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Continental gateways and the dynamics of mammalian faunas

Portes continentales et évolution des faunes mammifères

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A B S T R A C T

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.

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.

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 Riitters, 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