not unexpectedly, the impacts of Heinrich Events on the regional climate, and hence on potential biodiversity patterns, depend upon the prevailing orbital configuration.

In order to explore the extent to which the varying climatic conditions of the last glacial–interglacial cycle may have influenced the location of present centres of biodiversity and endemism in the region, Figure 5 maps minimum numbers of species of each biome, and endemic to southern Africa, for which each grid cell was suitable across all 17 palaeoclimate scenarios as well as the 1961–90 climate. As a result of the magnitude of the impacts of the simulated climatic changes, only a very small minority of grid cells remains suitable for any substantial number of species endemic to southern Africa in either group under all 18 climates examined. Only 8 0·5° grid cells consistently support 11 or more of the 19 endemics associated with Karoo, four of them consistently supporting 12 of these species and a single grid cell consistently supporting 13 of them. The areas that larger numbers of species were able consistently to occupy lie in the Tanqua and Little Karoo and the coastal Richtersveld areas, coinciding with areas of high present floristic diversity (Thuiller *et al.*, 2006). In the Fynbos, 11 0·5° grid cells consistently support 7 or more of the 24 endemics associated with this biome, with just four supporting 8 of these species. Once again, the areas able consistently to be occupied by larger numbers of species coincide with areas of higher present floristic and overall diversity within the biome (Thuiller *et al.*, 2006).

Discussion

In regions such as southern Africa, where relatively few terrestrial records of late-Quaternary palaeoclimatic conditions have been investigated, and many of those records are fragmentary or discontinuous, leading to a reliance upon often rather imprecise dates when making any comparisons amongst records, a modelling approach such as we have adopted potentially can provide important insights and/or generate new testable hypotheses. Of course, to be of value in such ways the models used must first be demonstrated to give simulated palaeoclimates that are consistent with those records that are available from the region. However, making the necessary comparison of model results and palaeoclimate records is itself rendered difficult when, as in the present case, at least some of the palaeoclimatic evidence appears contradictory. This difficulty is compounded by the lack of continuous, high-resolution terrestrial palaeoclimatic records that might record the millennial climatic fluctuations that characterise the last glacial stage. For this reason we first explore comparisons between the results of the AOGCM experiments and marine records from the South Atlantic that are both continuous and of sufficient resolution to reveal millennial fluctuations, especially those associated with Heinrich Events.

As described above, the largest magnitude regional climatic changes were seen in the experiments designed to mimic Heinrich Events and thus to generate climatic conditions characteristic of extreme Greenland Stadial intervals. In the South Atlantic, the “hosing” simulations produce a general warming which is a consistent and robust feature of GCM simulations seeking to mimic Heinrich Events (Kageyama *et al.*, 2010), and is consistent with ice-core evidence for a bi-polar see-saw (Blunier & Brook, 2001) with respect to temperatures during the last glacial. The “hosing” also shifts the position of the ITCZ and changes the overall latitudinal temperature gradient. These changes are intimately linked to a weakening of the south-east trade winds that are a major driver of the Benguela current which changes significantly. There is also a poleward shift of the Angola–Benguela front. At present, and under the orbitally-forced scenarios, the Benguela Current (which is a cold eastern boundary current) maintains cool dry conditions in the west of southern Africa. In the “hosing” simulations, the weaker trade winds and current shifts result in a broad change in upwelling waters along the west coast of southern Africa; this is supported by evidence from marine sediment cores indicating such changes coincident with the timing of Heinrich Events (Kim *et al.*, 2003). Similar evidence indicates a reduced contrast in temperature between waters north and south of the Angola–Benguela Front at these times (Kim *et al.*, 2003). There is also evidence linking the vigour of the south-east trade winds to the extent of Antarctic sea ice (Stuut *et al.*, 2004), with weakening of the trade winds when Antarctic sea ice extent is reduced, as it was during the Antarctic warming episodes that coincide with Heinrich Events in the North Atlantic. The AOGCM modelling results, and the palaeoclimate scenarios derived from them, thus appear consistent overall with the available evidence from marine sediment cores in the South Atlantic.

When we turn to the terrestrial palaeoclimatic records, comparisons are more difficult because the records are often fragmentary and because of limitations of dating precision; in particular, few if any of the available terrestrial records either can unequivocally be attributed to an interval between Heinrich Events or shown to coincide with a Heinrich Event. Nonetheless, aside from the generally cooler conditions, and moister conditions in the west, for time slices spanning the LGM, a number of more detailed points of potential agreement do emerge. One such relates to the conflicting evidence of linear dune fields in the north-eastern Kalahari that were active during the last glacial stage, and that are interpreted as evidence of arid conditions, and evidence from cave sites of humid conditions in the same region during the last glacial, leading to the inference that dune construction in the region during the last glacial stage was ‘punctuated’ (Stokes *et al.*, 1997; Thomas *et al.*, 2000). The AOGCM experiments indicate conditions in the area generally similar to or moister than present for the majority of last glacial time slices (Figure 2), but with episodes of marked aridity associated with Heinrich Events. A similar inference of episodic dune activity during the last glacial stage associated with arid conditions has been made for western coastal regions (Chase & Thomas, 2007) where other palaeoclimatic records are interpreted as indicating generally moister conditions during much of the last glacial (Chase & Meadows, 2007). Once again, however, the AOGCM experiments indicate contrasting conditions during Heinrich Events and other last glacial time slices, although in this case the prevalent condition is similar to or marginally drier than present, with the Heinrich Event climates being markedly moister, especially in more northern parts of the region. A further point of detailed agreement relates to the evidence from a number of localities, including Nelson Bay Cave, Boomplaas Cave and Vankervelsvlei wetland, reviewed by Chase and Meadows (2007) and interpreted as indicating an interval of cooler and drier conditions in the Eastern Cape spanning the LGM and extending as late as *ca*. 14 ka BP. The climates of the relevant AOGCM time slices (24, 21, 18 and 15 ka BP, Figs. 1 and 2) indicate a consistent area with conditions cooler and drier than present in the Eastern Cape.

We thus conclude that, given the limitations of the terrestrial palaeoclimatic records, there is overall general agreement between the AOGCM results and these records in terms of spatio-temporal patterns of climatic change, with some striking examples of detailed agreement. Furthermore, the contrasting AOGCM results for Heinrich Events and other last glacial time slices lead us to hypothesise that apparently conflicting evidence of drier and moister conditions from discontinuous records in some parts of the region can likely be accounted for by millennial climatic fluctuations, such fluctuations being evident in marine sediment records from the South Atlantic. However, testing this hypothesis requires much more precise dating of the discontinuous records or, ideally, recovery and examination of continuous records, although the lack of maar lakes or other geological formations favouring the development of deep-water lakes likely to offer such records in southern Africa may render this an unachievable goal.

Turning to the potential role of late-Quaternary climatic changes in determining patterns of biodiversity in the Cape region, we have demonstrated coincidence between areas of current highest species diversity and endemism within the Karoo and Fynbos biomes and limited areas that potentially were most consistently suitable, throughout at least the last glacial–interglacial cycle, for species associated with these biomes (Figure 5). This represents compelling evidence that historical factors have been of primary importance in determining present diversity patterns (see e.g. Thuiller *et al.*, 2006 for plant species-richness patterns). Furthermore, our results show that, rather than orbitally-forced changes in potential species' ranges, it was the much reduced extent of areas potentially occupied by species of the two biomes during extreme Greenland Stadial intervals, corresponding to Heinrich Events, that was of greatest importance in defining these patterns, and hence the locations of present centres of diversity.

The paramount role of historical factors in determining present diversity patterns in the Cape Floristic Province has important implications for conservation. In particular, demonstrating coincidence between centres of present diversity and areas showing greatest continuity of suitability for species associated with these centres not only helps understand the origins of present patterns but also focuses attention upon the potential impacts of projected anthropogenic climatic changes (Meehl *et al.*, 2007) upon these centres of diversity. Forecast changes in climatic conditions will result in conditions in these areas no longer suitable for many of their associated species (Huntley & Barnard, 2012) as climatic patterns develop that appear to be without analogues today in the Quaternary record (Jansen *et al.*, 2007). This would lead to substantial changes in potential distributions of species in southern Africa in ways that are likely to result in the areas of greatest present diversity, and hence the areas of greatest historical suitability, suffering large reductions in species richness (Huntley & Barnard, 2012). Whilst changes of similar magnitude occurred in the past, especially during Heinrich events, geographical responses of species' distributions to future anthropogenic climatic change will differ from their past responses, some future climates being likely to lack analogues and some present climates being likely to disappear (Williams *et al.*, 2007). The impacts of future anthropogenic climatic change will also be compounded by pressures arising from other aspects of global change. Increasing atmospheric concentrations of carbon dioxide have direct impacts upon vegetation, altering the balance between woody plants and grasses (Bond *et al.*, 2003); these impacts are likely to render some areas currently within these centres of diversity no longer suitable in future in terms of habitat structure. Habitat loss and fragmentation as a result of the increasing extent and intensity of human land use further exacerbates the problems. Furthermore, the responses of human populations to climatic change may result in intensified pressures upon habitats (Watson & Segan, 2013). Developing effective conservation strategies for these important centres of biological diversity must thus be informed by integrated modelling of the impacts of projected changes in climate, atmospheric composition and land use on their species and ecosystems. Such an approach is urgently needed if internationally agreed targets to stem biodiversity losses are to be achieved.

Acknowledgements

Research was supported by Leverhulme Grant F/00 128/BI (BH). We are grateful to Prof. Les Underhill (University of Cape Town) for making the Southern African Bird Atlas Project data available to us, and to the numerous birders without whose efforts these data would not exist. Rob Simmons drew our attention to the presence of stable but sparsely-vegetated dunes in north-east Namibia and north-west Botswana. We are grateful to two anonymous reviewers and the Editor for their helpful comments upon an earlier version of the paper.

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Biosketch

Brian Huntley is a palaeoecologist, ecologist and biogeographer with research interests in the interactions between species, ecosystems and their changing environment. His work encompasses studies of the palaeoecology and palaeoenvironments of the Quaternary, of present ecosystems and biogeographic patterns, and of the potential impacts of anthropogenic global change on species and ecosystems. His research has considered a range of taxonomic groups, from plants to extinct Quaternary mammals, and various ecosystems, from Arctic tundra to Fynbos. He has a particular interests in birds and climatic change, and in the development of conservation strategies informed by research into how species and ecosystems respond to environmental changes.

BH, GFM and PB conceived the study. PJV performed the palaeoclimate simulations. BH carried out the species' modelling, analysed the results, prepared the figures and drafted the manuscript. All authors commented upon and contributed to the final version of the manuscript.

Editor: John Stewart

Tables

Table 1: Karoo and Fynbos bird species

Scientific name*	Common name*	Karoo[1]	Fynbos[2]	Endemic[3]	AUC[4]
Afrotis afra / A. afroides	Black Korhaan	K	F	E	0·926
Anthobaphes violacea	Orange-breasted Sunbird		F	E	0·972
Anthoscopus minutus	Cape Penduline-Tit	K			0·816
Anthus crenatus	African Rock Pipit	K		E	0·961
Aquila pennatus	Booted Eagle	K			0·801
Bradornis infuscatus	Chat Flycatcher	K			0·929
Bradypterus sylvaticus	Knysna Warbler		F	E	0·956
Calandrella cinerea	Red-capped Lark	K			0·841
Calendulauda albescens	Karoo Lark	K		E	0·973
Cercomela familiaris	Familiar Chat	K			0·849
Cercomela schlegelii	Karoo Chat	K			0·958
Cercomela sinuata	Sickle-winged Chat	K	F	E	0·964
Cercomela tractrac	Tractrac Chat	K			0·966
Cercotrichas coryphoeus	Karoo Scrub-Robin	K	F	E	0·958
Certhilauda curvirostris	Longbilled Lark	K	F	E	0·899
Chaetops frenatus	Cape Rock-jumper		F	E	0·965
Chersomanes albofasciata	Spike-heeled Lark	K			0·932
Cinnyris afer	Greater Double-collared Sunbird		F	E	0·978
Cinnyris chalybeus	Southern Double-collared Sunbird	K	F	E	0·956
Cinnyris fuscus	Dusky Sunbird	K			0·946
Circus maurus	Black Harrier		F	E	0·910
Cisticola subruficapilla	Grey-backed Cisticola	K	F		0·977
Crithagra albogularis	White-throated Canary	K			0·933
Crithagra flaviventris	Yellow Canary	K			0·911
Crithagra leucopterus	Protea Seedeater		F	E	0·991
Crithagra symonsi	Drakensberg Siskin		F	E	0·978
Crithagra totta	Cape Siskin		F	E	0·964
Cryptillas victorini	Victorin's Warbler		F	E	0·976
Emberiza capensis	Cape Bunting	K	F		0·921
Emberiza impetuani	Lark-like Bunting	K			0·918
Eremomela gregalis	Karoo Eremomela	K		E	0·979
Eremopterix australis	Black-eared Sparrowlark	K		E	0·964
Eremopterix verticalis	Grey-backed Sparrowlark	K			0·879
Euplectes capensis	Yellow Bishop		F		0·966

Table 1: Karoo and Fynbos bird species (continued)

Scientific name*	Common name*	Karoo[1]	Fynbos[2]	Endemic[3]	AUC[4]
Eupodotis vigorsii	Karoo Korhaan	K		E	0·975
Euryptila subcinnamomea	Cinnamon-breasted Warbler	K		E	0·953
Falco naumanni	Lesser Kestrel	K			0·925
Falco rupicolis	Rock Kestrel	K			0·826
Galerida magnirostris	Large-billed Lark	K		E	0·982
Hirundo fuligula	Rock Martin	K			0·881
Hirundo spilodera	South African Cliff-Swallow	K			0·937
Malcorus pectoralis	Rufous-eared Warbler	K		E	0·953
Melierax canorus	Southern Pale Chanting Goshawk	K			0·910
Merops apiaster	European Bee-eater		F		0·883
Mirafra apiata	Clapper Lark	K	F	E	0·930
Monticola explorator	Sentinel Rock-Thrush		F	E	0·964
Myrmecocichla formicivora	Anteating Chat	K		E	0·905
Nectarinia famosa	Malachite Sunbird		F		0·964
Neotis ludwigii	Ludwig's Bustard	K			0·932
Oenanthe monticola	Mountain Wheatear	K			0·906
Oenanthe pileata	Capped Wheatear	K			0·855
Parus afer	Grey Tit	K		E	0·966
Ploceus capensis	Cape Weaver		F	E	0·964
Prinia flavicans	Black-chested Prinia	K			0·914
Prinia maculosa / P. hypoxantha	Spotted Prinia	K	F	E	0·975
Promerops cafer	Cape Sugarbird		F	E	0·984
Promerops gurneyi	Gurney's Sugarbird		F	E	0·980
Pycnonotus capensis	Cape Bulbul		F	E	0·966
Saxicola torquatus	African Stonechat		F		0·948
Serinus alario	Black-headed Canary	K		E	0·962
Serinus canicollis	Cape Canary		F	E	0·976
Sphenoeacus afer	Cape Grassbird		F	E	0·964
Spizocorys sclateri	Sclater's Lark	K		E	0·960
Struthio camelus	Common Ostrich	K			0·802
Telophorus zeylonus	Bokmakierie	K	F		0·971
Turnix hottentotta	Black-rumped Buttonquail		F	E	0·967

* Scientific and common names follow Hockey *et al*. (2005).

[1] K indicates species associated with Karoo; [2] F indicates species associated with Fynbos;

[3] E indicates species endemic to southern Africa;

[4] Area under the curve for a receiver operating characteristic plot for a model fitted to all data.

Figure Legends

Figure 1 Mean temperature of the coldest month

Mean temperature of the coldest month (MTCO) for the present (1961–90) climate (top left panel) and MTCO anomalies for 17 time slices derived from experiments made using the HadCM3 AOGCM (Singarayer & Valdes, 2010). Sea levels are shown lowered following Fairbanks (1989) and Lambeck *et al*. (2002), relative sea levels for the 17 time slices being as follows: -5, -25, -55, -95, -105, -110, -120, -125, -125, -110, -80, -80, -80, -80, -80, -60 and 0 m respectively.

Figure 2 Ratio of actual to potential evapotranspiration

Annual integral of the ratio of actual to potential evapotranspiration (APET) for the present (1961–90) climate (top left panel) and APET anomalies for 17 time slices derived from experiments made using the HadCM3 AOGCM (Singarayer & Valdes, 2010). Sea levels are shown lowered following Fairbanks (1989) and Lambeck *et al*. (2002), relative sea levels for the 17 time slices being as follows: -5, -25, -55, -95, -105, -110, -120, -125, -125, -110, -80, -80, -80, -80, -80, -60 and 0 m respectively.

Figure 3 Contrasting species-richness patterns for Karoo and Fynbos birds

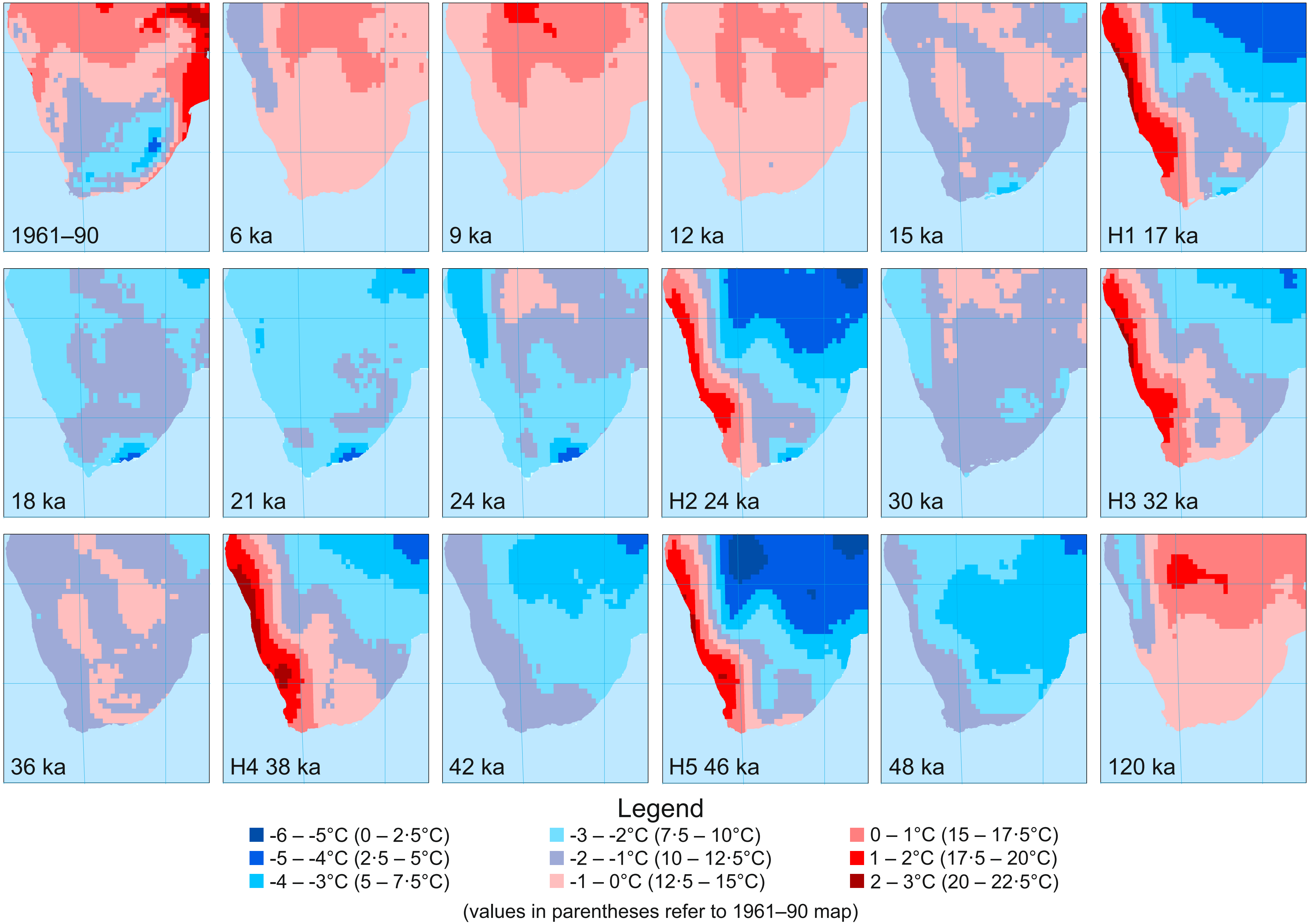
Potential species richness for Karoo (a – d) and Fynbos (e – h) species for 1961–90 (a, e), 6 ka BP (b, f), 21 ka BP (c, g) and Heinrich Event 2 (24 ka BP; d, h). Sea level shown lowered by 120 m for 21 and by 125 m for 24 ka BP; background shading indicates topography with contours at 500, 1000, 2000 and 3000 m. Darker shaded dots represent higher potential species richness.

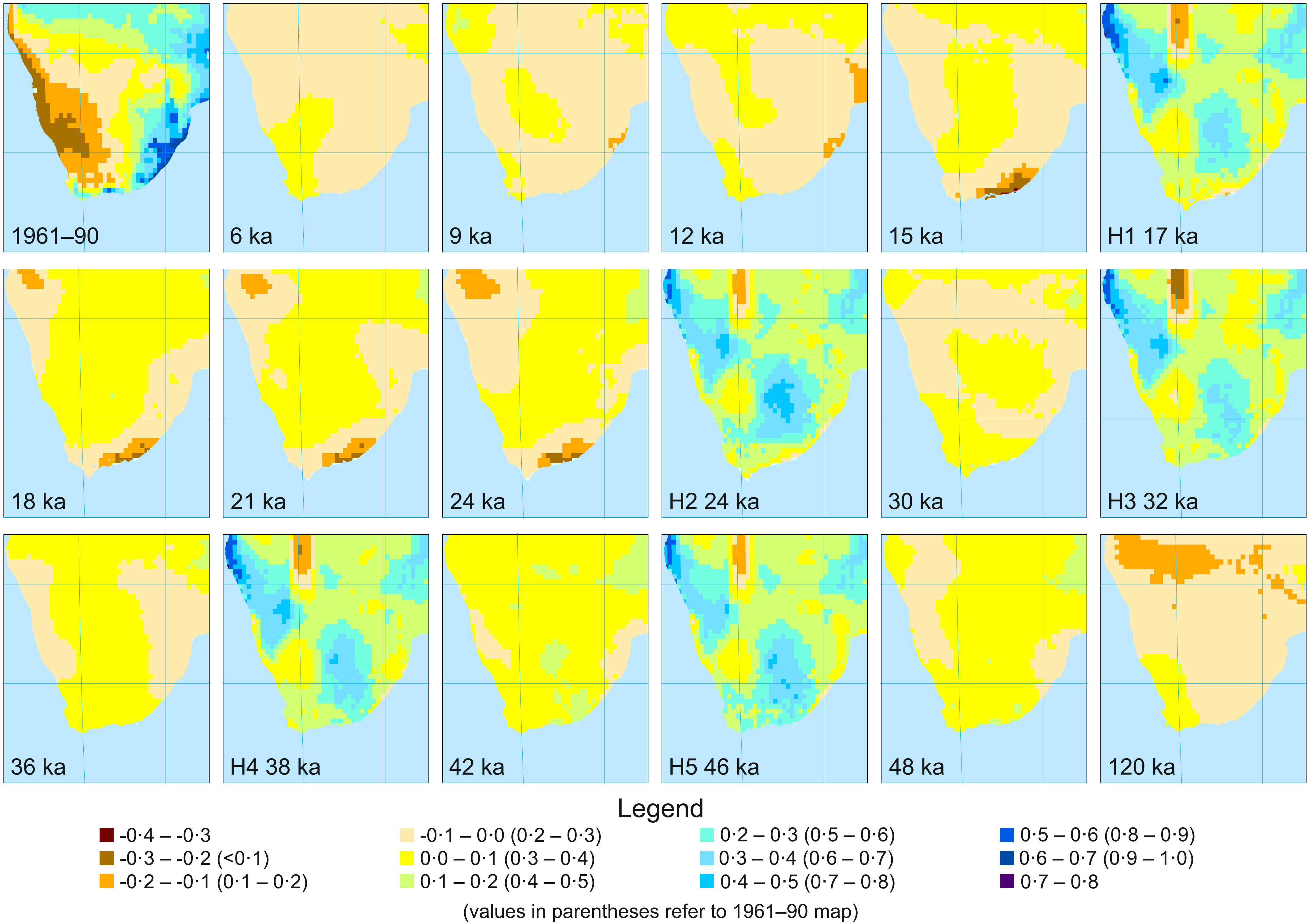
Figure 4 Variation between palaeoclimate scenarios in numbers of species-rich grid cells

Numbers of grid cells potentially occupied by >20 Karoo species (filled black diamonds), >30 Karoo species (unfilled diamonds), >10 Fynbos species (filled black triangles) and >15 Fynbos species (unfilled triangles) for the present climate and 17 palaeoclimate scenarios. Hatched vertical bars indicate palaeoclimate scenarios for experiments designed to mimic Heinrich Events. The curve shows the summer (December 21st – January 20th) insolation at 30°S calculated following Laskar *et al*. (2004).

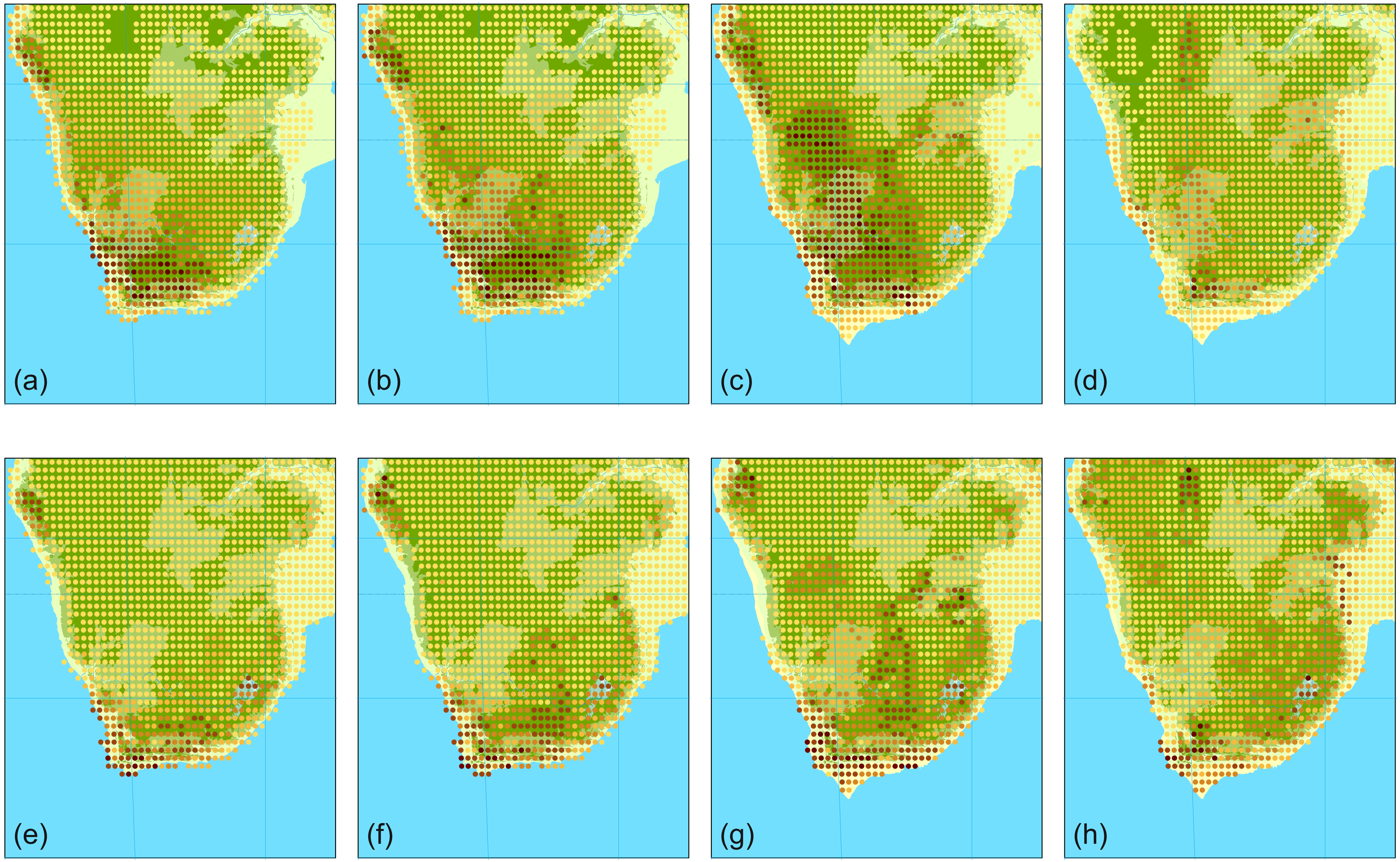
Figure 5 Grid cells consistently supporting higher numbers of southern African endemic species of each biome

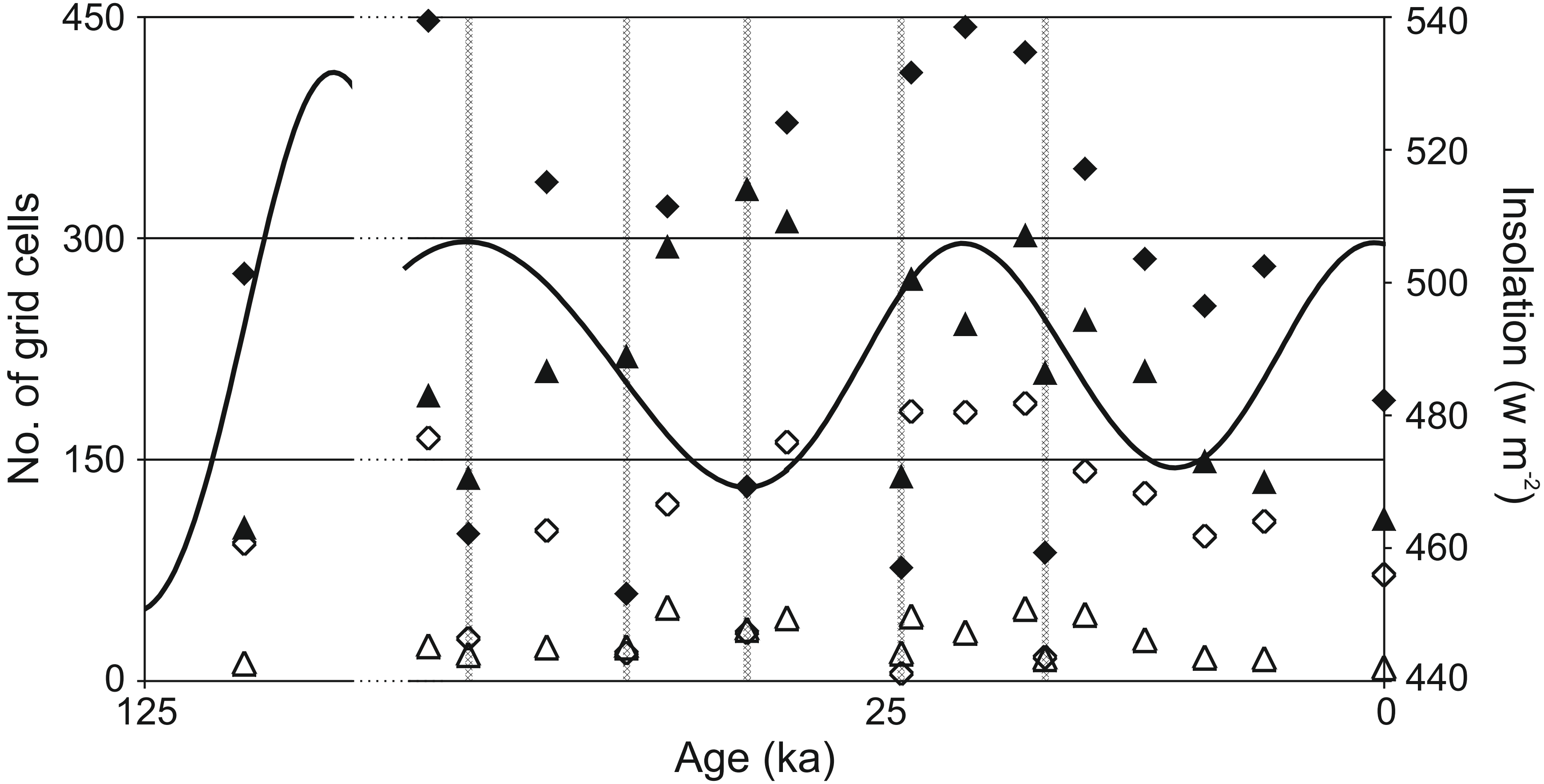
Grid cells potentially occupied (a) by a minimum of 7 – 13 Karoo species endemic to southern Africa for the 1961–90 climate and all 17 palaeoclimate scenarios and (b) by a minimum of 6 – 8 Fynbos species endemic to southern Africa for the 1961–90 climate and all 17 palaeoclimate scenarios. No grid cells potentially occupied at all times by species of either group endemic to southern Africa achieved higher minima than 13 and 8 for Karoo and Fynbos species respectively. Darker shaded dots indicate grid cells potentially occupied by a higher minimum number of species; background shading indicates topography with contours at 500, 1000, 2000 and 3000 m.

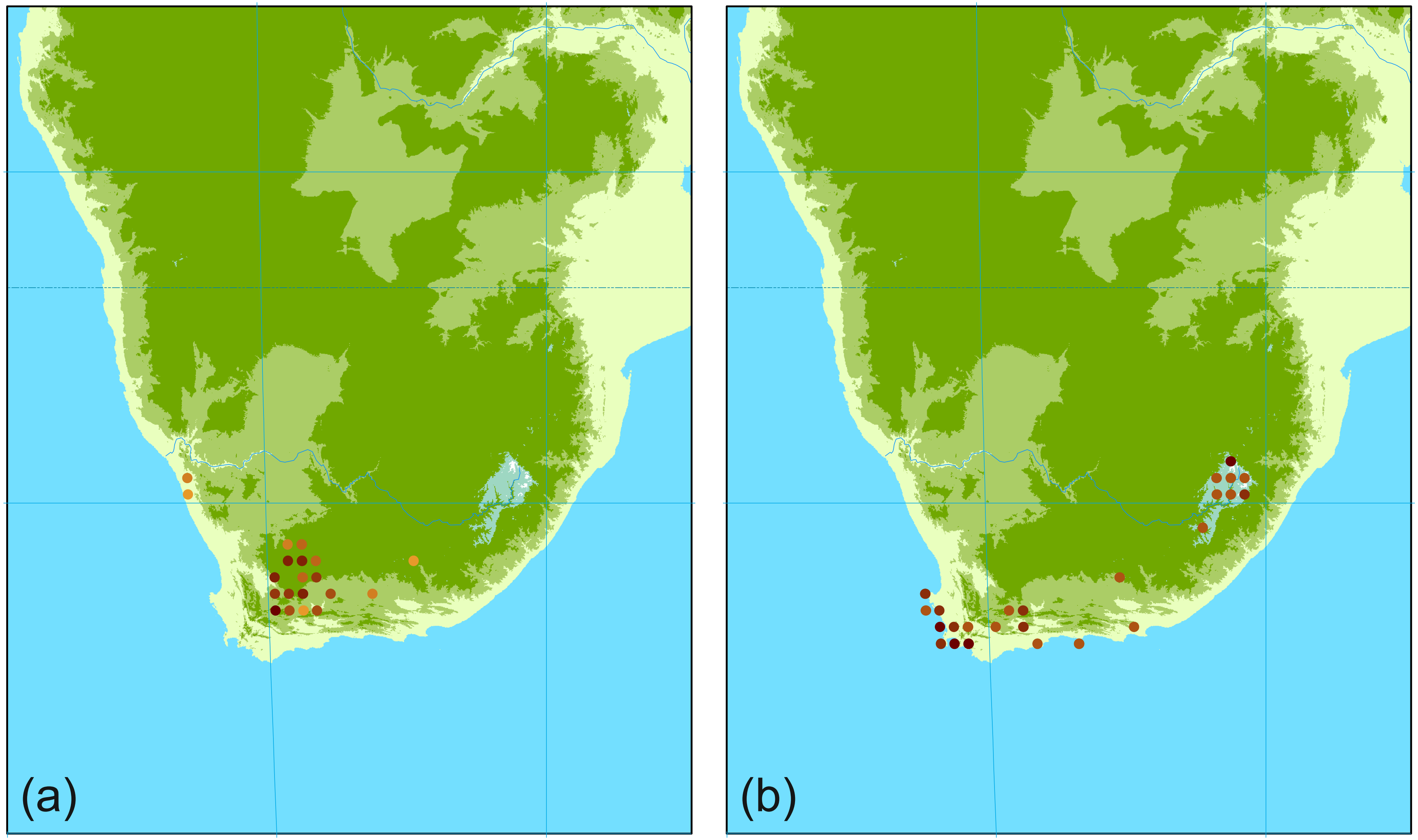

1961–90
6 ka
9 ka
12 ka
15 ka
H1 17 ka
18 ka
21 ka
24 ka
H2 24 ka
30 ka
H3 32 ka
36 ka
H4 38 ka
42 ka
H5 46 ka
48 ka
120 ka
Legend
-6 – -5°C (0 – 2·5°C)
-5 – -4°C (2·5 – 5°C)
-4 – -3°C (5 – 7·5°C)
-3 – -2°C (7·5 – 10°C)
-2 – -1°C (10 – 12·5°C)
-1 – 0°C (12·5 – 15°C)
0 – 1°C (15 – 17·5°C)
1 – 2°C (17·5 – 20°C)
2 – 3°C (20 – 22·5°C)
(values in parentheses refer to 1961–90 map)



1961–90
6 ka
9 ka
12 ka
15 ka
H1 17 ka
18 ka
21 ka
24 ka
H2 24 ka
30 ka
H3 32 ka
36 ka
H4 38 ka
42 ka
H5 46 ka
48 ka
120 ka
Legend
-0·4 – -0·3
-0·3 – -0·2 (<0·1)
-0·2 – -0·1 (0·1 – 0·2)
-0·1 – 0·0 (0·2 – 0·3)
0·0 – 0·1 (0·3 – 0·4)
0·1 – 0·2 (0·4 – 0·5)
0·2 – 0·3 (0·5 – 0·6)
0·3 – 0·4 (0·6 – 0·7)
0·4 – 0·5 (0·7 – 0·8)
0·5 – 0·6 (0·8 – 0·9)
0·6 – 0·7 (0·9 – 1·0)
0·7 – 0·8
(values in parentheses refer to 1961–90 map)


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)


450
300
150
0
125
25
0
Age (ka)
No. of grid cells
540
520
500
480
460
440
Insolation (w m-2)


(a)
(b)