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Range size heritability patterns in Carnivora arise from the interplay between evolutionary and geographic constraints

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Annotation:

The thesis explores how the range sizes of carnivorans are shaped by geographic and evolutionary constraints. Employing modern spatial analyses and phylogenetic comparative methods, we illustrate that phylogenetically conserved climate tolerances delimit species' geographic constraints, which in turn shape the species' range size. Range size heritability patterns emerge as a consequence of this interplay between geographic and evolutionary constraints.

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We hereby declare

that Antonin Machac has substantially contributed to our study

Machac A., Zrzavy J., Storch D. (2010) Range size heritability patterns in Carnivora arise from the interplay between evolutionary and geographic constraints.

Specifically, Antonin's contribution comprised

- conducting all the statistical analyses, GIS inference,
  analyses of phylogenetic signal and conservatism
- major contribution to the methodological design, text of the manuscript
- minor contribution to the phylogeny reconstruction

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» Geographical ranges are the Chinese-lantern shadows
produced by the different taxa on the continental screen:
it is like measuring, weighing, and studying
the behavior of ghosts. «

<Rapoport 1982>

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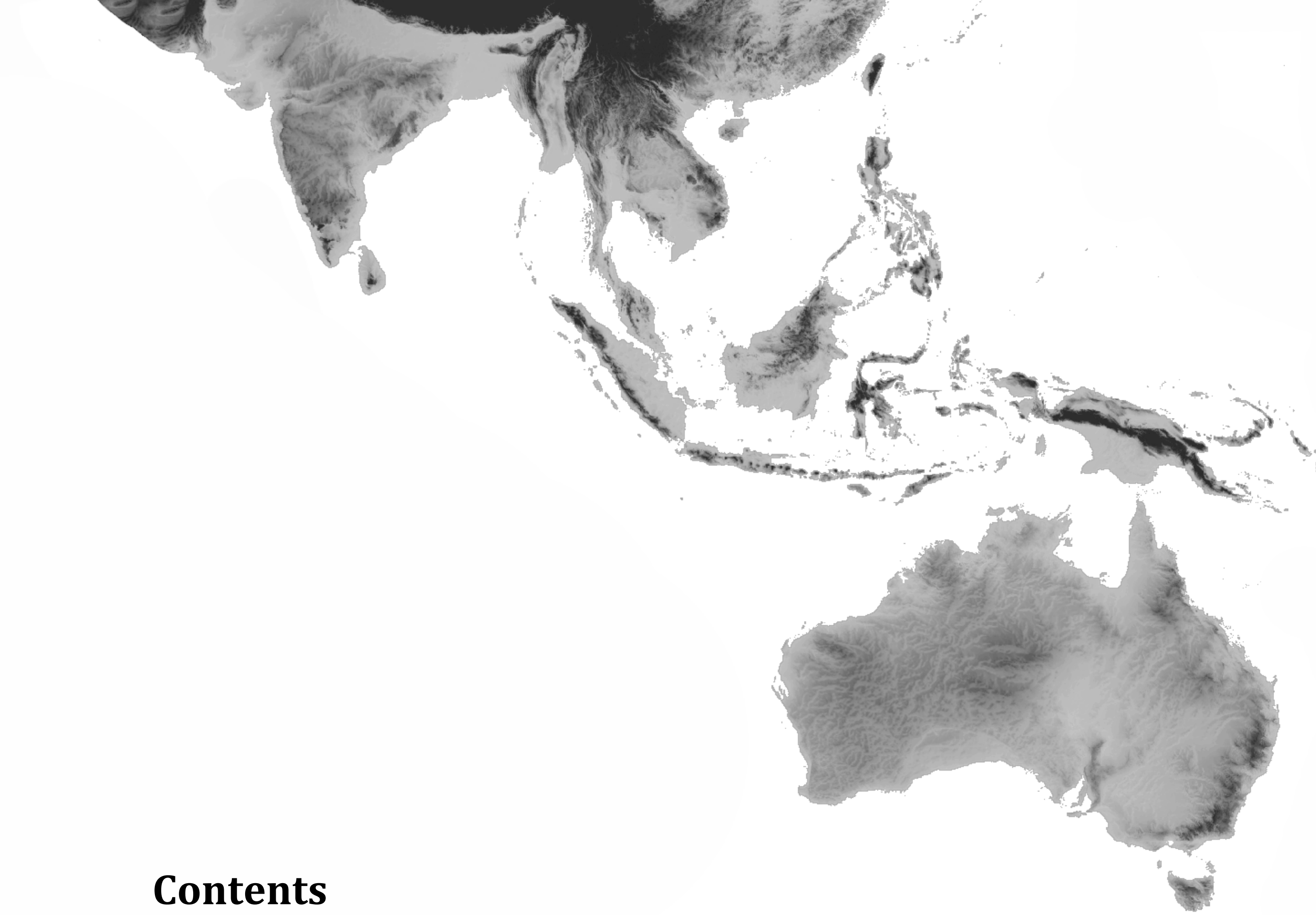

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Introduction

During the last two decades, range size heritability has been a subject of vigorous and sometimes controversial debates. The term "range size heritability" refers to a tendency of closely related species to retain more similar range sizes than distinct species do (Jablonski 1987). The appeal of range size heritability for biologists resides in its association with the species selection concept (Ricklefs and Latham 1992, Grantham 1995). Species selection is an outcome of heritable differences in speciation and extinction rates among phylogenetic lineages. It is widely accepted that differential speciation and extinction owing to purely emergent traits (collective properties of individuals within a species; e.g., geographic range size, sex ratio, intraspecific variability) has to be due to the species selection. However, for any selection process, heritability of the selected traits is a necessary prerequisite. Convincing evidence for range size heritability might therefore highlight the species selection as one of the central evolutionary processes (Gould and Lloyd 1999, Webb and Gaston 2003, Jablonski 2008, Rabosky and McCune 2010).

Tempted by this outlook for crucial findings, numerous studies have examined and variously documented (Jablonski 1987, Taylor and Gotelli 1994), refuted (Diniz-Filho and Torres 2002, Webb and Gaston 2003) and reaffirmed (Hunt et al. 2005, Jones et al. 2005) range size heritability via a spectrum of methods ranging from sister-species pairs comparison and phylogenetic autocorrelation to the construction of explicit models of range size evolution (see reviews by Gaston 2003, Waldron 2007). As recent discussions illustrate (Hunt et al. 2005, Webb and Gaston 2005), distinct methods may lead to different outcomes even when applied to the same dataset. The ambiguous conclusions prove the range size heritability to be a difficult conundrum. This is not only due to the methodological pitfalls but also due to presumably varied patterns among different taxonomic groups (Jones et al. 2005).

Despite the lack of compelling evidence for the pattern itself, many underlying mechanisms have been hypothesized and tested. For instance, phylogenetically conserved life history traits such as niche breadth, physiological tolerance, dispersal ability, and functional group membership may eventually lead to range size heritability (Mouillot and Gaston 2009).

Surprisingly, only rarely have geographic constraints such as spatial limits of continents or biomes been appraised (Freckleton and Jetz 2009, Bohning-Gaese et al. 2006).

Spatial structure is an inherent component of biogeographic data and is routinely considered when analyzing patterns in diversity or abundance (Legendre et al. 2002, Blackburn 2004, Rangel et al. 2006). It naturally affects range sizes as well. As Brown et al. (1996) highlighted in their keystone work, we need to consider "how geographic ranges are distributed on and constrained by the spherical geometry and basic geography of the earth”. A number of studies have documented that species occupying biogeographic provinces of vast spatial extent tend to have larger range sizes (Pagel et al. 1991, Smith et al. 1994, Gaston et al. 1998, Fortes and Absalao 2004). This means that we cannot make reliable conclusions about range size heritability without controlling for spatio-geographic constraints. However, only several studies so far have addressed simultaneously the evolutionary and geographic constituents of range sizes. Specifically, Freckleton and Jetz (2009) designed an integrated framework that allowed simultaneous evaluation of phylogenetic and spatial components of life history traits. Having detected spatial signal in range sizes of artiodactyls, the authors outline that range size variation may be driven by where species live rather than by evolutionary history. In the case of primates’ and carnivorans’ range sizes, however, Freckelton and Jetz (2009) did not detect any spatial signal. Neither did Bohning-Gaese et al. (2006) discover any substantial correlation when examining the relation between range sizes of 26 bird species and the area of corresponding ecoregions and biomes. These surprising conclusions are balanced by the findings of Mouillot and Gaston (2009) that imply spatial autocorrelation in an extensive dataset of 1136 bird species (the autocorrelation is therein manifested as a positive relationship between mutual overlap and similarity in size of sister species’ geographic ranges).

In our study, we thoroughly explore the impact of geographic constraints on carnivoran range sizes. As delimitation of specific geographic constraints might be contentious, we assess the constraints for several levels of geographic resolution (i.e., edges of continents, biomes, and climate envelopes). Subsequently, we contrast the effects of geographic and phylogenetic constraints on range size variation. We evaluate the stability of phylogenetic signal in range sizes after the correction for geographic constraints, and explore possible causes of the revealed patterns.

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Discussion

Biogeographic patterns are produced by a complex interaction among numerous factors whereby limits of continents, montane systems, and other physical barriers represent a crucial agent. Though their influence has been widely acknowledged, physical barriers appear rather difficult to grasp, and appropriate spatial analyses still represent a challenging issue. Herein, we aimed to verify and assess the effect of geographic constraints on range size heritability patterns. Employing an advanced method for analysis of phylogenetically and spatially structured data (PVR), we infer that edges of biomes are largely responsible for the observed patterns of range size heritability. Furthermore, we propose a mechanism whereby range size heritability patterns emerge due to the interplay between geographic and phylogenetic constraints. Phylogenetically conserved physiological tolerances presumably shape the extent of geographic domains that, subsequently, underlie species' range size.

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