

Climate change and faunal turnover: testing the mechanics of the turnover-pulse hypothesis with South African fossil data

J. Tyler Faith and Anna K. Behrensmeyer

Abstract.—The turnover-pulse hypothesis (TPH) makes explicit predictions concerning the potential responses of species to climate change, which is considered to be a major cause of faunal turnover (extinction, speciation, and migration). Previous studies have tested the TPH primarily by examining temporal correlations between turnover pulses and climatic events. It is rarely possible to dissect such correlations and observe turnover as it is occurring or to predict how different lineages will respond to climate change. Thus, whether climate change drives faunal turnover in the manner predicted by the TPH remains unclear. In this study, we test the underlying mechanics of the TPH using well-dated Quaternary ungulate records from southern Africa's Cape Floristic Region (CFR). Changes in sea level, vegetation, and topographic barriers across glacial-interglacial transitions in southern Africa caused shifts in habitat size and configuration, allowing us to generate specific predictions concerning the responses of ungulates characterized by different feeding habits and habitat preferences. Examples from the CFR show how climatically forced vegetation change and allopatry can drive turnover resulting from extinction and migration. Evidence for speciation is lacking, suggesting either that climate change does not cause speciation in these circumstances or that the evolutionary outcome of turnover is contingent on the nature and rate of climate change. Migrations and extinctions are observed in the CFR fossil record over geologically short time intervals, on the order of Milankovitch-scale climate oscillations. We propose that such climate oscillations could drive a steady and moderate level of faunal turnover over 10^4 -year time scales, which would not be resolved in paleontological records spanning 10^5 years and longer. A turnover pulse, which is a marked increase in turnover relative to previous and subsequent time periods, requires additional, temporally constrained climatic forcing or other processes that could accelerate evolutionary change, perhaps mediated through biotic interactions.

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Introduction

Climate change has been considered a driving force in the evolution of Earth's biota since the nineteenth century, but its precise role in mediating the distribution, origination, and extinction of species has proven difficult to test in the fossil record. With respect to terrestrial mammals, a proposal for how late Cenozoic climate change drives faunal turnover (migration, speciation, and extinction) was formalized in Elisabeth Vrba's (1985, 1992, 1993, 1999) turnover-pulse hypothesis (TPH). Vrba proposed that climate-driven changes in habitats promoted faunal turnover among African mammals and that a major turnover pulse occurred during the onset of Northern Hemisphere glaciation between 2.8

and 2.5 Ma. Her ideas initially were aimed at explaining patterns in the evolution of late Cenozoic African Bovidae, and she also applied them to the human fossil record (Vrba 1988, 1995, 1999). The TPH has inspired considerable debate over the role of climate change in mammalian evolution, with opinions ranging from climate as a major force in faunal turnover (Behrensmeyer et al. 1992, 1997; Barnosky 2001; Raia et al. 2005; van Dam et al. 2006; Blois and Hadly 2009) to climate as incidental and relatively unimportant (Alroy 1996, 1998; Prothero and Heaton 1996; Prothero 1999, 2004; Alroy et al. 2000).

Causes of large-scale biotic turnover are the subject of continuing controversy among paleobiologists and evolutionary ecologists, and a detailed review of these debates is

outside the scope of this paper. Briefly, the main alternatives to climate forcing as an explanation for biotic turnover are (1) biological processes, including competition, disease, and predation; (2) tectonically driven changes in biogeographic barriers; and (3) random processes of dispersal, extinction, and speciation. Competition within trophic levels may occur between individuals and populations especially in resource-limited situations and also result from the immigration of new taxa into an established community (Mitchell et al. 2006). The importance of competition as a driver of biotic turnover has been the subject of continuing debate (Van Valen 1973; Masters and Rayner 1993; Jablonski 2008; Benton 2009), but some paleontological studies suggest that this may be a viable explanation for turnover in the absence of observed climate change (Alroy 1998; Alroy et al. 2000). Tectonics plays an important role in faunal turnover by creating or eliminating geographic barriers (e.g., the isthmus of Panama) (Vrba 1992), and this can occur either in the absence of climate change or in concert with it. The null model of community assembly (Unified Neutral Theory of Biodiversity and Biogeography) proposes that turnover in any particular place and time is a function of random dispersal, extinction, and speciation; thus, chance alone is a major driver of biotic change (Hubbell 2001). For all of these proposed causes of biotic turnover, the genetic capacity of any given lineage to adapt under a given set of environmental and biological conditions could affect the pattern and rate of turnover and also its visibility in the fossil record.

With regard to the TPH, debate has centered on the extent to which late Cenozoic faunal turnover occurs in a piecemeal fashion or as synchronized pulses during episodes of pronounced climate change (Behrensmeyer et al. 1997; Reed 1997; McKee 2001; Barry et al. 2002; Bobe et al. 2002; Bobe and Behrensmeyer 2004; DeMenocal 2004; Werdelin and Lewis 2005; Behrensmeyer 2006; van Dam et al. 2006; Frost 2007). The TPH has also stimulated debate over the role of climate change in human evolution (Behrensmeyer et al. 1997; Reed 1997; Potts 1998; Bobe et al. 2002; Bobe and Behrensmeyer 2004; DeMenocal 2004;

Behrensmeyer 2006), in part because of Vrba's (1988, 1995, 1999) proposal that global cooling between 2.8 and 2.5 Ma contributed to a major turnover pulse in African mammals, which included the originations of the hominin genera *Homo* and *Paranthropus*. This has been questioned because empirical evidence from compiled species first and last appearances fails to show marked turnover during this interval (Behrensmeyer et al. 1997; Bobe et al. 2002; Werdelin and Lewis 2005; Frost 2007) and also because insufficient chronological resolution and unequal sampling often confounds attempts to correlate turnover with climate change (Hill 1987; McKee 2001).

Regardless of the arguments about the African 2.8–2.5 Ma turnover pulse, Vrba constructed the TPH with broad theoretical underpinnings that allowed her to make explicit predictions about *how* climate change can drive faunal turnover. If these predictions can be supported by evidence from the fossil record, this would have broad implications for understanding the role of climate in macroevolution and ecosystem change at a finer scale than has previously been possible. Investigations that focus solely on temporal correlations between faunal turnover and climate change can at best provide circumstantial rather than process-based tests for the predictions of the TPH. Here, we take a process-based approach to test the mechanics of the TPH using well-documented faunal histories from the Quaternary fossil record of southern Africa. The primary question asked here is, Does climate change drive turnover in accordance with the mechanisms outlined in Vrba's TPH?

Mechanics of Turnover

The central premise of Vrba's TPH is that all species are habitat-specific and able to persist only under a specific range of environmental conditions (e.g., temperature, rainfall, vegetation). Changes in the physical environment drive turnover by fragmenting or altering the composition of a species' habitat, which leads to the division of populations into geographically and genetically isolated groups (i.e., migration and vicariance). This vicariance results in a phase of allopatry, which has long

been argued to be a necessary precursor to speciation and extinction (Mayr 1942, 1963, 1970). Because climate change is a common driver of physical environmental change, the TPH predicts that faunal turnover will occur as synchronous pulses across multiple lineages in conjunction with temporally constrained climatic events.

In debates concerning the roles of biotic versus climatic drivers in macroevolution (e.g., Red Queen vs. Court Jester), the TPH is often emphasized for its predictions concerning speciation (e.g., Barnosky 2001, 2005; Benton 2009). Although this is one crucial component of the TPH, it is important to note that the TPH more broadly concerns the influence of climate on all manners of faunal turnover, which include speciation, extinction, and migration (Vrba 1985, 1992, 1993, 1995). As initially formulated by Vrba (1985, 1992, 1993), the TPH predicts several potential responses of species to climate change (Fig. 1). If the distribution of habitats preferred by a species remains unchanged, that species will persist with no change in distribution (Fig. 1A). Alternatively, if the preferred habitat moves in response to climate change, a species will persist but with a change in distribution (i.e., migration) (Fig. 1B). Lastly, if climate change causes preferred habitats to become discontinuously subdivided, a species will undergo vicariance either without (Fig. 1C) or with evolutionary change (Fig. 1D–H). Evolutionary responses include extinction (Fig. 1D), intraspecific evolution (Fig. 1E), and speciation (Fig. 1F–H). Vrba (1985) proposed that evolutionary change will only occur when a species' environmental tolerance threshold is exceeded.

We consider these responses to climate change as the fundamental mechanics of the TPH, which drive the combination of migration, extinction, and speciation that characterize a turnover pulse. Previous studies have tested the TPH by looking for peaks in turnover, often using first and last appearances of fossil taxa that can be associated with climatic events (Behrensmeyer et al. 1997; McKee 2001; Bobe et al. 2002; Bobe and Behrensmeyer 2004; Raia et al. 2005; Werdelin and Lewis 2005; van Dam et al. 2006; Frost

2007). However, even when turnover pulses are detected and can reasonably be explained by contemporaneous climate change, the fossil record rarely provides the resolution needed to observe the mechanics of the TPH or to predict how different lineages will respond to climate change. As a result, the crucial links between climate change and faunal turnover have been largely invisible in the vertebrate fossil record, leaving open the question of whether climate drives faunal turnover in the manner predicted by the TPH.

Southern Africa's Cape Floristic Region

The fossil record of Southern Africa's Cape Floristic Region (CFR; Fig. 2) provides an ideal opportunity to explore the mechanics of Vrba's turnover-pulse hypothesis owing to the combined effects of late Quaternary climate change, sea-level fluctuations, and biogeographic barriers for large mammals. The CFR encompasses approximately 90,000 km² along the southern and western coast of South Africa and is characterized by exceptional floral diversity of ~9000 plant species, more than two-thirds of which are endemic (Linder 2003). The primary vegetation types include fynbos and renosterveld. Fynbos is dominant and characterized by hard-leaved evergreen shrubland occurring on nutrient-poor soils. Renosterveld is found on more nutrient-rich soils and is composed of evergreen asteraceous shrubs with a sparse understory of grasses. The shrubby CFR vegetation provides poor forage for large mammalian herbivores, supporting a low-biomass ungulate community dominated by small-bodied browsers, including duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), and Cape grysbok (*R. melanotis*) (Klein 1983; Skead 2011). The rare large grazers, including hartebeest (*Alcelaphus buselaphus*), bontebok (*Damaliscus dorcas*), buffalo (*Syncerus caffer*), and zebras (*Equus zebra* and *E. quagga*), preferentially utilize the grasses in renosterveld habitats (Boshoff and Kerley 2001).

In terms of climate, vegetation, and the fauna, the coastal lowlands of the CFR can be divided into two distinct subregions: the southern coastal plain (SCP) and the western coastal plain (WCP) (Klein 1983; Chase and

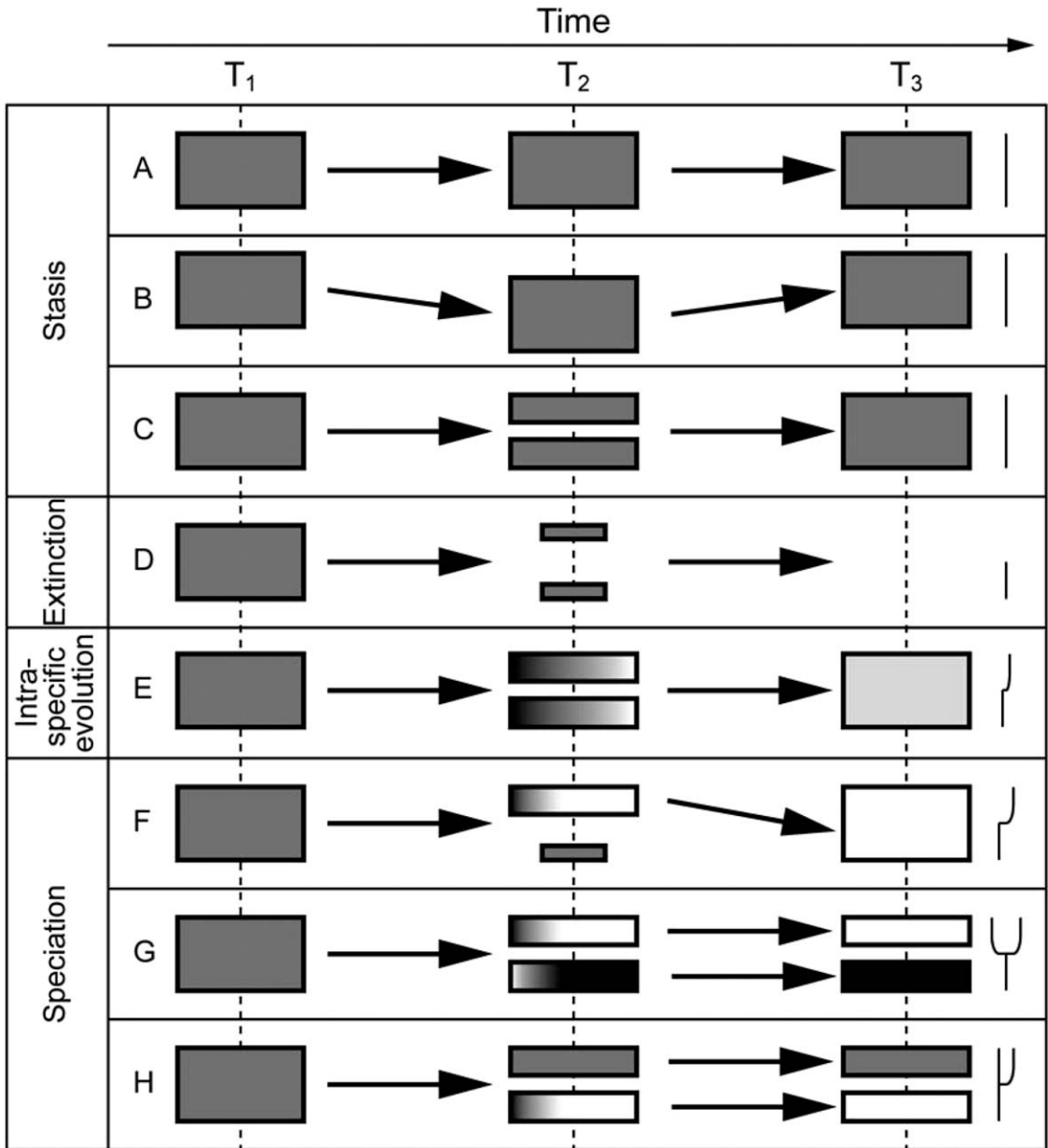


FIGURE 1. Potential responses of species to climate change through time, including stasis (A–C), extinction (D), intraspecific evolution (E), and speciation (F–H). Boxes represent the geographic distributions and habitats occupied by a species. Schematic phylogenetic trees shown at far right. Modeled after Vrba (1985). Note that line drawings to the right indicate the pattern as it would appear if projected through time.

Meadows 2007; Radloff 2008; Compton 2011; Skead 2011). The WCP receives most of its rainfall during the winter months, whereas the SCP receives rainfall more evenly throughout the year, with summer rainfall increasing from west to east (Chase and Meadows 2007). The variation in rainfall seasonality has an impor-

tant effect on the distribution of C_3 and C_4 grasses, with the sparse grass cover of the WCP dominated by C_3 grasses (>75%) and the SCP including greater grass biomass and a larger proportion of C_4 grasses (Vogel et al. 1978; Rebelo et al. 2006; Radloff 2008). The combination of year-round rainfall and greater

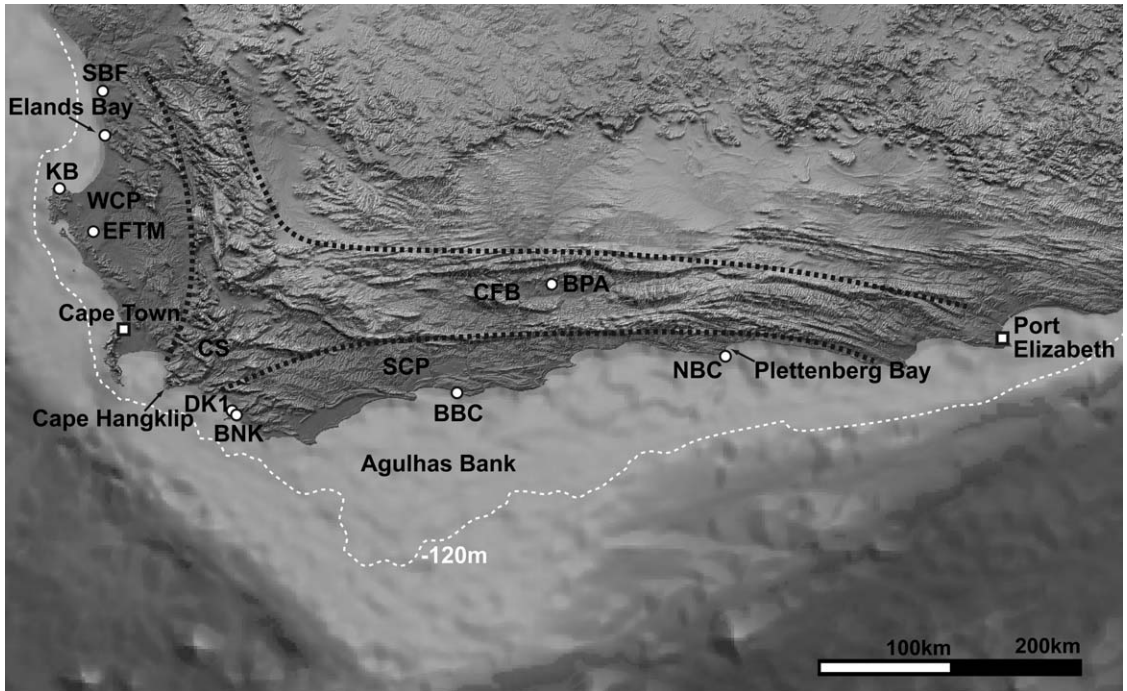


FIGURE 2. Map of southern Africa showing the location of the southern coastal plain (SCP) and the western coastal plain (WCP) relative to the Cape Fold Belt (CFB: dashed black line) and the Cape Syntaxis (CS). Dashed white line indicates the -120-m sea-level contour corresponding to the Last Glacial Maximum coastline (Van Andel 1989; Compton 2011). Fossil sites include Boomplaas Cave (BPA), Nelson Bay Cave (NBC), Blombos Cave (BBC), Byneskranskop 1 (BNK), Die Kelders Cave 1 (DK1), EFTM (Elandsfontein Main), KB (Kasteelberg A & B), Steenbokfontein (SBF), and the Elands Bay sites (Elands Bay Cave, Elands Bay Open, Spring Cave, Tortoise Cave, Pancho's Kitchen Midden).

availability of grass allows the SCP to support several large grazers that have been absent historically from the WCP (Radloff 2008), including bontebok, buffalo, and extinct blue antelope (*Hippotragus leucophaeus*) (Klein 1983; Boshoff and Kerley 2001; Skead 2011).

The SCP and WCP are isolated from each other and from the South African interior by the rugged Cape Fold Belt, which is divisible into southern and western branches that intersect at the Cape Syntaxis (Fig. 2). The southern branch consists of a series of folded mountains that rise up to 2 km in elevation and run parallel to the coast for >600 km from Port Elizabeth in the east to Cape Hangklip in the west. Cape Hangklip represents the coastal spur of the Cape Syntaxis, from which the western branch extends ~ 250 km to the north and defines the eastern boundary of the WCP. The intersection of the Cape Syntaxis with the shoreline at Cape Hangklip creates a biogeographic barrier in a series of rocky cliffs

that restrict movement of large terrestrial mammals between the SCP and the WCP (Compton 2011). With the exception of the Cape mountain zebra (*Equus zebra zebra*), which tolerates rugged terrain, most large grazers are unable to find adequate habitat or forage across the Cape Syntaxis barrier (Boshoff and Kerley 2001), restricting their potential for migration between the two regions. In contrast, the Cape Syntaxis presents a more permeable barrier for smaller browsers, such as Cape grysbok, steenbok, and klipspringer (*Oreotragus oreotragus*) (Boshoff and Kerley 2001).

Migration beyond the eastern margins of the SCP, particularly for open-habitat species, is inhibited by dense Afromontane forest along the narrow coastal plain (4 km wide) near Plettenberg Bay and deeply incised river gorges (Compton 2011). The WCP is likewise cut off from the interior by an arid corridor to the north, which receives less than 300 mm

annual rainfall (Chase and Meadows 2007; Compton 2011) and is characterized by the prevalence of succulent plant species (Succulent Karoo vegetation). This arid corridor restricts migration of many large mammal species, with the possible exceptions of springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazella*), both of which tolerate arid conditions, and elephant (*Loxodonta africana*), which is capable of migrating long distances between water sources (Skinner and Chimimba 2005; Skead 2011).

The physical barriers and environments that influence the large mammals in the CFR today were fundamentally altered during Pleistocene marine regressions (Fig. 3). Reduced sea levels exposed the shallow continental shelf off the SCP (the Agulhas Bank), creating a broad coastal plain and increasing landmass by upwards of 60,000 km² (Van Andel 1989; Fisher et al. 2010). Drawing upon bathymetric evidence, Compton (2011) showed that marine regressions would have allowed large mammals to move between the SCP and WCP unimpeded by the outer spur of the Cape Syntaxis. Likewise, movement between the exposed coastal plain to the east and the interior was facilitated by the expanded 40–60 km-wide coastal portal near Plettenberg Bay (Compton 2011).

Changes in paleogeography during marine regressions correspond to substantial environmental and vegetational shifts. On the WCP, charcoal and pollen records from Elands Bay Cave show that the Last Glacial Maximum (LGM) through Lateglacial was characterized by increased moisture availability and a higher proportion of grassland habitats compared to the Holocene (Cowling et al. 1999; Parkington et al. 2000). Micromammal assemblages from Byneskranskop 1 and Boomplaas Cave (SCP and Cape Fold Belt) indicate peak frequencies of grassland species during the LGM–Lateglacial (Avery 1982). These vegetation shifts are likely related to altered rainfall regimes and diminished atmospheric CO₂ concentrations (Chase and Meadows 2007; Faith 2013). Thus, paleoenvironmental records independent of the large mammal record from both the SCP and WCP provide evidence for an expansion of grasslands. Consistent with

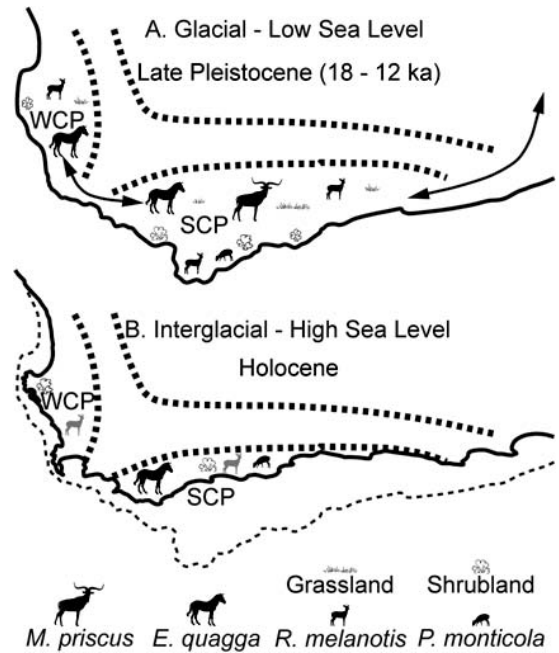


FIGURE 3. Changes in paleogeography, vegetation, and faunas during glacial maxima and interglacial highstands with four representative taxa: (1) *Megalotragus priscus* (grazer), which becomes extinct; (2) *E. quagga* (grazer), which exhibits a range contraction; (3) *R. melanotis* (browser), which retains a stable distribution but with evolutionary change (represented by gray shading in B); and (4) *P. monticola* (browser), which exhibits an apparent range expansion when its habitat shifts north into the vicinity of neo-coastal sites. Arrows indicate migration routes for grassland species.

this vegetation change, fossil evidence indicates that the large mammal community that inhabited the exposed coastal plain was species rich and dominated by large grazing ungulates, including equids and alcelaphine antelopes (Schweitzer and Wilson 1982; Klein 1983; Klein and Cruz-Urbe 1987; Rector and Reed 2010; Faith 2011b). Grazing species may have migrated seasonally across the coastal platform, following the winter rains in the WCP and the summer rains along the eastern SCP (Marean 2010; Faith and Thompson in press). Given the presence of grassland faunas on the coastal lowlands and in the highlands of the Cape Fold Belt (Klein 1983; Faith 2012b), fynbos and its associated browser-dominated mammal community likely occurred along a narrow zone adjacent to the expanded paleo-coastline (Bar-Matthews et al. 2010; Marean 2010; Compton 2011).

Rapidly rising sea levels during glacial terminations created a vicariance event by flooding the coastal plain and isolating the SCP from the WCP and the interior (Compton 2011). Grassland species that once ranged across the continuous coastal plain were split into the two subregions of the CFR. At the same time that ranges were being divided, altered rainfall regimes and rising atmospheric CO₂ concentrations contributed to a contraction of grasslands. As sea level rose, the band of fynbos and other shrubby vegetation types moved northward across the formerly grassy coastal lowlands. This is consistent with fossil mammal sequences spanning the Pleistocene–Holocene transition, which show the replacement of open-habitat grazers by small browsers typical of CFR shrublands, with an essentially modern fauna in place by ~5000 years ago (Schweitzer and Wilson 1982; Klein 1983; Faith 2012b). There is also evidence for comparable shifts in faunal composition across glacial-interglacial stages earlier in the late Pleistocene (Klein 1983). Taken together, the changes in paleogeography and vegetation structure across the Pleistocene–Holocene transition set up an important distinction between those species whose habitats fragmented or disappeared (open-habitat species—large grazers) and those whose habitats shifted their distribution (shrubland species—small browsers).

Testing the Mechanics of Faunal Turnover

The combination of habitat change and vicariance across glacial-interglacial transitions in the CFR (Fig. 3) provides ideal circumstances for testing the mechanics of faunal turnover according to the TPH. Current understanding of Quaternary climate, vegetation, and faunal change in the CFR allows us to make several predictions relevant to turnover:

Prediction 1: The loss of grassland habitats and the isolation of the SCP and WCP at the onset of the Holocene should lead to extinction, extirpation, and range contraction primarily in species that are grazers or prefer open grassland habitats. Range contractions should be characterized primarily by the disappearance of taxa from the WCP, which

is less productive and grassy than the year-round rainfall zone on the SCP.

Prediction 2: Rising sea levels and expanding shrubland (e.g., fynbos) at the onset of the Holocene will allow browsing species that prefer closed or shrubby habitats to shift distribution into the vicinity of neo-coastal sites along the SCP. Such species are expected to be absent from the SCP during the LGM–Lateglacial but present in the Holocene. We expect fewer range shifts among small browsers along the WCP, where coastline changes during glacial-interglacial cycles were less substantial (Fig. 3).

Prediction 3: Lineages adapted to open grassland habitats will be characterized by elevated incidences of extinction and speciation over the long term (i.e., the Quaternary). This results from the repeated expansion and contraction of grassland habitats during glacial-interglacial cycles together with the isolation of grassland species on the SCP during marine transgressions. The former (habitat loss) will promote extinction or speciation by exceeding a species' environmental tolerance threshold, whereas the latter (isolation) is a necessary precursor to allopatric speciation but also increases the probability of extinction (Vrba 1985).

These predictions encompass the range of potential responses to climate change, as outlined by Vrba's TPH (1985, 1992, 1993, 1999), including migration (Predictions 1 and 2), extinction (Predictions 1 and 3), and speciation (Prediction 3). Testing such predictions requires a fossil record with multiple, geographically widespread, reliably dated assemblages of well-studied taxa along with independent evidence for environmental shifts linked to climate change. The CFR late Pleistocene to Holocene fossil record meets these criteria, allowing us to examine the predictions using the biogeographic histories of bovids, equids, and suids, which have been reconstructed from previously reported fossil assemblages together with Skead's (2011) assessment of species distributions in historic times (1600 A.D. to present). We focus our analysis on these ungulates because they are well represented in CFR the fossil record and because most species are linked by their

TABLE 1. SCP and WCP faunal samples from the last ~21,000 ¹⁴C years. Age ranges provide for Holocene (H) and Pleistocene (P) (LGM–Lateglacial) faunal aggregates.

Site	Context	Age range	Reference
SCP assemblages			
Blombos Cave	Coastal cave	H: 2–0.3 ¹⁴ C Ka	Henshilwood et al. 2001
Boomplaas Cave	Inland Cave	H: 9.1–1.5 ¹⁴ C Ka P: 21.2–10.4 ¹⁴ C Ka	Klein 1983; Faith 2012b
Byneskranskop Cave 1	Near-coastal cave	H: 9.8–0.3 ¹⁴ C Ka P: 12.7–>9.8 ¹⁴ C Ka.	Schweitzer and Wilson 1982; Faith 2012a
Die Kelders Cave 1	Coastal cave	H: 2–1.5 ¹⁴ C Ka	Klein and Cruz-Urbe 2000
Nelson Bay Cave	Coastal cave	H: 9.0–0.5 ¹⁴ C Ka P: 18.7–10.2 ¹⁴ C Ka	Klein 1983; Inskeep 1987; Faith 2012a
WCP assemblages			
Elands Bay Cave	Coastal cave	H: 9.6–0.3 ¹⁴ C Ka P: 13.6–10.7 ¹⁴ C Ka	Klein and Cruz-Urbe 1987
Elands Bay Open	Open-air midden	H: 1.5–0.6 ¹⁴ C Ka	Klein and Cruz-Urbe 1987
Kasteelberg A & B	Open-air midden	H: 1.9–0.3 ¹⁴ C Ka	Klein and Cruz-Urbe 1989
Pancho's Kitchen Midden	Open-air midden	H: 3.6–0.6 ¹⁴ C Ka	Jerardino 1998
Spring Cave	Near-coastal cave	H: <2 Ka	Klein and Cruz-Urbe 1987
Steenbokfontein	Near-coastal cave	H: 6–2.2 ¹⁴ C Ka	Jerardino and Yates 1996
Tortoise Cave	Near-coastal cave	H: 7.7–0.8 ¹⁴ C Ka	Klein and Cruz-Urbe 1987

dietary ecology to specific habitats, making them appropriate candidates for exploring the mechanics of the TPH as outlined by Vrba. However, we caution that the applicability of our results to other mammalian lineages will require further investigation.

To explore patterns of ungulate community change across the Pleistocene–Holocene transition, we make use of presence-absence data from four well-sampled and well-dated LGM and Lateglacial assemblages and 12 Holocene assemblages across the present-day southern and western coastal plain (Table 1, Fig. 2). We note that Boomplaas Cave is not located on the SCP proper, but rather is located ~80 km inland on the flanks of the Swartberg Mountains (Cape Fold Belt). Its inclusion in the broader SCP sample is justified by the fact that it shares most of the same species present in other SCP sites, suggesting interchange between the two regions, and because it shows a similar faunal transition from grasslands to shrublands across the Pleistocene–Holocene transition (Avery 1982; Klein 1983; Faith 2012b).

The faunal remains from all sites were recovered from stratified cave and open-air deposits, with age estimates established by radiocarbon dates primarily on charcoal (see age ranges in Table 1). These presence-absence data are used to test Predictions 1 and 2, by providing evidence for extirpation and range

shifts from the LGM–Lateglacial to the Holocene (Table 2). Given the small number of LGM–Lateglacial assemblages, it is possible that rare species have not been documented due to sampling artifacts. In a broader quantitative analysis of CFR Pleistocene assemblages, Faith (2011b: p. 224) showed that rare species tend to be grazers. The possibility that grazers are under-represented in the LGM–Lateglacial could lead to (1) a failure to recognize grazer extirpations across the Pleistocene–Holocene transition or (2) the erroneous impression of grazer expansions across the Pleistocene–Holocene transition. As demonstrated below, however, these possibilities do not seem to have detracted from the overall pattern.

For geographic reasons, we have omitted the Holocene ungulates from Klasies River Mouth. Although Klasies River Mouth is located within the CFR proper, it is situated east of Plettenberg Bay and may have been contiguous with the SCP only during marine regressions (Compton 2011). However, we note that the inclusion of this site in our analysis does not alter the results.

The LGM–Lateglacial and Holocene fossil assemblages examined here are derived from archaeological contexts, with ungulate remains largely representing food refuse deposited at hunter-gatherer residential sites. Ethnographic data from southern Africa indi-

TABLE 2. The presence/absence of ungulates in LGM–Lateglacial (21.2–10 ¹⁴C Ka) and Holocene (<10 ¹⁴C Ka) assemblages on the SCP and WCP.

Taxon	Habitat	Diet	LGM–Lateglacial		Holocene		Shift?
			WCP	SCP	WCP	SCP	
Cape zebra (<i>Equus capensis</i>)†	Open	Grazer	1	1	1**	0	Extinct
Plains zebra (<i>Equus quagga</i>)	Open	Grazer	1	1	0	1	Contract
Warthog (<i>Phacochoerus aethiopicus</i>)	Open	Grazer	0	1	0	1	Stable
Bushpig (<i>Potamochoerus larvatus</i>)	Closed	Omnivore	0	1	0	1	Stable
Eland (<i>Taurotragus oryx</i>)	Intermediate	Mixed	1	1	1	1	Stable
Bushbuck (<i>Tragelaphus scriptus</i>)	Closed	Browser	0	1	0	1	Stable
Kudu (<i>Tragelaphus strepsiceros</i>)	Intermediate	Mixed	0	1	0	1	Stable
Roan antelope (<i>Hippotragus equinus</i>)	Intermediate	Grazer	0	1	0	1*	Stable
Blue antelope (<i>Hippotragus leucophaeus</i>)†	Open	Grazer	1	1	1*	1	Stable
Southern reedbuck (<i>Redunca arundinum</i>)	Intermediate	Grazer	0	1	0	1*	Stable
Mountain reedbuck (<i>Redunca fulvorufula</i>)	Intermediate	Grazer	0	1	0	1	Stable
Hartebeest (<i>Alcelaphus buselaphus</i>)	Open	Grazer	1	1	1	1	Stable
Black wildebeest (<i>Connochaetes gnou</i>)	Open	Grazer	0	1	0	0	Extirpated
Bontebok (<i>Damaliscus dorcas</i>)	Open	Grazer	0	1	0	1	Stable
Giant wildebeest (<i>Megalotragus priscus</i>)†	Open	Grazer	0	1	0	0	Extinct
Blue duiker (<i>Philantomba monticola</i>)	Closed	Browser	0	0	0	1	Expand
Unnamed caprine†	Open	Grazer	0	1	0	1*	Stable
Common duiker (<i>Sylvicapra grimmia</i>)	Intermediate	Browser	1	0	1	1	Expand
Grey rhebok (<i>Pelea capreolus</i>)	Intermediate	Mixed	0	1	0	1	Stable
Southern springbok (<i>Antidorcas australis</i>)†	Open	Mixed	0	1	0	0	Extinct
Klipspringer (<i>Oreotragus oreotragus</i>)	Intermediate	Browser	1	1	0	1	Contract
Oribi (<i>Ourebia ourebi</i>)	Intermediate	Grazer	0	1	0	1	Stable
Steenbok (<i>Raphicerus campestris</i>)	Intermediate	Browser	1	1	1	1	Stable
Cape grysbok (<i>Raphicerus melanotis</i>)	Intermediate	Browser	1	1	1	1	Stable
African buffalo (<i>Syncerus caffer</i>)	Intermediate	Grazer	1	1	1*	1	Stable
Long-horn buffalo (<i>Syncerus antiquus</i>)†	Open	Grazer	0	1	0	0	Extinct

† Extinct.

* Historically absent (since 1600 A.D.).

** Persists only into the earliest Holocene (9600 ± 90 ¹⁴C yr B.P.).

cate a typical hunter-gatherer foraging radius of 8–12 km from a residential site (e.g., Lee 1972). We assume that the ungulate species identified in these assemblages represent animals that lived within a similar distance of the archeological sites (Table 1) and thus provide a reliable record of the local herbivore communities and how they changed through time. The fact that previously documented changes in large mammal community composition at CFR archeological sites are consistent with independent evidence for vegetation change (e.g., Avery 1982) supports this as a reasonable assumption.

All species documented in the sites listed in Table 1 are classified according to their dietary and habitat preferences (Table 2). Dietary preferences follow Rector and Verrelli (2010) and are based on behavioral observations, analysis of stomach contents, and isotopic data. We follow Plummer and Bishop (1994) in assigning species to three broadly defined

habitat categories: open (grasslands), intermediate (bushland, shrubland, woodland, ecotones), and closed (continuous tree cover, including forest). Extinct species include the long-horn buffalo (*Syncerus antiquus*), southern springbok (*Antidorcas australis*), giant wildebeest (*Megalotragus priscus*), blue antelope (*Hippotragus leucophaeus*), an unnamed caprine antelope, and Cape zebra (*Equus capensis*). Taxonomic analogy, morphology, and palaeoenvironmental associations suggest that these taxa inhabited open habitats (Klein 1980, 1983, 1994; Faith 2012b) and stable carbon isotopes indicate that the long-horn buffalo, giant wildebeest, and Cape zebra were grazers (Lee-Thorp and Beaumont 1995; Codron et al. 2008). Both the blue antelope and southern springbok are dentally similar to their living congeners (Klein 1974, 1980), and they are assigned to the grazer and mixed feeder category, respectively. The extreme

TABLE 3. Extant and extinct bovids, equids, and suids known from the CFR. See Table 2 for common names.

Family	Tribe	Taxon	Extant	Extinct			
				Middle Pleistocene	Late Pleistocene	Holocene	
Bovidae	Tragelaphini	<i>Taurotragus oryx</i>	1	-	-	-	
		<i>Tragelaphus strepsiceros</i>	1	-	-	-	
		<i>Tragelaphus scriptus</i>	1	-	-	-	
	Hippotragini	<i>Oryx gazella</i>	1	-	-	-	
		<i>Hippotragus equinus</i>	1	-	-	-	
		<i>Hippotragus gigas</i>	-	1	-	-	
	Reduncini	<i>Hippotragus leucophaeus</i>	-	-	-	1*	
		<i>Redunca arundinum</i>	1	-	-	-	
	Alcelaphini	<i>Redunca fulvorufula</i>	1	-	-	-	
		<i>Alcelaphus buselaphus</i>	1	-	-	-	
	Caprini	<i>Rabaticeras arambourgi</i>	-	1	-	-	
		<i>Damaliscus aff. lunatus</i>	-	1	-	-	
		<i>Damaliscus dorcas</i>	1	-	-	-	
		<i>Damaliscus niro</i>	-	1	-	-	
		<i>Damaliscus sp. nov.</i>	-	1	-	-	
		<i>Parmularius sp. nov.</i>	-	1	-	-	
		<i>Connochaetes gnou</i>	1	-	-	-	
		<i>Megalotragus priscus</i>	-	-	1	-	
		Unnamed caprine	-	-	-	1	
		Cephalophini	<i>Sylvicapra grimmia</i>	1	-	-	-
			<i>Philantomba monticola</i>	1	-	-	-
	Peleini	<i>Pelea capreolus</i>	1	-	-	-	
	Antilopini	<i>Gazella sp.</i>	-	1	-	-	
		<i>Antidorcas recki</i>	-	1	-	-	
		<i>Antidorcas australis</i>	-	-	1	-	
		<i>Antidorcas marsupialis</i>	1	-	-	-	
		<i>Oreotragus oreotragus</i>	1	-	-	-	
	Neotragini	<i>Raphicerus melanotis</i>	1	-	-	-	
		<i>Raphicerus campestris</i>	1	-	-	-	
		<i>Ourebia ourebi</i>	1	-	-	-	
		<i>Syncerus antiquus</i>	-	-	1	-	
		<i>Syncerus caffer</i>	1	-	-	-	
	Equidae	<i>Equus capensis</i>	-	-	1	-	
<i>Equus zebra</i>		1	-	-	-		
<i>Equus quagga</i>		1	-	-	-		
<i>Kolpochoerus paiceae</i>		-	1	-	-		
Suidae	<i>Metridiochoerus andrewsi</i>	-	1	-	-		
	<i>Phacochoerus aethiopicus</i>	1	-	-	-		
	<i>Potamochoerus larvatus</i>	1	-	-	-		

* Extinction in historic times.

hypsodonty of the unnamed caprine suggests it was a grazer (Brink 1999).

To examine extinction and speciation trends in the long term (Prediction 3), we compiled presence-absence data for bovids, equids, and suids reported from CFR fossil assemblages spanning the last 1 million years (Table 3) (Klein 1983; Brink 1999; Cruz-Urbe et al. 2003; Klein et al. 2007; Rector and Reed 2010; Faith 2012a,b). The fossil site of Elandsfontein, located on the WCP and dated to between 1 Ma and 600 Ka on the basis of faunal correlations (Klein et al. 2007), represents the oldest assemblage considered here.

Turnover in the Cape Floristic Region

The temporal and geographic distributions of ungulate species are reported in Table 2 and illustrated in Figure 4. We recognize four groupings of species, based on their distributional shifts across the Pleistocene–Holocene transition: (1) those with an expanded distribution, (2) those with a contracted distribution, (3) those that went extinct or were extirpated from the CFR, and (4) those whose distributions remained stable. We use these data as the basis for evaluating Predictions 1 and 2.

Prediction 1.—The loss of grassland habitats and the isolation of the SCP and WCP at the onset

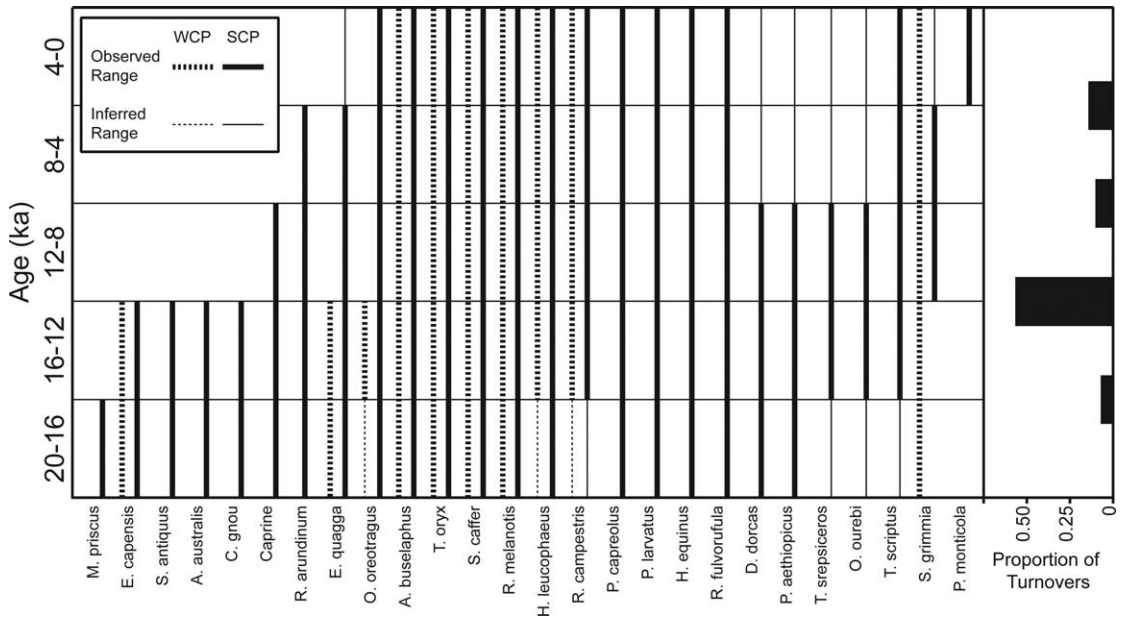


FIGURE 4. Temporal ranges of ungulate species from the WCP and SCP of the CFR across 4000-year time bins. The most pronounced phase of turnover, involving 7/26 (27%) of the species, occurs across the Pleistocene–Holocene transition. This could be considered a turnover pulse relative to the adjacent time intervals but is much less than levels of turnover proposed for African Plio–Pleistocene bovids on a million-year time scale (Vrba 1995).

of the Holocene should lead to extinction, extirpation, and range contraction primarily in species that are grazers or prefer open grassland habitats. The transition from the Pleistocene to the Holocene is associated with the extinction of four open-habitat species, including long-horn buffalo, Cape zebra, giant wildebeest, and southern springbok, as well as extirpation of black wildebeest (*Connochaetes gnou*). Two species, plains zebra (*Equus quagga*) and klipspringer (*Oreotragus oreotragus*), which are present on both the SCP and WCP during the Pleistocene, are found only on the SCP during the Holocene. Consistent with Prediction 1, extinctions, extirpations, and range contractions across the Pleistocene–Holocene transition were biased toward open-habitat species, with 6 of 11 of these species undergoing range contraction or extinction, compared to only 1 of 15 species that prefer intermediate or closed habitats (Fisher's exact test: $p = 0.021$). Diet alone, however, does not explain the overall pattern of species declines across the Pleistocene–Holocene transition. Range contractions or extinctions are observed in 5 of 15 grazers compared to 2 of 11 species

representing other dietary classes, a difference that is not statistically significant (Fisher's exact test: $p = 0.658$).

There are five species with Holocene fossil distributions broader than those observed historically: blue antelope, roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), southern reedbuck (*Redunca arundinum*), and the extinct caprine antelope. Buffalo and blue antelope, although present on the WCP and SCP in Holocene fossil assemblages, were absent from the WCP in historic times (Skead 2011). The blue antelope ultimately went extinct ca. 1800 A.D., evidently the result of non-viable population size in its limited geographic range on the SCP (Kerley et al. 2009). The southern reedbuck is documented in the Pleistocene and Holocene fossil record along the SCP. However, Boshoff and colleagues (in Skead 2011) concluded that it never occurred on the coastal lowlands of the CFR in historic times. A possible historic account of roan antelope, which is found in Holocene fossil assemblages along the SCP (Klein 1974; Faith 2012a), is ambiguous (Skead 2011). If roan antelope were indeed present on

the SCP in historic times, they were extirpated around the same time that blue antelope went extinct and likely for the same reasons (Faith 2012a). The extinct caprine makes its last appearance during the early Holocene at Boomplaas Cave, between 6400 ± 75 ^{14}C yr B.P. and 9100 ± 135 ^{14}C yr B.P. (Faith 2012b). The biogeographic histories of these bovids suggest that geographic isolation and limited availability of grassy forage since the Pleistocene–Holocene transition contributed to a gradual decline of grazers well into the Holocene. If we add these species to the list of taxa that experienced range contraction or extinction since the Pleistocene, then diet does become a significant correlate of change, with grazers disproportionately represented (10 of 15 grazers involved in range contraction or extinction compared to 2 of 11 species from other dietary classes; Fisher's exact test: $p = 0.021$).

Prediction 2.— *Rising sea levels and advancing shrubland at the onset of the Holocene will allow browsing species that prefer closed or shrubby habitats to shift distribution into the vicinity of neo-coastal sites along the SCP.* Two species show an apparent range expansion across the Pleistocene–Holocene transition: blue duiker (*Philantomba monticola*) and common duiker (*Sylvicapra grimmia*). Blue duiker, a small browser with a preference for closed habitats, is present only in the Holocene deposits at Nelson Bay Cave on the SCP (Klein 1983). It evidently expanded into the vicinity of the neo-coastal SCP in conjunction with the advancing fynbos. Common duiker, a small browser with a preference for shrubby vegetation, is present on the WCP during the Pleistocene and on both the WCP and SCP in the Holocene. This gives the impression of a range expansion from the WCP to the SCP across the Pleistocene–Holocene transition. However, it is possible that these species occurred near the paleo-coastline of the SCP during the LGM and Lateglacial, in which case the fossil evidence represents only an apparent range expansion. In agreement with Prediction 2, range expansions (or apparent range expansions) across the Pleistocene–Holocene transition were biased in favor of browsers, with 2 of 6 browsing species

exhibiting a range expansion versus 0 of 20 species from other dietary classes (Fisher's exact test: $p = 0.044$). We are unable to find any statistically significant signal relating to the specific habitat preferences of this subset of two browsing taxa, although both prefer closed or intermediate habitats.

Prediction 3.— *Lineages adapted to open grassland habitats will be characterized by elevated incidences of extinction and speciation over the long term.* We predict that the repeated expansion and contraction of grassland habitats across multiple glacial-interglacial cycles, together with the isolation of grassland species on the SCP during marine transgressions, should promote extinction and speciation in lineages adapted to open habitats. There are 39 bovid, equid, and suid taxa documented in the CFR over the last 1 million to 600,000 years, of which 16 are extinct (Table 3). In agreement with Prediction 3, extinction is clearly biased toward open-habitat lineages. For example, the bovid tribes Alcelaphini (wildebeest and allies) and Antilopini (gazelles and springboks), both of which are characterized by species with hypsodont dentitions and cursorial limbs, are considered archetypal open-habitat lineages (Greenacre and Vrba 1984; Bobe and Behrensmeier 2004; Bobe 2006). These antelopes represent only 17% (4/23) of extant species, yet they account for 56% of extinctions (9/16). The bias toward extinctions among alcelaphines and antilopines is significant (Fisher's exact test: $p = 0.017$). Morphology and stable isotope data indicate that at least five of the remaining extinct species were also grazers, with a preference for open habitats including *Syncerus antiquus*, *Hippotragus leucophaeus*, the unnamed caprine, *Equus capensis*, and *Metridiochoerus andrewsi* (Klein 1974, 1980, 1994; Marean 1992; Brink 1999; Harris and Cerling 2002).

Although the evidence for extinction is abundant, with the loss of 23% (6/26) of ungulate species since the LGM (Fig. 4) and 41% (16/39) of ungulate species over the last 1 million to 600,000 years, the CFR record provides only one example for the origination of a new taxon, and only at the subspecies level. *Damaliscus dorcas* is an open-habitat

grazer that includes two allopatric subspecies: bontebok (*Damaliscus dorcas dorcas*), which is endemic to the CFR, and blesbok (*D. dorcas phillipsi*), which is found in the South African interior (Skinner and Chimimba 2005). Vrba (1997) places the first appearance of *D. dorcas* in the early Pleistocene at Swartkrans Member 2, now dated to ca. 1.4 Ma (Sutton et al. 2009). The earliest record of *D. dorcas* in the CFR dates to the end of the middle Pleistocene (ca. 151 Ka) at Pinnacle Point (Rector and Reed 2010), coinciding with a marine regression during Marine Isotope Stage (MIS) 6. The evidence suggests that *D. dorcas* first emerged in the South African interior and later migrated into the CFR during a middle Pleistocene marine regression (MIS 6 or earlier), when reduced sea levels and expanded grasslands facilitated interchange between the CFR and the interior. Subsequent isolation during interglacial highstands likely allowed allopatric divergence at the subspecies level.

An Example of Intraspecific Evolution.—At least one of the CFR ungulates responded to changes across the Pleistocene–Holocene transition with a combination of phenotypic and behavioral evolution (i.e., intraspecific evolution). The Cape grysbok is a small-bodied (8–12 kg) bovid that is endemic to the CFR, where it is sympatric with its geographically widespread relative, the steenbok (*Raphicerus campestris*) (Klein 1976; Skinner and Chimimba 2005). Consistent with the fynbos-dominated vegetation throughout its range, the modern Cape grysbok selectively browses various dicot species (Skinner and Chimimba 2005).

Unlike some browsers, the Cape grysbok range remains constant across the Pleistocene–Holocene transition (Table 2) and it is found in association with grazer-dominated mammal communities during the Pleistocene and browser-dominated mammal communities during the Holocene (Klein 1976, 1983; Faith 2011a). Its persistence can be attributed in part to dietary flexibility. Dental mesowear analysis shows that Cape grysbok consumed greater amounts of grass when open grasslands were more widespread during the Pleistocene (Faith 2011a). Fossil samples from the Nelson Bay Cave stratigraphic sequence show a steady increase in the proportion of

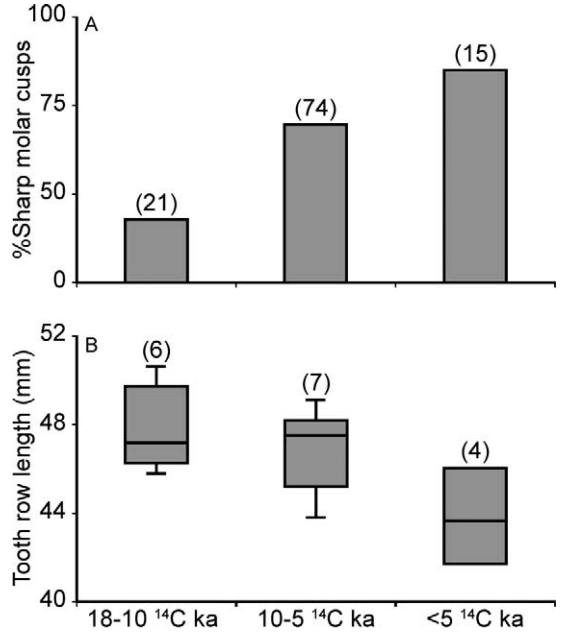


FIGURE 5. Increasing frequencies of sharp maxillary molar cusps (A) and reductions in maxillary tooth row length (B) in the Cape grysbok (*Raphicerus melanotis*) assemblage from Nelson Bay Cave. Mesowear data from Faith (2011a). Sample sizes in parentheses.

dicots in its diet over the past 18,000 ^{14}C years (Faith 2011a). This is illustrated in Figure 5, which shows increasing proportions of sharp maxillary molar cusps across late Pleistocene ($\sim 18,500$ – $10,000$ ^{14}C yr B.P.), early Holocene ($\sim 10,000$ – $5,000$ ^{14}C yr B.P.), and late Holocene (5000 ^{14}C yr B.P. to Recent) samples ($\chi^2_{\text{trend}} = 12.103$, $p = 0.001$). The increase in sharp molar cusps reflects elevated consumption of dicots, paralleling the increased abundance of browsing species (Faith 2011a). The dietary shift corresponds to a significant reduction in mean maxillary tooth-row length at Nelson Bay Cave (Fig. 5) ($F = 5.066$, $p = 0.022$). This indicates a less robust masticatory apparatus, consistent with diminished grass consumption.

Discussion

The combination of changes in sea level, vegetation, and biogeographic barriers across the Pleistocene–Holocene transition in the CFR (Fig. 3) provides a unique opportunity to test the mechanics of faunal turnover with respect to the specific predictions of Vrba's

TPH. The CFR fossil record clearly shows how changes in the physical environment, transmitted to ungulates through vegetation and habitat area shifts, can initiate migration and extinction (Fig. 4). Loss of grassland habitat and vicariance (i.e., separation of the SCP and WCP) at the onset of the Holocene contributed to elevated extinctions and range contractions (migration) in species that are grazers or favor open habitats (Fig. 3), with the effects of climate change extending well into the Holocene. The corresponding migration of fynbos toward the neo-coastline resulted in a concurrent range shift (migration) within two small browsing species (Fig. 3). These patterns are supported over the long term, with the past 600,000 to 1 million years associated with 16 (41%) documented extinctions primarily in open-habitat lineages (Table 3). It is possible that the pattern of extinction-dominated turnover observed since the LGM also occurred during each of the previous glacial cycles, leading to a cumulative decline in CFR ungulate diversity. If so, this suggests that any periodic or longer-term moderation of Pleistocene biodiversity loss would have depended on the rate of new species migrating into the CFR from other parts of southern Africa.

The many examples of extinction far outweigh the minimal evidence for speciation. The subspecific divergence of the bontebok from blesbok provides the only evidence for climatically driven allopatry leading to the emergence of a novel taxon. This can be attributed to migration of *D. dorcas* into the CFR during MIS6, or perhaps an earlier marine regression, followed by geographic isolation in the CFR during the subsequent marine transgression, which promoted allopatric evolution of the two subspecies. This is roughly consistent with genetic evidence, which suggests the subspecies diverged ~250,000 years ago (Essop et al. 1991).

Vrba (1985) proposed that evolutionary change will only occur when a species' environmental tolerance threshold is exceeded. The CFR record shows that such thresholds were surpassed for many ungulate species, both during the Pleistocene–Holocene transition and probably during previous de-

glaciations, but with the dominant evolutionary outcome being extinction. If the requirements for turnover are met—as suggested by the instances of migration and extinction—then why is there no evidence for speciation across the Pleistocene–Holocene transition or earlier? For example, Vrba (1995) documents 48 first appearance dates for African bovids from 3–2 Ma, most of which are broadly associated with the proposed 2.8–2.5 Ma turnover pulse. One possibility for the lack of speciation observed here is that climate change is an effective driver of migration and extinction, but that other mechanisms (e.g., biotic interactions) are necessary for speciation over these time scales. A lack of evidence for climatically mediated speciation elsewhere has prompted others to favor alternative drivers (Alroy 1998; Alroy et al. 2000; Prothero 1999). The hypothesis that climate does not drive speciation remains viable for the CFR record, but the absence of speciation precludes a detailed exploration of the alternatives. One alternative is that climate change drives all aspects of faunal turnover, but that the evolutionary outcome is contingent on the nature (e.g., unidirectional vs. cyclical) and rate of change relative to the evolutionary response time of the species under consideration. The Quaternary is characterized by rapid high-amplitude climatic shifts during glacial-interglacial cycles, with the amplitude of the cycles and potential stress on organisms increasing toward the present (Jouzel et al. 2007). This may favor extinction over speciation by limiting the amount of time a species has to adapt to change or by surpassing the habitat threshold of a species to such a point that it is unable to adapt. Conversely, the evolutionary scales may be tipped in favor of speciation when climatic changes are gradual, of lower magnitude, or unidirectional rather than cyclical.

The possibility that Quaternary climate cycles are not conducive to promoting speciation in ungulates is supported by other African records. Bobe (2006) demonstrates that the onset of the Pleistocene signals a steady decline in the generic richness of large herbivores in broad regions of Africa. Faith et al. (2012) similarly observed elevated inci-

dences of ungulate extinction relative to speciation over the last 780,000 years in East Africa, a pattern they attribute to the loss of specialist grazers during high-amplitude climate shifts. This broader continental perspective is consistent with the decline of diversity in the CFR and suggests that elevated extinction rates in ungulates are characteristic of the African Quaternary.

It should be noted that although Africa has long been regarded as the exception to end-Pleistocene megafaunal extinction seen on other continents (Koch and Barnosky 2006), the CFR fossil record documents five prehistoric extinctions during the late Pleistocene to Holocene (Table 3). Whether or not any of these extinctions involved human hunting is unclear, with some authors invoking a combination of climate change and anthropogenic contributions (Klein 1980) and others arguing that climate change alone is an adequate explanation (Brink 1999; Faith 2011b). Regardless of the potential role humans may have played in the late Pleistocene to Holocene extinctions, it is clear that grassland species suffered numerous extinctions in the CFR long before the appearance of modern humans (Table 3).

The evidence for dietary and morphological evolution within Cape grysbok requires some modification to the underlying mechanics of Vrba's TPH, which predicts evolutionary change only when a species' range is divided (vicariance) and its environmental tolerance threshold exceeded. The transition from the Pleistocene to the Holocene witnessed no change in Cape grysbok distribution (Table 2), and it is a common element in glacial and interglacial assemblages (Klein 1976, 1983; Schweitzer and Wilson 1982; Rector and Reed 2010; Faith 2012b). Rising sea levels and the geographic separation of the SCP from the WCP are unlikely to have presented a substantial barrier to migration, as this species is capable of inhabiting the rugged terrain along the Cape Syntaxis (Boshoff and Kerley 2001). Although Vrba (1992) proposed that most species will respond to climate change by shifting their distributions while maintaining habitat fidelity, Cape grysbok responded to climate change with in situ evolution (pheno-

typic change), in the *absence* of vicariance or migration. Rapid dietary responses to vegetation change have also been documented in modern populations of Cape grysbok (Kerley et al. 2010). This raises the possibility of an alternative evolutionary strategy: a species with the genetic or phenotypic plasticity to change its behavior (diet) and morphology (dental apparatus) over geologically short time frames does not have to respond to habitat change by migrating, but can instead adapt with evolutionary change. Such intra-specific evolution may be easier in some lineages than in others (Vrba 1999). The ability to evolve while maintaining a relatively stable range has also been documented in the classic study of Darwin's finches (Grant and Grant 2008), and suggested by recent research on dietary shifts in mammal lineages during Miocene climate change in Pakistan (Badgley et al. 2008). This is also consistent with predictions of the variability selection hypothesis of Potts (1998), in which species with the capacity to change rapidly under shifting environmental conditions preferentially survive relative to specialized species lacking this capacity.

By using Quaternary ungulate records in South Africa to test the mechanics of the TPH, our analyses show how climate change translated through environmental shifts can play an important role in mammalian evolution by driving migration and extinction, although they leave unresolved the precise role of climate change in driving speciation. Nevertheless, the CFR record shows that faunal turnover can operate over relatively short time scales, on the order of Milankovitch-scale climate oscillations (i.e., 10^4 – 10^5 years) (Fig. 4). This poses an interesting inconsistency between average species durations and the effect of cyclic environmental change. With the geologic life span of fossil mammal species averaging ~ 2.5 Myr (Alroy 2000), most species must endure numerous Milankovitch-scale climate cycles. This has led some to suggest that Milankovitch cycles cannot be responsible for mammal speciation and extinction (Dynesius and Jansson 2000; Barnosky 2001). Our observations suggest that this viewpoint requires some modification, at least

with respect to the extinction component. We propose that climate change associated with Milankovitch oscillations should contribute to a steady and relatively low degree of turnover through time. This could explain the “background” turnover often observed in long fossil sequences (Behrensmeyer et al. 1997; Barry et al. 2002; van Dam et al. 2006) and the numerous middle Pleistocene extinctions in the CFR (Table 3). Why some species undergo evolutionary change across a climate cycle and others do not could depend on the nature and rate of climate change or the distributions of populations relative to topography or vegetation, and may be purely stochastic on a large scale. Major turnover pulses, in contrast, would require alternative climatic drivers, perhaps including changes associated with long-period (1.0 and 2.4 Myr periods) astronomical forcing (van Dam et al. 2006) or shifts in community structure associated with novel predators, disease, or loss and gain of key-stone species.

Conclusion

Elisabeth Vrba's Turnover Pulse Hypothesis has inspired a sustained debate over the role of climate change in mammalian evolution. Although this hypothesis continues to be important in macroevolutionary thinking, limited temporal resolution in fossil and paleoclimatic records has made it difficult to observe the TPH in operation (Vrba 1992: p. 12) and to predict how different lineages will respond to climate change.

Previous investigations of turnover have generated mixed support for the TPH (Behrensmeyer et al. 1997; Prothero 1999; Alroy et al. 2000; Barry et al. 2002; Bobe et al. 2002; Raia et al. 2005; van Dam et al. 2006), prompting some to argue that climate change plays little role in mammalian evolution (Prothero 1999, 2004; Alroy et al. 2000). However, problems of temporal and spatial scale are known to plague analyses of turnover relative to climate change (Barnosky 2001; Raia et al. 2005), and this could explain why some studies fail to observe climatic effects on turnover (e.g., Alroy 1998; Prothero 1999; Alroy et al. 2000). Our analyses represent a relatively fine-grained test of the TPH, on a temporal scale

of 10^3 – 10^5 years and a geographic scale of 10^4 km². This perspective allows us to explore the underlying mechanics of the TPH (i.e., Does it work as proposed by Vrba?), and examine *how* climate change drives ungulate turnover via vicariance and habitat change, and in rare cases, in situ evolution without vicariance. Our results provide conclusive evidence that climate change drives faunal turnover in the form of migration and extinction, but the role of climate as a driver of speciation remains uncertain. It is possible that climate plays little role in driving speciation, or that the evolutionary outcome of a turnover event may depend on the *nature* (e.g., unidirectional vs. cyclical) and *rate* of climate change. Although the speciation component of the TPH is unclear, we conclude that climate change can be an important driver of significant faunal turnover in ungulates, even over geologically short time intervals.

A remaining challenge in exploring the relationship between climate change and faunal communities is to understand why some climatic events are associated with major turnover and others are not. What explains the observed variability in turnover rates through time and space? Answers to this question will help to further clarify the role of climate change in evolution, especially with respect to potential alternative evolutionary processes (e.g., biotic interactions, biogeographic barriers and connections, random ecological, and genetic drift), or thresholds involving the additive effects of multiple processes, and may also provide a better understanding of the role of climate versus human impact in the contentious problem of late Quaternary mammal extinctions across the continents.

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