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## Continental gateways and the dynamics of mammalian faunas

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## ABSTRACT

Continental gateways occur where mountainous topography interacts with changing climate and sea level to open or close dispersal corridors. The interaction of permeable or impermeable montane barriers with changing or stable climate yields four biogeographic states, each associated with changes in diversification rates and ecological structure of faunas. For example, permeable montane barriers and climatic stability result in low rates of immigration and extinction, elevated endemic speciation, and stable ecological structure. Three examples from the mammalian fossil record test these scenarios. (1) In Miocene faunas of Pakistan, immigration rates peaked and faunal proportions changed during an interval of cooling and open corridors. (2) In Miocene faunas of Spain, elevated extinction and origination rates and changing trophic structure occurred during regional aridification with open corridors. (3) In Quaternary faunas of South Africa, ungulates experienced range reductions and elevated extinction during the transition from glacial to interglacial climates as corridors closed.

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## R É S U M É

Les portes continentales se forment là où une topographie montagneuse interfère avec les variations climatiques qui déterminent le niveau marin, ainsi que l'ouverture et la fermeture des seuils qu'elles représentent. La perméabilité de ces barrières montagneuses, sous l'emprise d'un climat changeant ou stable, connaît quatre états biostratigraphiques, chacun d'eux associé à des variations du taux de diversification et de la structure écologique de la faune. Une barrière montagneuse perméable, par exemple sous un climat stable, résulte en des taux faibles d'immigration et de disparition, une spéciation endémique élevée et une structure écologique stable. Trois exemples provenant des mammifères testent ces scénarios. (1) Dans les faunes du Miocène du Pakistan, les taux d'immigration ont culminé et les rapports des différentes classes de faune ont changé durant un intervalle de refroidissement et d'ouverture des seuils. (2) Les faunes miocènes d'Espagne sont caractérisées par

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des taux de disparition et d'apparition élevés, avec des niveaux trophiques changeant en fonction d'une aridification associée à des seuils ouverts. (3) Dans les faunes du Quaternaire d'Afrique du Sud, l'aire de répartition des ongulés a été réduite et le taux de disparition élevé, à la transition des climats glaciaire à interglaciaire lors de la fermeture des seuils.

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## 1. Introduction

Geographically isolated populations are more likely than connected populations to speciate, change adaptively, or become extinct (Badgley, 2010; Brown, 2001; Cracraft, 1985; Vrba, 1992). Isolated populations are usually exposed to environments that differ in physical and biotic qualities from those prevailing over the rest of the species' geographic range and thereby experience a different selective regime from those of conspecifics. Such populations may accumulate enough genetic changes relative to conspecifics over the rest of the geographic range to acquire unique characters and reproductive isolation (Mayr, 1963). Isolated populations are also vulnerable to stochastic fluctuations in population size, sex ratios, and inbreeding effects that may elevate the risk of extinction (Gaston, 2003). Geographic isolation has both spatial and temporal components. At one extreme are geographic ranges with high spatial continuity that maintain gene flow over years to millennia. At the other extreme are spatially fragmented ranges such that dispersal among fragments is improbable over tens to thousands of generations. Between these extremes are various configurations of metapopulations (Hanski, 1999; Lomolino et al., 2010).

Factors that determine whether populations are continuously distributed or in isolated fragments over their geographic range include the environmental tolerances of the species, dispersal ability, the topographic complexity of the landscape, and the temporal variability of seasons and climate (Gaston, 2009; Janzen, 1967; Lomolino et al., 2010). In continental environments, populations become chronically isolated when environmental gradients are steep and discontinuous for thousands of years or more. For example, mountain ranges, deep canyons, and extensive water bodies are effective barriers to dispersal for terrestrial populations.

From a community perspective, chronic geographic isolation occurs when geographic barriers are impermeable over extended periods of time. No immigration or emigration is then possible, and changes in community composition occur via endemic speciation or local extinction (Ricklefs and Schluter, 1993). Adaptive change within the isolated region may result in allopatric speciation with respect to conspecifics outside the isolated region, without adding new lineages to the isolated community. The fossil record presents many examples of ecosystems that have experienced different degrees of spatial and temporal isolation (Hoorn et al., 2010; Stigall, 2015; Vrba, 1985).

Here we present and evaluate a conceptual framework of contrasting conditions of geographic isolation and environmental change and their implications for evolutionary processes and community dynamics over geologic time. Our conceptual framework involves the interactions of

regional tectonics, sea level, and climate in determining whether geographic barriers are permeable or impermeable and whether species' geographic ranges are likely to shift in location or remain stable. Different combinations of these geohistorical factors generate four different biogeographic states, each with unique predictions for evolutionary and ecological processes. In this paper, we introduce the conceptual framework and develop its implications for evolutionary processes and community dynamics of continental mammalian faunas at the scale of the sedimentary basin. We then present three Neogene records of mammalian faunal change with different configurations of tectonic barriers and climatic change and evaluate these records in terms of the predictions of the conceptual framework. We conclude by evaluating how well the conceptual framework predicts the faunal changes in each record and consider the relevance of this framework for other geohistorical sequences.

## 2. Conceptual framework of four biogeographic states

The interactions of tectonic history, sea level, and climate determine whether a particular region is relatively open or closed to immigrants for a focal group of organisms (Behrensmeyer et al., 1992; Lomolino et al., 2010). Landscape barriers to biotic interchange can range from fully permeable to impermeable, determining rates of immigration, emigration, and the spatial continuity of geographic ranges. Climate may be changing or stable (fluctuating around a stable mean), determining both annual and seasonal temperature and precipitation, and thereby the regional vegetation within the focal region (Bradley, 2015; Woodward, 1987). Four combinations of permeable versus impermeable boundaries and changing versus stable climate represent alternative biogeographic states that correspond to different intervals of regional geological history, with different implications for ecological and evolutionary changes in mammalian faunas (Table 1). While this scheme of four biogeographic states simplifies the interactions of geological processes, it highlights fundamental differences in physical and biotic drivers of faunal change.

Mountain ranges may act as barriers to dispersal of mammals as a consequence of rugged topography, absence of vegetation and shelter, or inhospitable life zones at high elevations (Coblentz and Ritters, 2004). In terms of locomotion, breeding cycles, and food habits, the life habits of most mammals are adapted for ecosystems at low to middle elevations below the treeline. Species with special adaptations to high elevations – in terms of thermal tolerance, ability to hibernate or enter torpor, ability to walk on steep, rocky slopes – tend to be limited to these

**Table 1**

Four biogeographic states determined by the interaction of geologically controlled barriers to immigration and presence or absence of regional climatic change. Each state results in a unique combination of evolutionary and ecological changes in mammalian faunas during the time interval in which the external conditions prevail. See text for references.

**Tableau 1**

Quatre états biogéographiques déterminés par l'interférence des barrières géologiquement contrôlées et la présence ou l'absence de variations climatiques régionales. Chaque état résulte en une combinaison unique de changements évolutifs et écologiques dans les faunes mammifères pour la période caractérisée par les conditions prévalentes. Voir texte pour les références.

	Permeable barriers	Impermeable barriers	Differentiation
Changing climate	<b>A: Open access during climatic change</b> 1 – High immigration rate 2 – Moderate speciation rate 3 – High extinction rate 4 – Change (↑ or ↓) in species richness 5 – Lineage replacement: rapid, adaptively different 6 – Change in ecological structure	<b>B: No access during climatic change</b> 1 – No immigration 2 – Moderate speciation rate 3 – Moderate to high extinction rate 4 – Decline in species richness 5 – Lineage replacement: rapid, adaptively mixed 6 – Change in ecological structure	A and B: 1, 5
Stable climate	<i>Faunal turnover by addition and loss</i> <b>C: Open access during climatic stability</b> 1 – Low immigration rate 2 – Low speciation rate 3 – Low extinction rate 4 – Small increase in species richness 5 – Lineage replacement: slow, adaptively mixed 6 – Stable ecological structure	<i>Faunal turnover by loss</i> <b>D: No access during climatic stability</b> 1 – No immigration 2 – Low speciation rate 3 – Low extinction rate 4 – Stable species richness 5 – Lineage replacement: slow, adaptively similar 6 – Stable ecological structure	C and D: 1, 4, 5
Differentiation	<i>Stable faunal composition, regional endemism</i> A and C: 1, 2, 3, 5, 6	<i>Stable faunal composition, strong regional endemism</i> B and D: 2, 3, 4, 5, 6	

elevations as well (e.g., mountain goats, pikas). For the majority of terrestrial mammals, mountain ranges act as barriers if they are high enough to support multiple life zones and are not breached by river valleys. These circumstances may persist for millions of years during orogeny. The size of a mountain range, particularly its length and relationship to other barriers, such as coastlines, determine whether or not the mountain range acts as a barrier. The Himalayas and the Andes today are high enough and long enough to act as barriers to most lowland mammals and have distinctive faunas on either side of the range. In contrast, the many mountain ranges of the Great Basin in western North America are high enough to support multiple life zones but are relatively short (200–400 km) and are surrounded by gently sloping alluvial fans and flat basins that serve as conduits for dispersal (Grayson, 2011). Mammalian faunas of the Great Basin are similar at lower elevations (Badgley et al., 2014).

Climate change and erosion can both affect the permeability of montane barriers. Both regional and global climates influence thermal lapse rates and thereby the relationship between elevation and temperature (Poulsen and Jeffery, 2011). Thermal lapse rates are lower during warm periods, resulting in smaller differences in temperature between low and high elevations. These circumstances could effectively reduce the number of bioclimatic zones on mountains during warm periods, thereby increasing the permeability to dispersing mammals. Changes in the direction or seasonal timing of air masses may alter orographic effects, which could also change the permeability of topographic barriers. Climate also affects erosional processes and rates (Molnar, 2004). The presence of glaciers and glacial-interglacial cycles has potent effects on erosion, on the height of mountain ranges, and on elevational shifts in life zones (Egholm et al., 2009; Herman et al., 2013).

Weathering and erosion may increase montane uplift from isostatic response of the lithosphere to removal of mass during valley incision (Molnar and England, 1990). After orogenic episodes have terminated, weathering and erosion diminish elevation and relief such that mountain ranges become quite permeable to dispersal.

The conceptual framework of Table 1 was developed for regions with tectonic barriers that potentially could be closed, partly open, or fully open. Examples of such barriers include straits separating or connecting water bodies, depending on plate motions or sea level (e.g., the Strait of Gibraltar) and geomorphically youthful mountain ranges that separate a peninsula from the continental interior (e.g., the Alps in relation to the Italian Peninsula). Changes in sea level, whether eustatic or isostatic, may enhance or diminish the effectiveness of topographic barriers. Climatic change causes geographic ranges of most species and biomes to shift and may facilitate the breaching of former barriers to dispersal or establish new barriers of climatically unsuitable habitat, especially along steep topographic gradients (Lomolino et al., 2010). These interacting factors may alter the size and continuity of habitats, steepen or reduce environmental gradients, and facilitate or impede immigration, extinction, and speciation (Badgley, 2010; Barnosky, 2001; Cracraft, 1985; Endler, 1977). In their analysis of foraminiferan and molluscan faunas from the late phases of the Paratethys Sea, Harzhauser and Piller (2007) proposed “the toggle switch of biogeography” for regions that have experienced alternating closed and open boundaries to immigration. They noted pulses of immigration and faunal enrichment when the Paratethys Sea was connected to the Mediterranean Sea or the North Atlantic Ocean, in contrast to intervals of endemic evolution and extinction when the Paratethys was isolated from these marine connections by complex collisional interactions between the

African and European plates. We note parallels in the terrestrial realm in the examples presented below.

Four hypothetical configurations of tectonic barriers, sea level, and regional climate correspond to four biogeographic states (Table 1). The evolutionary consequences of these states refer to mammal diversity and composition at the regional spatial scale and from  $10^4$  to  $10^5$  years in terms of temporal scale and resolution. At smaller spatial and temporal scales, local habitat variation, taphonomic effects, and short-term climatic variations could lead to high variability in faunal composition of individual localities or depositional environments. Such effects should be minimized when aggregating data over entire sedimentary basins or tectonic provinces. The four biogeographic states do not represent an idealized geomorphological sequence; a region could, in principle, pass back and forth among all four states in any order, depending on the particular circumstances of topography and climate.

In state A, barriers are permeable and climatic conditions are changing. Under these circumstances, geographic ranges should shift as species track their preferred habitats (Vrba, 1985). Shifting geographic ranges should bring immigrants into the focal region and lead some former residents to emigrate as they follow the relocation of their preferred habitats. Climatic change should increase environmental heterogeneity during the transient phase via fragmentation of habitats as well as the appearance of novel habitats (Williams et al., 2007). Both the increase in environmental heterogeneity as well as ecological interactions among immigrant and resident species should stimulate speciation (Hernández Fernández and Vrba, 2005; Hopkins, 2005; Vrba, 1992), since habitats, potential predators, and competitors are in flux. Such circumstances may drive some immigrant or resident species to extinction. Species richness within the focal region should increase or decrease significantly depending on whether immigration and endemic speciation exceed emigration and extinction or not. Changes in richness should be accompanied by changes in the ecological structure of mammalian faunas in response to climatically driven changes in vegetation (Andrews et al., 1979; Badgley et al., 2008) and to morphological evolution in dental traits linked to feeding adaptations (Barnosky, 2005; Eronen et al., 2010). This scenario corresponds to a classic turnover pulse (Vrba, 1985, 1992, 1995).

In state B, barriers are closed as climate is changing. No immigrants should enter the focal region, except by rare sweepstake events (Lomolino et al., 2010; Vrba, 1995). Shifting and fragmenting geographic ranges within the focal region, in combination with changes in vegetation, as climatic gradients change, should stimulate anagenetic changes and some endemic speciation (Barnosky and Kraatz, 2007; Davis et al., 2008; Simpson, 1964). As the climatic tolerances of some species are exceeded, some local extinctions should occur. Species richness should remain stable or decline, with changes in ecological structure tracking changes in vegetation.

State C involves permeable barriers while climatic conditions are stable. Immigration should be feasible as a consequence of expanding populations or changing resource use within lineages. However, resistance from

resident species should keep immigration rates low (Jablonski, 2008). Both endemic speciation and local extinction rates should be low (Moen and Morlon, 2014). Species richness may remain stable or increase slightly without significant change in ecological structure.

In state D, barriers are closed and climate is stable, resulting in low environmental heterogeneity at the regional scale. Immigrations should be rare (Vrba, 1995). Endemic speciation may occur in response to ecological specialization (Schluter, 2009). Biotic interactions may also promote anagenetic changes (Van Valen, 1973). Species richness and ecological structure should remain stable.

Although we present the conceptual framework in terms of binary modes of barriers and climatic conditions, we recognize that realistic intermediate states should be common. We can only estimate rather coarsely the actual status of ancient barriers and paleoclimates. In the three examples that follow, we analyze time intervals that correspond closely to one of the four states, based on geological and biogeographic evidence inside and outside the focal region, and compare the predicted patterns of diversification to observed faunal changes from the fossil record.

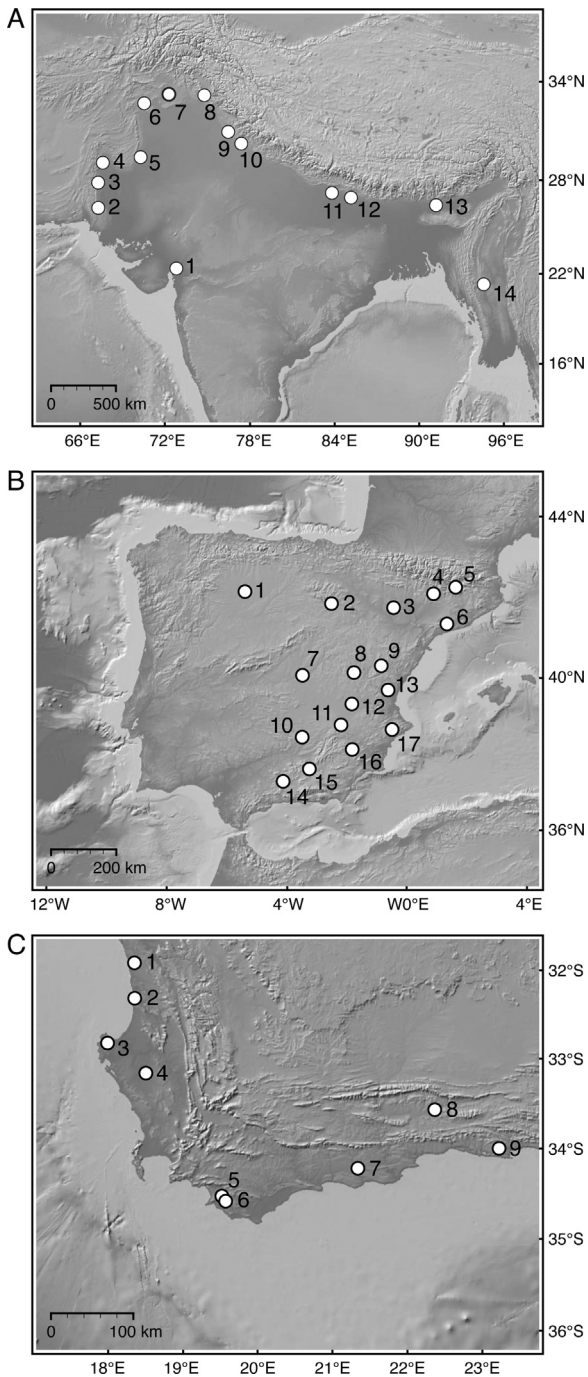
### 3. Three examples from Neogene records of mammals

Three case studies from the Neogene mammalian record exemplify geological settings in which strong barriers were alternately open or closed for extended periods of time. We evaluated the record of large mammals (> 1 kg) in order to compare results among the three examples (data for small mammals were not available for two cases). Data for the first example are published here for the first time; data for the other examples are from recently published studies. All of the faunal data come from terrestrial depositional sequences.

#### 3.1. The Miocene Siwalik record from Pakistan

Siwalik sediments and fossils are continental deposits derived from the southern margin of the Himalayas and associated mountain ranges bounding the contact between the Indian and Asian tectonic plates (Fig. 1A, Barry et al., 2002). Although outcrops of the Siwalik Group extend from western Pakistan to Myanmar, the most thorough studies of sediments, faunas, geochronology, and environmental history have focused on sequences in Pakistan, ranging from Oligocene through Quaternary in age (Barry et al., 2013; Flynn et al., 2013, 2016). Here we present faunal data from the extensive record of the Potwar Plateau in northern Pakistan. We originally developed the conceptual framework of Table 1 for analyzing Siwalik faunal change in relation to changing configurations of montane barriers and regional climate affecting the entire Siwalik faunal province, encompassing the area in Fig. 1A with Siwalik fossil sequences.

The Siwalik record of the Potwar Plateau occurs in fluvial deposits that accumulated in a foreland basin over much of the Neogene (Barry et al., 2002). Boundary faults between the Indian and Asian plates now underlie the Potwar Plateau, which has been uplifted and deformed



**Fig. 1.** Three regions where mountain ranges, sea level, and climate have interacted to create permeable or impermeable barriers to mammalian dispersal. Each region has a Neogene fossil record of mammals for evaluating the macroevolutionary consequences of barriers and climate change over geologic time. Circles indicate the location of major fossiliferous sequences, with bold circles being the source of data used for faunal analyses presented here. A. Indian subcontinent with extensive deposits of Siwalik sediments and faunas. Major sequences: 1 = Perim Island, 2 = Sehwan, Manchar Formation, 3 = Gaj, Manchar Formation, 4 = Bugti Hills, 5 = Zinda Pir Dome, 6 = Kohat, 7 = Potwar Plateau, 8 = Kashmir, 9 = Haritalyangar, 10 = Pinjor, 11 = Surai Khola, Nepal, 12 = Tinau Khola, Nepal, 13 = Garo Hills, Assam, 14 = Chiang Muan Basin, Thailand. B. Iberian peninsula with Pyrenees Mountains and Strait of Gibraltar

into a shallow syncline with thousands of meters of sediments exposed along modern river valleys. The Neogene deposits represent the channels and floodplains of major and minor tributaries of the ancient Indo-Gangetic fluvial system (Barry et al., 2002; Willis, 1993), and are continuous between 18.0 and 5.0 Ma in the sense that no major unconformities are present (Barry et al., 2013). Over 300 species in 50 families of mammals have been documented from this sequence, recording both notable endemic groups and notable absences. The large-mammal record is dominated by ungulates, proboscideans, and carnivorous mammals (Barry et al., 2002). The data analyzed here include all groups of large mammals except Carnivora, whose lineages are not yet taxonomically resolved.

Siwalik ecosystems were isolated from faunal exchange with areas to the east, west, and north over much of the Neogene. Evidence for this isolation comes from the tectonic history of the Himalayas and accessory ranges on the eastern and western margins of the Indian subcontinent (e.g., Lukens et al., 2012; Najman and Garzanti, 2000) and discontinuities in faunal composition with regions adjacent to the Indian subcontinent (e.g., Brunet et al., 1984). Changes in sea level could have opened or closed coastal corridors between the Indian subcontinent and areas to the east and west. Based on these lines of evidence and

restricting access, depending on sea level. Major sequences: 1 = Duero Basin, 2 = Calatayud-Daroca Basin, 3 = Ebro Basin, 4 = Seu d'Urgell Basin, 5 = Cerdanya Basin, 6 = Vallès-Penedès Basin, 7 = Tagus Basin, 8 = Teruel Basin, 9 = Sarrión-Mijares Basins, 10 = Calatrava Basin, 11 = Júcar Basin, 12 = Cabriel Basin, 13 = Valencia Basin, 14 = Granada Basin, 15 = Guadix-Baza Basin, 16 = Fortuna Basin, 17 = Alicante North Prebetic Basin. C. Cape Fold Belt, South Africa, with mountain ranges separating western and southern coastal plains from each other and from the continental interior. Major Late Quaternary fossil sites: 1 = Steenbokfontein, 2 = Elands Bay sites, 3 = Kasteelberg, 4 = Elandsfontein Main, 5 = Die Kelders Cave 1, 6 = Byneskranskop 1, 7 = Blombos Cave, 8 = Boomplaas Cave, 9 = Nelson Bay Cave.

**Fig. 1.** Trois régions où les chaînes de montagne, le niveau marin, et le climat ont interféré, formant ainsi des barrières perméables ou imperméables à la répartition des mammifères. Chaque région a un registre de fossiles de mammifères néogènes permettant l'évaluation macroévolutive de l'influence des barrières et du climat pour une certaine période géologique. Les cercles indiquent la position des séquences fossilifères majeures, les cercles en ligne grasse indiquent la source des données servant aux analyses présentées ici. A. Le sous-continent Indien, représenté par les faunes et les sédiments abondants de Siwaliks. Séquences majeures : 1 = île de Perim, 2 = Sehwan, formation de Manchar, 3 = Gaj, formation de Manchar, 4 = collines de Bugti, 5 = dôme de Zinda Pir, 6 = Kohat, 7 = plateau de Potwar, 8 = Cachemire, 9 = Haritalyangar, 10 = Pinjor, 11 = Surai Khola, Népal, 12 = Tinau Khola, Népal, 13 = collines de Garo, Assam, 14 = bassin du Chiang Muan, Thaïlande. B. Péninsule Ibérique avec la chaîne des Pyrénées et le détroit de Gibraltar permettant le passage en fonction du niveau marin. Séquences majeures : 1 = bassin du Douro, 2 = bassin de Calatayud-Daroca, 3 = bassin de l'Èbre, 4 = bassin de la Seu d'Urgell, 5 = bassin de Cerdagne, 6 = bassin de Vallès-Penedès, 7 = bassin du Tage, 8 = bassin de Teruel, 9 = bassins de Sarrión-Mijares, 10 = bassin de Calatrava, 11 = bassin de Júcar, 12 = bassin de Cabriel, 13 = bassin de Valence, 14 = bassin de Grenade, 15 = bassin de Cadix-Baza, 16 = bassin de Fortuna, 17 = bassin pré-bétique nord d'Alicante. C. Ceinture du cap Fold, Afrique du Sud, avec chaînes montagneuses séparant les plaines côtières de l'est et de l'ouest entre elles mais aussi de l'intérieur du continent. Majeurs sites fossiles du Quaternaire supérieur : 1 = Steenbokfontein, 2 = Elands Bay, 3 = Kasteelberg, 4 = Elandsfontein Main, 5 = grotte de Die Kelders 1, 6 = Byneskranskop 1, 7 = grotte de Blombos, 8 = grotte de Boomplaas, 9 = grotte de Nelson Bay. Base maps from GeoMapApp ([www.geomapp.org](http://www.geomapp.org)).

**Table 2**

Analysis intervals in the Siwalik record of the Potwar Plateau, Pakistan. Each interval corresponds to one of the four biogeographic states in Table 1. The geological evidence in support of the boundary conditions for each analysis interval is summarized briefly.

**Tableau 2**

Intervalles d'analyse du registre fossilifère pour le plateau de Potwar de Siwaliks, Pakistan. Chaque intervalle correspond à un des états biogéographiques indiqués dans le Tableau 1. L'évidence géologique en accord avec les conditions limitrophes pour chaque intervalle est brièvement résumée.

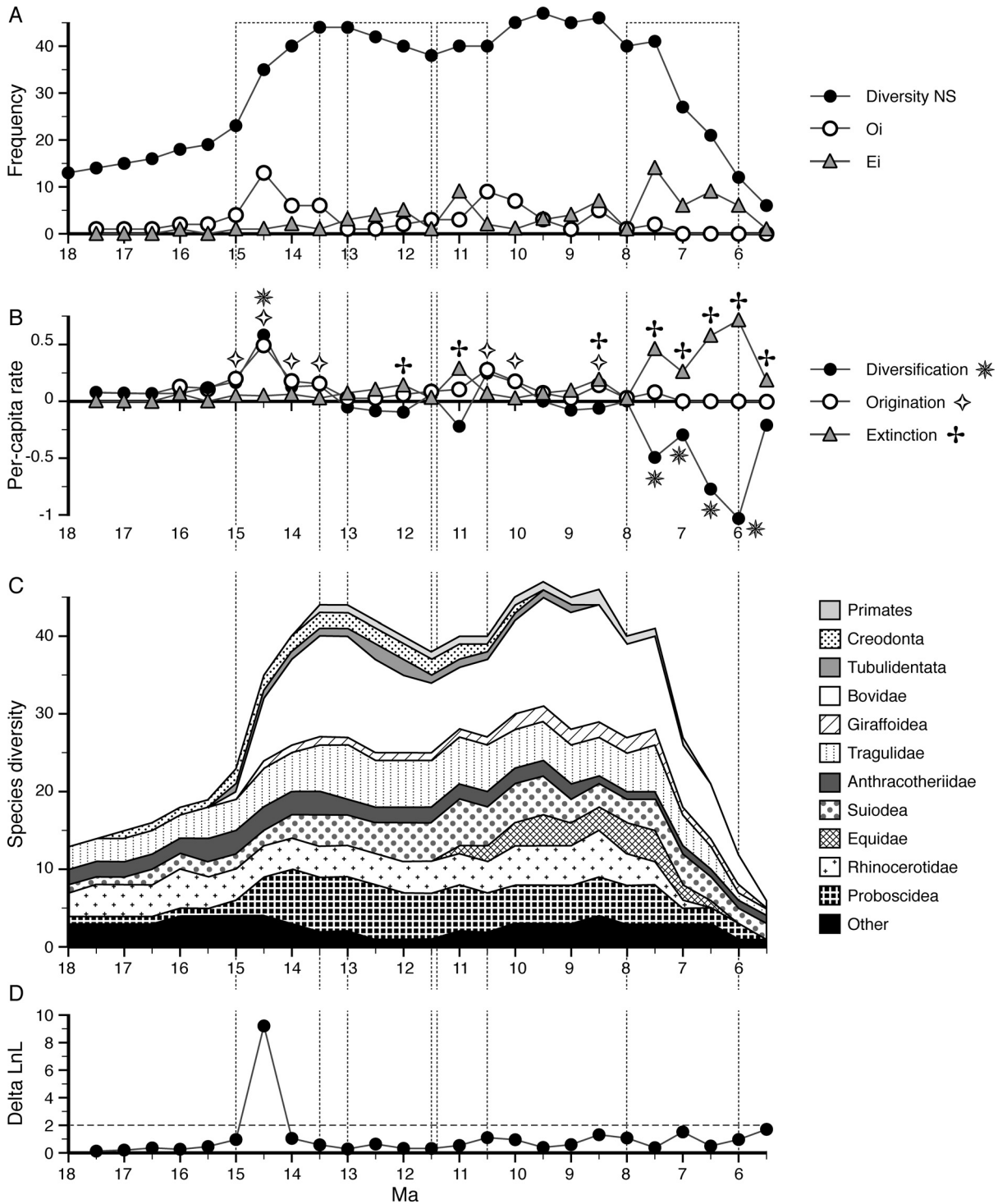
State	Age (Ma)	Evidence
A: Permeable barriers, changing climate	15.0–13.6	Cooling at end of Miocene climatic optimum; fall in sea level; change in source area of sediments References: Clift et al., 2002; Najman et al., 2003; Holbourn et al., 2013
D: Impermeable barriers, stable climate	13.0–11.6	Stable source area and drainage system; stable climate References: Willis, 1993; Cheng et al., 2004
C: Permeable barriers, stable climate	11.4–10.6	Change in source area and drainage system; fall in sea level; stable climate References: Westerhold et al., 2005; Lirer et al., 2009
A: Permeable barriers, changing climate	8.0–6.1	Regional aridification; intensification of S. Asian monsoon; sea level close to modern References: Quade and Cerling, 1995; Huang et al., 2007

records of regional to global climate change, we identified four analysis intervals between 18.0 and 5.0 Ma that correspond to three biogeographic states of the conceptual framework.

Table 2 lists the four analysis intervals and the evidence for assigning each interval to a biogeographic state. The oldest interval, from 15.0 to 13.6 Ma (using a precision of 0.1 myr), corresponds to the end of the Miocene climatic optimum, with a transition from a period of global warming from 17–14 Ma to abrupt cooling at 13.9 Ma and at least one major low stand in sea level (Betzler et al., 2013; Holbourn et al., 2005, 2013; Zachos et al., 2008). In the Potwar Plateau, a major change in fluvial facies signaled tectonically controlled change in source area and drainage system (Najman et al., 2003). The next interval, from 13.0 to 11.6 Ma, corresponds to a period of global climatic stability and stable to slightly rising sea level, according to regional marine oxygen-isotope records; Milankovitch fluctuations had low amplitude through this interval (Cheng et al., 2004; Holbourn et al., 2013; Zhao et al., 2001). The third interval, from 11.4 to 10.6 Ma, was also a period of global and regional climatic stability, culminating in minor cooling (Holbourn et al., 2013). A major coarsening of Siwalik macrofacies and increase in sediment accumulation rate at this time suggest that an increase in tectonic uplift occurred in the western Himalayas (Willis, 1993). Stable isotopes of C and O from Siwalik sediments and faunas show no significant changes during this interval. The first appearance of equids and immigrant genera of suids and bovids implies faunal connections to other regions of Asia. The youngest analysis interval, extending from 8.0 to 6.1 Ma, covers a period of regional aridification and change from C<sub>3</sub> to C<sub>4</sub> vegetation across the floodplain ecosystem (Badgley et al., 2008; Behrensmeyer et al., 2007; Quade and Cerling, 1995).

In order to evaluate the macroevolutionary predictions of the conceptual framework for the analysis intervals of the Siwalik record, we analyzed the diversification history of large mammals to identify periods of high or low origination and extinction rates. For most artiodactyl and perissodactyl lineages, we noted whether originations were likely to have occurred from immigration or endemic speciation following the procedure of Flynn et al. (2014). In addition, we evaluated changes in taxonomic composition and faunal structure from one time interval to the next. We compiled the stratigraphic distribution of

species-level occurrences between 18.0 and 5.6 Ma in 0.5-myrr intervals (with interval boundaries from 18.00–17.51, 17.50–17.01, etc.) for a total of 137 species. We lumped species denoted as anagenetic members of single lineages, and evaluated the entire unit as one lineage. We used the range-through assumption between first and last occurrences. For species known from older Siwalik strata outside the Potwar Plateau, we used the older age as the first occurrence within the Siwalik faunal province. We estimated confidence intervals on species durations based on the observed first and last occurrences, and the number of 0.1-myrr horizons in each species' record, following the method of Marshall (1990). We calculated 50% confidence limits, then excluded species with confidence intervals greater than 1.0 myr from further analysis. We also excluded species whose occurrences lie entirely within a single 0.5-myrr time bin. After these adjustments, the dataset contained 89 species. The endpoints of the confidence intervals were taken as inferred first and last occurrences for the diversification analysis. Following methods of Foote (2000), we calculated the per-capita rates of origination, extinction, and net diversification; this approach standardizes the number of first and last occurrences by the number of species passing through each time step. Thus, a particular number of first occurrences might give rise to a high per-capita rate of origination if the number of species passing through the interval is small, but to a low per-capita rate if the number of species passing through the interval is large. In order to assess the statistical significance of the observed rates, we performed a bootstrap analysis of randomized stratigraphic ranges and then calculated rates of origination, extinction, and diversification. The confidence intervals for each rate were based on 500 iterations of randomized ranges as a null model. We determined confidence intervals (CIs) as 2 standard deviations about the mean of the bootstrap distribution for each diversification variable (Finarelli and Badgley, 2010). For each time interval, if the bootstrap CI for the observed rate did not include 0, then the observed rate was considered significant. Fig. 2A illustrates species richness and the number of origination (O<sub>i</sub>) and extinction (E<sub>i</sub>) events per 0.5-myrr interval, with per-capita rates of origination, extinction, and diversification per interval in Fig. 2B. Rather than plot all of the CIs, we noted with special symbols which rates are statistically significant.



**Fig. 2.** Diversity, diversification metrics, and changes in faunal composition between 18 and 5.6 Ma for large mammals (> 1 kg) from the Siwalik record of the Potwar Plateau, northern Pakistan. In each graph, the horizontal axis is geologic time in myr. A. Species diversity (with 50% confidence intervals and singletons omitted), number of originations (Oi), and number of extinctions (Ei) in 0.5-myr intervals. The four analysis intervals are noted in light gray outlines. B. Per-capita rates of origination, extinction, and diversification (origination – extinction) for data in (A). Significant per-capita rates, according to a bootstrap of confidence intervals, are noted by symbols above or below the data symbols. C. Species diversity of large mammals in family and other higher taxonomic units. The category “other” contains groups for which at most 1 species occurred for all time intervals in which the group was present. D. Change in log-likelihood ratios for comparison of the faunal proportions from (C) for each 0.5-myr interval with the preceding interval. Substantial change between adjacent time intervals occurs when Delta LnL rises above 2.0. See text for explanation of calculations.

**Fig. 2.** Diversité, diversification métrique, et changements dans la faune entre 18 and 5,5 Ma pour le registre des grands mammifères (> 1 kg) de Siwalik du plateau de Potwar, Nord du Pakistan. Dans chaque graphique, l'axe horizontal représente le temps en millions d'années. A. Diversité

For assessing changes in taxonomic composition, we conducted a likelihood analysis of faunal composition between adjacent pairs of 0.5–myr time bins (Fig. 2C). The likelihood analysis assesses how well the faunal proportions of one time interval predict the faunal proportions of the next younger interval, based on comparison of the likelihoods of faunal proportions for the two intervals (the log-likelihood ratio, or Delta LnL, Fig. 2D). When faunal proportions of the older interval fail to predict well the proportions of the younger interval (such that the log-likelihood ratio exceeds 2.0), then change in faunal proportions was deemed significant. If the log-likelihood ratio lies below 2.0, then change in taxonomic composition was not considered significant. This procedure and the diversification metrics are explained in greater detail in Badgley and Finarelli (2013) and Domingo et al. (2014).

#### Diversification of Siwalik mammals

The diversification of Siwalik large mammals proceeded sporadically over the Middle to Late Miocene record of the Potwar Plateau (Fig. 2). Although the lithofacies of Siwalik formations and the frequency of fluvial depositional environments within formations change over time, the facies transitions do not correspond closely to the intervals of major faunal turnover. Adjusted species diversity (Diversity NS, with no singletons) rose from 13 to 47 species from 18.0 to 9.0 Ma. After 8.5 Ma, diversity declined to fewer than 10 species at 5.5 Ma (Fig. 2A). Notable peaks in the number of originations occurred at 14.5 and 10.5 Ma; in contrast, peaks in extinction events occurred at 11.0 and 7.5 Ma. In terms of per-capita rates, intervals of significant origination rates occurred in the early and middle portions of the record, with the highest rate at 14.5 Ma (Fig. 2B). Significant but relatively low extinction rates occurred at 12.0, 11.0, and 8.5 Ma; significant and relatively high extinction rates occurred from 7.5 to 5.5 Ma, with the highest rate at 6.0 Ma. A significant positive diversification rate occurred at 14.5 Ma and significant negative diversification rates occurred from 7.5 to 6.0 Ma.

Faunal composition changed substantially over the entire record, but gradually enough that only one time bin showed significant change relative to the previous interval (Fig. 2D). At 15.0 Ma, an increase in the number of bovid species represents the largest rapid change in faunal proportions over the record. The appearance of equid species at 11.5 Ma marks an interval in which the log-likelihood ratio lies just below the threshold value. The primary changes in trophic structure of large mammals, as indicated by dental morphology, stable carbon isotopes from enamel, and dental microwear analysis, occurred from 8.5 to 6.0 Ma. During this interval, frugivorous and browsing species, all consumers of C<sub>3</sub> vegetation, largely disappeared from the Siwalik record. Mixed feeders and grazing species, with

stable carbon isotopes indicative of C<sub>3</sub>, mixed C<sub>3</sub>-C<sub>4</sub>, and C<sub>4</sub> vegetation, appeared and disappeared through this interval (Badgley et al., 2008). These changes in trophic structure tracked changes in floodplain vegetation as recorded in the carbon-isotope record from soil carbonates (Quade and Cerling, 1995).

Recalling the four analysis intervals proposed for the Siwalik record (Table 2), we can evaluate the observed changes in diversity and faunal composition in relation to the predicted changes of the conceptual framework (Table 3). For the oldest analysis interval, which corresponds to the biogeographic state of permeable barriers and changing climate, three of the observed changes match the four predicted faunal changes (Table 3). The highest per-capita origination rates of the entire sequence occur during this interval (Fig. 2B), and most of these originations are immigrants to the region. The observed low extinction rates do not match the prediction of high extinction rate through this analysis interval. Immigrants joined the resident fauna, contributing to the substantial Middle Miocene increase in diversity (Fig. 2A). Faunal composition changed significantly due to the influx of bovid species at 15.0 Ma (Fig. 2C, D). For the next analysis interval, representing an interval of impermeable barriers and stable climate, all of the observed changes match predicted changes in diversification and faunal structure. The only mismatch concerns the balance between immigrant and endemic originations. Although both values are low, a few immigrations did occur, suggesting that barriers were not fully closed. For the third analysis interval, which represents the state of permeable barriers and stable climate, all of the observations match the predictions. Moderate but significant origination and extinction rates occurred, with immigration exceeding endemic originations. The youngest analysis interval, corresponding to permeable barriers and climate change, features the highest extinction rates of the entire record and the highest (negative) diversification rates (Fig. 2B). Although faunal composition did not change significantly between adjacent time intervals (Fig. 2D), substantial change in trophic structure occurred between 8.0 and 6.1 Ma as most frugivores and browsers disappeared (Badgley et al., 2008). The only observed change that does not match the prediction is the origination rate, which is low and declines to 0 over the younger part of this analysis interval (Fig. 2B). Originations were dominated by immigration, consistent with expectations.

In summary, most of the predictions of the conceptual framework match the observed changes in diversity and faunal structure for the four analysis intervals of the Siwalik record. The major discrepancies involve the two intervals of permeable barriers and changing climate. During the first,

d'espèces (en négligeant les 50 % des intervalles de confiance et les « singletons »), taux d'origination (O<sub>i</sub>), et de disparition (E<sub>i</sub>) en intervalles de 0,5 million d'années. Les quatre intervalles d'analyse sont notés en lignes grises. B. Taux d'origination, de disparition et de diversification (= origination moins disparition) *per capita*, basé sur les données dans (A). Taux significatifs *per capita*, suivant un degré de confiance se rapportant à un *bootstrap*, indiqués par un symbole au-dessous ou au-dessus de ceux qui indiquent les données générales. C. Diversité d'espèces de grands mammifères par famille et niveaux taxonomiques supérieurs. La catégorie « autre » représente des groupes pour lesquels une espèce au plus représente tous les intervalles durant lesquels le groupe fut représenté. D. Changement en *log-likelihood* des taux servant à la comparaison des rapports entre les différentes catégories de faunes de (C) pour chaque intervalle de 0,5 million d'années en fonction de l'intervalle précédent. Un changement entre deux intervalles consécutifs est considéré comme significatif quand le Delta LnL dépasse 2,0. Voir le texte pour l'explication des calculs.



**Table 3**

Observed changes in species diversity and faunal composition in the Siwalik record of large mammals from the Potwar Plateau, Pakistan, compared to predicted changes from the conceptual framework of Table 1. Observed changes that match predictions are highlighted in bold font. I = immigration, E = endemic speciation.

**Tableau 3**

Changements observés dans la diversité et la composition de la faune pour le registre fossilifère des grands mammifères de Siwalik du plateau de Potwar, Pakistan, comparés avec la prédiction des changements provenant du cadre conceptuel du Tableau 1. Les changements démontrés reflétant les changements prédits sont présentés en lettres grasses. I = immigration, E = spéciation endémique.

Analysis interval	Predicted change	Observed change
15.0–13.6 Ma Permeable barriers, changing climate	High to moderate origination rate High extinction rate Change in species diversity Change in ecological structure	<b>Highest origination rate (I &gt; E)</b> Low extinction rate <b>Increase in diversity</b> <b>Change in faunal proportions</b>
13.0–11.6 Ma Impermeable barriers, stable climate	Very low origination rate Low extinction rate Stable diversity Stable ecological structure	<b>Low origination rate (I ≈ E)</b> <b>Low extinction rate</b> <b>Stable diversity</b> <b>Stable faunal proportions</b>
11.4–10.6 Ma Permeable barriers, stable climate	Moderate origination rate Low to moderate extinction rate Small increase in species diversity Stable ecological structure	<b>Moderate origination rate (I ≈ E)</b> <b>Low extinction rate</b> <b>Small increase in diversity</b> <b>Stable faunal proportions</b>
8.0–6.1 Ma Permeable barriers, changing climate	High to moderate origination rate High extinction rate Change in species diversity Change in ecological structure	Low origination rate (I > E) <b>Highest extinction rate</b> <b>Decline in diversity</b> <b>Change in ecological structure</b>

Middle Miocene interval, regional cooling coincided with a pulse of immigrations along with several endemic speciation events but with little extinction. During the last, Late Miocene interval, regional aridification coincided with a pulse of extinctions, a few immigrations, and no endemic origination. This contrast suggests that the direction of climate change may determine whether faunal responses are dominated by originations or extinctions.

### 3.2. Late Miocene record from Spain

The Iberian Peninsula contains an excellent fossil record of Neogene mammals from intermontane basins across the peninsula (Fig. 1B). Although no single basin sequence spans the entire Neogene, many sequences contain several million years or more of continental sediments and fossil localities. Many Neogene basins contain a transition from coarse alluvial deposits along the basin margins to finer sediments with lacustrine carbonates and evaporites in the center (Civis, 2004). Fossil assemblages occur across this spectrum of facies. A recent analysis of the diversification history of Late Miocene mammals from Spain (Domingo et al., 2014) provides the opportunity to evaluate faunal change from three analysis intervals that correspond to two biogeographic states from our conceptual framework. The diversification analysis is similar in most respects to the one presented for the Siwalik record.

Mammalian faunas documented from 17 Iberian basins were dated and correlated by radiometric estimates, paleomagnetic stratigraphy, and appearance-event ordination (Domingo et al., 2014). The study interval extends from 12.0 to 5.5 Ma and includes 155 species of large mammals (> 1 kg in body weight), including carnivores. The inclusion of several families of carnivores makes it difficult to compare patterns of faunal change in detail between the Siwalik and Spanish records since carnivores were

omitted from the Siwalik data. Our primary goal, however, is to evaluate each record in terms of the conceptual framework in Table 1, not in comparison with each other. Taxonomic differences between the Spanish and Siwalik records should not impede this goal. Domingo et al. (2014) estimated 50% confidence intervals for each lineage, using the method of Marshall (1990), and excluded species with CI's greater than 1.0 myr from the analysis. Singletons were also removed. Diversification metrics identical to those described for the Siwalik sequence above were calculated for time bins of 0.5 myr. (Time bins preceding and following the record were analyzed and then truncated to avoid edge effects.) Computational details for the diversification metrics, bootstrap procedures, and likelihood analysis of changes in faunal composition — all identical in methods to those described for the Siwalik record — are given by Domingo et al. (2014).

The three analysis intervals in the Late Miocene Spanish record focus on periods of faunal change (Table 4). The earliest interval extends from 12.0 to 10.6 Ma and represents the state of permeable barriers and changing climate. Across Eurasia, this interval is notable for high-latitude cooling, immigrant lineages from North America, including the earliest hipparionine equids in Eurasia, and mobility of large mammals across Europe (Garcés et al., 1997; Tedford et al., 2004). Immigrants in the Spanish record during this time came from Asia and other regions of Europe (Domingo et al., 2014). Palynological data and stable isotopes from large-mammal teeth indicate that vegetation was stable through this interval (Domingo et al., 2013). The second interval, also representing permeable barriers and changing climate, extends from 9.5 to 7.6 Ma. This interval witnessed increasing seasonality of precipitation and aridification, accompanied by widespread vegetation change from forest to open woodland (Agustí et al., 1999a, b, 2003; Barrón et al., 2010; Domingo et al., 2013; Fortelius

**Table 4**

Analysis intervals for the large-mammal record of Spain. Each interval corresponds to one of the biogeographic states in Table 1. Geological evidence in support of the boundary conditions for each interval is summarized briefly.

**Tableau 4**

Intervalles d'analyse pour le registre de grands mammifères d'Espagne. Chaque intervalle correspond à un des états biogéographiques du Tableau 1. L'évidence géologique en accord avec les conditions limitrophes pour chaque intervalle est brièvement résumée.

State	Age (Ma)	Evidence
A: Permeable barriers, changing climate	12.0–10.6	High-latitude cooling, immigrations via Bering Land Bridge; high mobility of mammals across Europe; stable vegetation in Spain References: <a href="#">Garcés et al., 1997</a> ; <a href="#">Pound et al., 2012</a>
A: Permeable barriers, changing climate	9.6–7.6	Increase in aridity and seasonality of precipitation; forests change to woodland References: <a href="#">Agustí et al., 1999a, b</a> ; <a href="#">Barrón et al., 2010</a> ; <a href="#">Domingo et al., 2013</a> ; <a href="#">Fortelius et al., 2006</a>
B: Impermeable barriers, changing climate	6.5–5.6	Alpine uplift restricts access; Mediterranean drying; regional aridity; stable vegetation in Spain References: <a href="#">Barrón et al., 2010</a> ; <a href="#">Domingo et al., 2013</a> ; <a href="#">Eronen et al., 2009</a> ; <a href="#">Jiménez-Moreno et al., 2010</a> ; <a href="#">Kuhlemann, 2007</a>

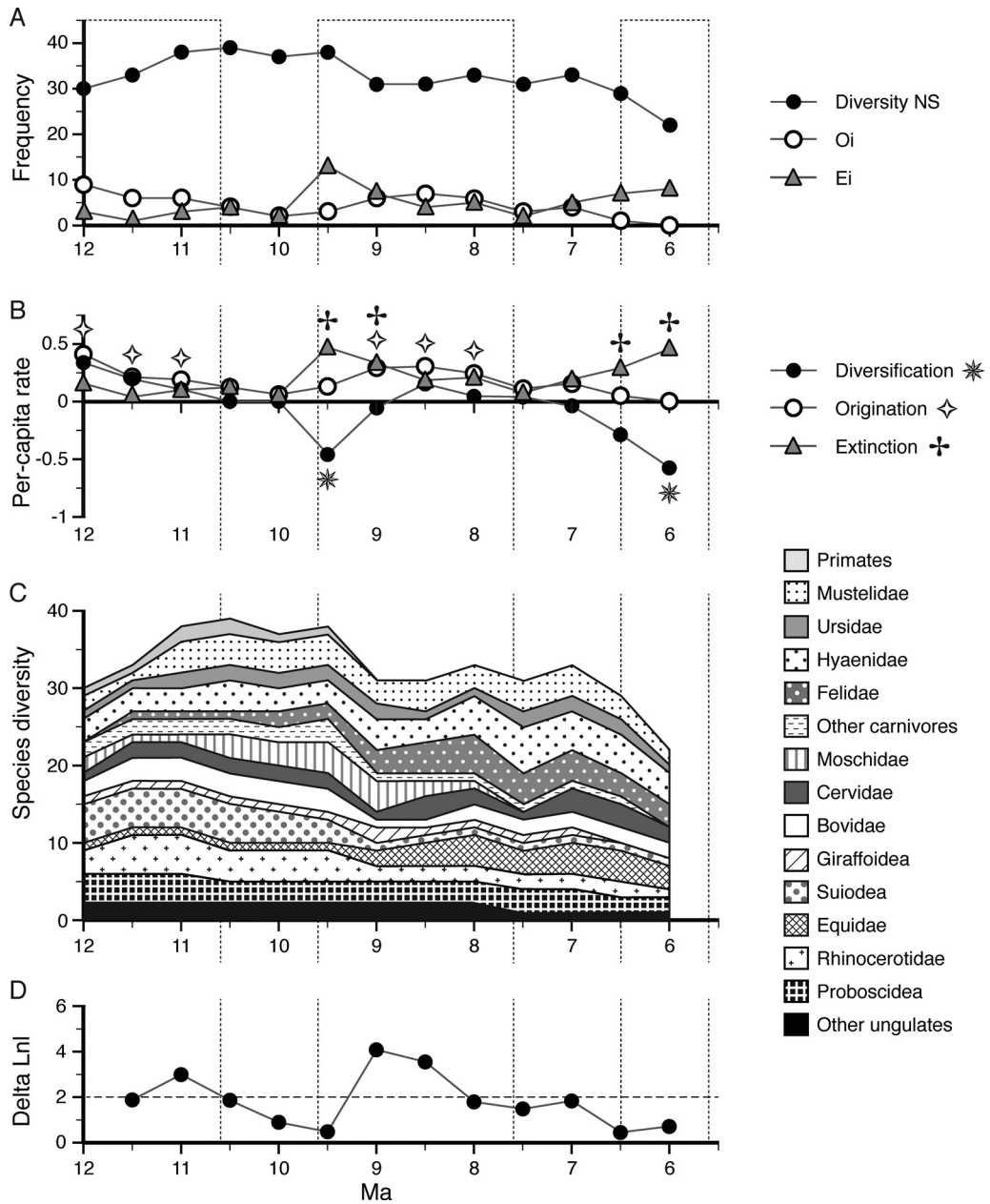
et al., 2006; Jiménez-Moreno et al., 2010; Marmi et al., 2012). This interval includes the “Vallesian Crisis” in the European mammal record. The third interval, from 6.5 to 5.6 Ma corresponds to the state of impermeable barriers with changing climate. This interval includes the onset of the Messinian Salinity Crisis, when sea level of the Mediterranean Sea fell drastically ([Krijgsman et al., 1999](#)). Although much of the Mediterranean Basin was dry, increased erosion rates in the western Alps imply rapid uplift ([Kuhlemann, 2007](#)), potentially obstructing dispersal of mammals from Western and Central Europe into the Iberian Peninsula. Mammalian faunas of the eastern and western Mediterranean from this time interval show low levels of similarity compared to earlier and later periods ([Costeur and Legendre, 2008](#); [Eronen et al., 2009](#)), implying the presence of dispersal barriers.

#### Diversification of Spanish mammals

Species diversity rose at the beginning and declined at the end of the Late Miocene Spanish record (Fig. 3A). Peaks in origination rate occurred in the early and middle portions of the record, whereas peaks in extinction rate occurred in the middle and late intervals. Significant per-capita diversification rates occurred in two intervals, at 9.5 and 6.0 Ma, and both involved loss of diversity (Fig. 3B). Faunal composition and structure changed significantly during the first and second analysis intervals (Fig. 3C, D). Changes in faunal composition at 11.0 Ma were dominated by an increase in the number of mustelids (weasels). Changes between 9.0 and 8.1 Ma (two successive time intervals) were dominated by multiple families, including equids, moschids, giraffids, hyenids, felids, and especially cervids. Principal components analysis of taxonomic composition (number of species in 22 families) separated time intervals on the first principal component according to those older versus younger than 9.0 Ma ([Domingo et al., 2014](#), fig. 5). A separate principal components analysis of trophic structure (number of species in seven trophic categories) also separated time bins into those older than 9.0 Ma, dominated by browsers, in contrast to those younger than 9.0 Ma, dominated by grazers and mixed feeders ([Domingo et al., 2014](#), fig. 6). These changes in trophic structure tracked changes in the  $\delta^{13}\text{C}$  values of herbivore enamel that indicate increased aridity across the Iberian Peninsula between ~9.5 and 7.0 Ma ([Domingo et al., 2013](#)).

Observed changes for the Iberian record are largely in agreement with the predicted changes from the conceptual framework (Table 5). The earliest analysis interval features the highest per-capita origination rate, dominated by immigration into the Iberian Peninsula. The only observation that does not match its prediction is the low extinction rate. The second analysis interval involves the greatest amount of faunal turnover, with high origination and extinction rates. All of the observed changes match the predictions. Originations were dominated by immigrants from Europe and Asia, and some extinctions affected all Iberian members of entire families ([Domingo et al., 2014](#); for micromammals, see [García-Paredes et al., 2016](#)). The third analysis interval represents a biogeographic state not observed in the Siwalik sequence – impermeable boundaries and changing climate – with tectono-sedimentary and eustatic evidence supporting isolation of the Iberian Peninsula to mammalian dispersal. Confidence intervals on species durations imply that one of the few dispersals from North Africa to Spain, interpreted previously as a crossing of the dry Mediterranean around 6 Ma, more likely occurred almost 1 myr earlier ([Domingo et al., 2014](#)). The only observation that does not match the predicted change is the low origination rate. [Domingo et al. \(2014\)](#) noted that the origination rate may have been underestimated for this interval. The conceptual framework, however, does specify no immigration (Table 1), which accords with the sole origination of an endemic equid. High endemism characterized the large-mammal faunas of the Iberian Peninsula during this interval ([Casanovas-Vilar et al., 2010](#); [Costeur and Legendre, 2008](#); [Eronen et al., 2009](#)). Extinctions removed widely distributed species, leaving a high proportion of Iberian endemics and increasing the proportion of grazers among herbivorous mammals (see also [Casanovas-Vilar et al., 2016](#), for micromammals). Paleoenvironmental indicators, including pollen records and C and O stable isotopes from mammalian enamel, suggest that the climate and vegetation did not undergo fundamental changes but continued the aridification trend that began ca. 9.0 Ma ([Domingo et al., 2013](#); [Fauquette et al., 2006](#); [Jiménez-Moreno et al., 2010](#)).

Overall, the Late Miocene Spanish record satisfies most of the predictions of the conceptual framework for the three analysis intervals. Notably, regional aridification in



**Fig. 3.** Diversity, diversification metrics, and changes in faunal composition between 12 and 5.6 Ma for large mammals (> 1 kg) from Spain. In each graph, the horizontal axis is geologic time in myr. A. Species diversity (with 50 % confidence intervals and singletons omitted), number of originations (Oi), and number of extinctions (Ei) in 0.5-my intervals. The three analysis intervals are noted in light gray outlines. B. Per-capita rates of origination, extinction, and diversification (origination – extinction) for data in (A). Significant per-capita rates, according to a bootstrap of confidence intervals, are noted by symbols above or below the data symbols. C. Species diversity of large mammals by family and other higher taxonomic units. The categories of “other carnivores” and “other ungulates” contain groups for which at most 1 species occurred for all time intervals in which the group was present. D. Change in log-likelihood ratios for comparison of the faunal proportions from (C) for each 0.5-my interval with the preceding interval. Substantial change between adjacent time intervals occurs when Delta LnL rises above 2.0. See text for explanation of calculations.

**Fig. 3.** Diversité, diversification métrique, et changements dans la composition de la faune entre 12 et 5,5 millions d’années pour de grands mammifères (> 1 kg) d’Espagne. Dans chaque graphique, l’axe horizontal représente le temps en millions d’années. A. Diversité d’espèces (en négligeant les 50 % des intervalles de confiance et les « singletons »), taux d’origination (Oi), et d’extinction (Ei) en intervalles de 0,5 million d’années. Les quatre intervalles d’analyse sont notés en lignes grises. B. Taux d’origination, d’extinction et de diversification (= origination moins extinction) *per capita*, basé sur les données dans (A). Taux significatifs *per capita*, suivant un degré de confiance se rapportant à un *bootstrap*, indiqués par un symbole au-dessus ou au-dessous des symboles indiquant les données. C. Diversité d’espèces de grands mammifères par famille et niveaux taxonomiques supérieurs. Les catégories « d’autres carnivores » et « d’autres ongulés » comprennent des groupes pour lesquels au plus une espèce est présente pour tous les intervalles temporels pour lesquels le groupe a été présent. D. Changement en *log-likelihood* des taux servant à la comparaison des rapports entre les différentes catégories de faunes de (C) pour chaque intervalle de 0,5 million d’années en fonction de l’intervalle précédent. Un changement entre deux intervalles consécutifs est considéré comme significatif quand le Delta LnL dépasse 2,0. Voir texte pour l’explication des calculs.

**Table 5**

Observed changes in diversity and faunal composition of large mammals from Spain compared to predicted changes from the conceptual framework of Table 1. Observed changes that match predictions are highlighted in bold. I = Immigration, E = endemic speciation.

**Tableau 5**

Changements dans la diversité et la composition de la faune pour le registre fossilifère des grands mammifères d'Espagne, comparés à la prédiction des changements provenant du cadre conceptuel du Tableau 1. Les changements démontrés réfléchissant les changements prédits sont présentés en lettres grasses. I = Immigration, E = spéciation endémique.

Analysis interval	Predicted change	Observed change
12.0–10.6 Ma Permeable barriers, changing climate	High to moderate origination rate High extinction rate Change in species diversity Change in ecological structure	<b>Highest origination rate (I &gt; E)</b> Low extinction rate <b>Increase in diversity</b> <b>Change in faunal proportions</b>
9.5–7.6 Ma Permeable barriers, changing climate	High to moderate origination rate High extinction rate Change in species diversity Change in ecological structure	<b>High origination rate (I &gt; E)</b> <b>High extinction rate</b> <b>Decline in diversity</b> <b>Change in ecological structure</b>
6.5–5.6 Ma Impermeable barriers, changing climate	Moderate origination rate High extinction rate Decrease in species diversity Change in ecological structure	Low origination rate (I < E) <b>High extinction rate</b> <b>Decline in diversity</b> <b>Change in ecological structure</b>

both the Siwalik record and the Spanish record was accompanied by high extinction rates for large mammals.

### 3.3. Late Quaternary mammals of the Cape Floristic Region, South Africa

The final example of mammalian faunas constrained by tectonic barriers, sea level, and climate history comes from the Late Quaternary mammalian faunas of the Cape Floristic Region, South Africa (Fig. 1C). Faith and Behrensmeyer (2013) analyzed the mammalian record from cave and open-air fossil sites of this region over the last 21 kyr in order to evaluate biogeographic predictions of the turnover-pulse hypothesis (Vrba, 1985, 1992). Data from Faith and Behrensmeyer (2013) serve as a test of the conceptual framework presented here.

The Cape Floristic Region includes a western coastal plain (WCP) and a larger southern coastal plain (SCP) separated by western and southern arms of the Cape Fold Belt (Fig. 1C). Rugged topography and unsuitable vegetation in the mountains of the Cape Fold Belt and its syntaxis present strong barriers to dispersal by large ungulates of the coastal plains, with the exception of the local race of zebra, but not to species of small bovids (antelopes) that can tolerate rugged terrain and browse on shrub vegetation (Faith and Behrensmeyer, 2013). The coastal plains are bounded to the east and west by steep topography or bioclimatic zones of unsuitable habitat for the ungulate residents of the WCP and SCP. In contrast, during glacial maxima, when sea level was ~120 m lower than at present, the coastal plains nearly doubled in area. In addition, the exposed continental shelf presented coastal corridors for dispersal between the WCP and SCP and from the coastal plains into the South African interior. Increased moisture characterized glacial intervals, resulting in widespread grassland vegetation on the coastal plains, in contrast with the arid shrublands during the current interglacial. The composition of mammalian faunas changed from glacial to interglacial periods, with grazing ungulates dominating the glacial intervals and browsing species dominating the interglacials (Faith, 2011; Faith and Behrensmeyer, 2013; Klein, 1983).

The changes in habitat area, strength and extent of montane barriers, and vegetation of the Cape Floristic Region over the last 20 kyr correspond to a transition from the biogeographic state of permeable barriers and changing climate (Table 1A) to the state of impermeable barriers and stable climate during the Holocene (Table 1D). This record provides an opportunity to evaluate predictions of the conceptual framework over a shorter time frame, by more than an order of magnitude, than the two Miocene examples. Table 6A presents four predicted responses from Faith and Behrensmeyer (2013) of the mammalian faunas to the glacial-interglacial transition and the corresponding predictions from the conceptual framework (Table 6B). The observed changes are based on the temporal ranges of ungulate species of different dietary habits (Fig. 4).

The temporal ranges of 26 large-mammal species include species whose geographic ranges expanded or contracted, species that became extirpated or extinct, and species whose geographic ranges were stable over the analysis interval (Faith and Behrensmeyer, 2013). The total species diversity of large mammals was greater during the Latest Pleistocene (10–20 ka) than during the Holocene, with disappearances occurring in a temporally staggered pattern (Fig. 4). Thirteen species present during the glacial period of the latest Pleistocene no longer occur in the Cape Floristic Region today, with five extinctions and eight range contractions. These disappearances differ by dietary category: 10 of 15 grazers disappeared (prior to the extinction of the blue antelope, *Hippotragus leucophaeus*, in historic times), whereas only two mixed feeders (2/4) disappeared, and no browsers (0/6) disappeared. These losses occurred disproportionately from the WCP, which is smaller in area than the SCP. In contrast, species that appeared or expanded their ranges during the glacial-interglacial transition and persist to the present day are all browsers. No species-level originations occurred in the Cape Floristic Region since the Middle Pleistocene (Faith and Behrensmeyer, 2013). The time span of this record is too short to capture speciation in ungulates, although one endemic subspecies of grazing antelope, *Damaliscus dorcas dorcas*, has arisen over this time period.

**Table 6**

Predicted changes in diversity and faunal composition of large mammals from the Cape Floristic Region during the transition since the last glacial maximum to the modern interglacial period, compared to observed changes in diversity and ecological structure. (A) Predicted changes in diversity and ecological structure from Faith and Behrensmeyer (2013). (B) Corresponding prediction from Table 1A (C). Observed changes, highlighted in bold when they match the corresponding prediction.

**Tableau 6**

Variations dans la diversité et la composition de la faune de grands mammifères de la région du cap Floristic au cours de la transition du dernier optimum glaciaire à l'interglaciaire moderne, comparées afin d'analyser leur diversité et leur structure écologique. (A) Changements dans la diversité et la structure écologique prédits selon Faith and Behrensmeyer (2013). (B) Prédiction suivant le Tableau 1A. (C). Les changements observés, réfléchissant les changements prédits, sont présentés en lettres grasses.

(A) Predictions for faunas of the Cape Floristic Region	(B) Predictions, conceptual framework	(C) Observed changes in faunas of the Cape Floristic Region
1 - Ungulates should experience high speciation rates because of expansion and contraction of habitat area	1 - High to moderate origination rate	1 - <b>Five immigrations but no speciation occurred during the last 20 ka</b>
2 - Grazing species should decline during transition from glacial to interglacial intervals from loss of grassland habitat	2 - High extinction rate	2 - <b>Grazing species became extinct, extirpated, or had range contractions at a higher frequency than species in other dietary categories</b>
3 - Diversity should be higher during glacial intervals, lower during interglacial intervals	3 - Change in species diversity	3 - <b>Diversity was higher during glacial maximum</b>
4 - Browsing species should be uncommon during glacial intervals, common during interglacial intervals	4 - Change in ecological structure	4 - <b>Browsing species increased and grazers declined during the climatic transition, resulting in altered trophic structure</b>

The observed changes in diversity and dietary habits of ungulates from the Cape Floristic Region match all four predictions from the conceptual framework (Table 6C). Although habitat area and the prevailing vegetation changed substantially between glacial and interglacial intervals, no new species are recorded in the fossil faunas. The five species that appear in the Cape Floristic Region represent regional range expansions or shifts (i.e., immigrations). In contrast, about one fourth of the ungulates present during the Latest Pleistocene became extinct, with selective disappearance (5/6) of grazing species. Overall species diversity declined, even though some browsers expanded their geographic ranges into or within the Cape Floristic Region. Trophic structure changed from grazer-dominated during the glacial period to a prevalence of browsers and mixed feeders during the Holocene interglacial.

Overall, the Late Quaternary mammalian record from the Cape Floristic Region matches the predictions of the conceptual framework well. Disappearances outnumbered appearances during the transition from the more humid glacial interval to the drier interglacial.

#### 4. Discussion

The conceptual framework presents four alternative geohistorical states with different constraints on biogeographic processes that affect evolution and faunal change or stability. These processes operate at the regional scale corresponding to substantial portions of typical mammalian geographic ranges. The temporal scale for geographic-range shifts, speciation, and extinction in mammals ranges from  $10^2$  to  $10^6$  years (Barnosky and Kraatz, 2007). The three faunal sequences presented here have comparable taxonomic resolution and spatial scale but differ in time depth, with the record from the Cape Floristic Region representing a much smaller time interval than a single time bin in the other two studies. The time depth is enough for geographic-range shifts,

extirpation, and extinctions to occur, but not enough for speciation in large mammals. All three examples feature landscapes interacting with regional and global climate changes that have the potential to isolate or connect ecosystems across formidable montane or marine barriers.

For each case study, most of the observed record matches the predicted faunal changes. All of the predictions regarding changes in diversity, faunal proportions, and ecological structure were confirmed. The mismatches between observed and predicted changes involved origination or extinction rates during periods of changing climate. These discrepancies suggest that we could modify the conceptual framework to account for the effects of different kinds of climate change on mammalian faunas. If indeed climatic changes were the primary drivers of geographic-range shifts into or out of the focal regions, then some kinds of climate change were stimulating mainly immigration (e.g., the first analysis intervals from the Siwalik and Spanish records), whereas other kinds of climate change led primarily to regional extinction (e.g., the last analysis intervals for the Siwalik and Spanish records, and the Cape Floristic Region). With further understanding of the paleobiology of the mammals in each record, we could potentially identify habitat generalists and specialists and then refine our predictions for how generalists versus specialists would respond to climate change. In addition, information about the abundance of species in each record would be useful, especially in combination with inferences about habitat specialization. For example, widespread habitat generalists should exhibit greater persistence during intervals of climate change than habitat generalists with small geographic ranges (Cantalapiedra et al., 2011; Gómez Cano et al., 2013; Vrba, 1992). Also, biotic interactions between resident and immigrant species need elaboration within the context of this framework.

Two additional considerations would strengthen the use of the conceptual framework. The first involves the assessment of permeability of mountain ranges. Our current assessment combines general tectonic history of the

Species	Dietary category	Temporal range (ka)					Extinct †	
		20	16	12	8	4		0
<i>Megalotragus priscus</i>	Grazer	—	—	—	—	—	—	†
<i>Equus capensis</i> *	Grazer	—	—	—	—	—	—	†
<i>Syncerus antiquus</i>	Grazer	—	—	—	—	—	—	†
<i>Connochaetes gnou</i>	Grazer	—	—	—	—	—	—	—
<i>Caprini indet</i>	Grazer	—	—	—	—	—	—	†
<i>Redunca arundinum</i>	Grazer	—	—	—	—	—	—	—
<i>Equus quagga</i> *	Grazer	—	—	—	—	—	—	—
<i>Damaliscus dorcas</i>	Grazer	—	—	—	—	—	—	—
<i>Phachochoerus aethiopicus</i>	Grazer	—	—	—	—	—	—	—
<i>Ourebia ourebi</i>	Grazer	—	—	—	—	—	—	—
<i>Alcelaphus buselaphus</i>	Grazer	—	—	—	—	—	—	—
<i>Syncerus caffer</i>	Grazer	—	—	—	—	—	—	—
<i>Hippotragus leucophaeus</i>	Grazer	—	—	—	—	—	—	†
<i>Hippotragus equinus</i>	Grazer	—	—	—	—	—	—	—
<i>Redunca fulvorufula</i>	Grazer	—	—	—	—	—	—	—
<i>Antidorcas australis</i>	Mixed feeder	—	—	—	—	—	—	†
<i>Tragelaphus strepsiceros</i>	Mixed feeder	—	—	—	—	—	—	—
<i>Taurotragus oryx</i>	Mixed feeder	—	—	—	—	—	—	—
<i>Pelea capreolus</i>	Mixed feeder	—	—	—	—	—	—	—
<i>Oreotragus oreotragus</i> *	Browser	—	—	—	—	—	—	—
<i>Raphicerus melanotis</i>	Browser	—	—	—	—	—	—	—
<i>Sylvicapra grimmia</i> **	Browser	—	—	—	—	—	—	—
<i>Raphicerus campestris</i>	Browser	—	—	—	—	—	—	—
<i>Tragelaphus scriptus</i>	Browser	—	—	—	—	—	—	—
<i>Philantomba monticola</i>	Browser	—	—	—	—	—	—	—
<i>Potamochoerus larvatus</i>	Omnivore	—	—	—	—	—	—	—

\* Species range was shorter in the WCP.

\*\* Species range was shorter in the SCP.

**Fig. 4.** Dietary category and temporal range of 26 ungulates in fossil localities of the Cape Floristic Region. Temporal range (solid line) refers to presence in either the Southern Coastal Plain (SCP) or the Western Coastal Plain (WCP) or both. Dashed line is inferred range when the species was present in older intervals or still lives today.

**Fig. 4.** Catégories de régimes alimentaires et intervalles de temps de 26 ongulés des localités de la région du cap Floristic. Les aires de répartition temporelles (ligne continue) se rapportent à leur présence, soit dans la plaine côtière du Sud (SCP), soit dans celle de l'Ouest (WCP), soit dans les deux. Les lignes pointillées représentent l'aire de répartition inférée d'espèces, soit pour les intervalles plus anciens, soit pour des espèces encore en vie.

Information from Faith and Behrensmeyer (2013).

focal area, associated sedimentological evidence (e.g., for montane-sourced mineral suites in basin sediments), and changes in regional sea level and climate. Additional relevant information could include estimates of paleoelevation from oxygen-isotope and clumped-isotope studies (Rowley and Garzzone, 2007), thermochronometric data for exhumation history (Reiners and Brandon, 2006), and additional analysis of basin sediments to distinguish between montane and trans-montane sediment sources. A more detailed analysis of modern geographic-range boundaries in different topographic settings would be useful for distinguishing the contributions of topography per se from the effects of elevational gradients in climate and vegetation on mammalian range boundaries.

The second consideration involves the depositional environments of fossil assemblages. In each record analyzed, fossil assemblages were preserved in a variety of depositional environments, including alluvial, natural-trap, open-air, and cave deposits. Siwalik fossil assemblages occur in a particular subset of fluvial environments (Behrensmeyer et al., 2005), which are present but change in relative frequency through the sequence analyzed. Taxonomic abundance varies among depositional environments, reflecting both environmental and preservational differences (Badgley, 1986; Barry et al., 2013). Consequently, changes over time in the frequency

of preservational environments should influence the probability of preservation of particular species. Analyses to date of taxonomic composition and abundance in relation to preservational environments indicate that the major trends in faunal composition over millions of years (Fig. 2) are a consequence of changes in paleoenvironment as well as immigration and extinction, but not preservational processes (Badgley et al., 2008; Barry et al., 2013). Comparable information about depositional environments and faunal composition is not available for the faunal records from Spain or the Cape Floristic Region of South Africa.

The conceptual framework is useful for placing geohistorical factors that have long been considered important drivers of mammalian evolution and faunal turnover into an analytical framework of alternate states or modes, each associated with a unique combination of ecological and evolutionary responses. In addition to the three records presented here, this framework could be applied to faunal records from the African Rift system, intermontane basins compared with lowland basins of the Andes, coastal regions compared to the Mexican Plateau, basins east and west of the Sierra Nevada Mountains of California, and intermontane basins compared with lowland basins of China. While proposed for tectonic settings with geographically restrictive barriers, such as the examples presented here, this framework can serve as a bridge to a more general model

that formalizes the influences of landscape history on the geography and diversity of mammals and other components of terrestrial ecosystems.

## 5. Conclusion

Biogeographers since the time of Alexander von Humboldt have understood that landscape history has profoundly influenced the geography of species diversity and diversification. Yet there have been relatively few efforts to develop predictive analytical frameworks for testing the effects of tectonic and climatic history on biotic change with data from the fossil record. The conceptual framework presented here has been tailored specifically to mammalian faunal change in the context of continental environments with strong montane barriers. This framework focuses on the interactions of tectonically controlled barriers, regional climate, and vegetation that stimulate or impede mammalian dispersal, alter the configuration of geographic ranges, and sort species according to their environmental tolerances.

For the three faunal sequences evaluated here, the conceptual framework has shown strong predictive capability. The mismatches between observations and predictions in each sequence highlight aspects of the framework that need reconsideration, including a model with more than four alternative states. Nevertheless, the conceptual framework has enabled us to progress from a narrative to an analysis of the impacts of landscape history on evolutionary and ecological changes in mammalian faunas in their geographic and environmental contexts.

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