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Co-diversity and co-distribution in phyllostomid bats: Evaluating the relative roles of climate and niche conservatism

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Abstract

Explaining the causes of geographic gradients in biodiversity remains an elusive task. Traditionally, correlative approaches have been used to relate species richness with contemporary climate, without actually explaining the causal factors. Recent approaches propose simulation models as more appropriate tools for assessing potential causes of macroecological patterns. Here we developed stochastic models to assess the relative contribution of climate and niche conservatism in determining compositional similarity among sites (co-diversity) and geographic association among species (co-distribution) in the bat family Phyllostomidae. We used range-diversity plots and variance-ratio tests to describe and evaluate such patterns. Our results supported a strong effect of climate in determining cohesive ranges causing positive co-diversity and co-distribution. We also demonstrated a marginal effect of niche conservatism, as modeled here, among species in shaping these patterns. However, climate and niche conservatism are not sufficient and other processes are still required to explain observed patterns. Our study highlights the importance of historical processes and demonstrates the usefulness of a simulation framework in testing biogeographical hypothesis to understand the relationship between diversity and distribution.

Zusammenfassung

Die Gründe für geographische Gradienten der Biodiversität zu erklären, bleibt eine schwer fassbare Aufgabe. Traditionell wurden korrelative Ansätze benutzt, um den Artenreichtum mit dem aktuellen Klima in Beziehung zu setzen ohne tatsächlich die kausalen Faktoren zu erklären. Neuere Ansätze schlagen Simulationsmodelle vor, als besser geeignete Werkzeuge, um die potentiellen Gründe von makroökologischen Mustern einzuschätzen. Hier entwickelten wir stochastische Modelle, um am Beispiel der Fledermausfamilie Phyllostomidae den relativen Beitrag von Klima und Nischenkonservatismus zur Bestimmung der Gemeinschaftsähnlichkeit zwischen Standorten (Ko-Diversität) und die geographische Assoziation zwischen Arten (Ko-Verteilung) abzuschätzen. Wir benutzten Verbreitungs-Diversitäts-Diagramme und Varianz-Verhältnis-Tests, um derartige Muster zu beschreiben und auszuwerten. Unsere Ergebnisse unterstützten einen starken Einfluss des Klimas bei der Bildung zusammenhängender Verbreitungsgebiete, was zu positiver Ko-Diversität und Ko-Verteilung führt. Wir zeigten mit der gewählten

Modellierung außerdem einen marginalen Einfluss des Nischenkonservatismus unter den Arten auf die Bildung dieser Muster. Indessen genügen Klima und Nischenkonservatismus nicht und weitere Prozesse werden benötigt, um die beobachteten Muster zu erklären. Unsere Studie hebt die Bedeutung historischer Prozesse hervor und zeigt die Nützlichkeit eines Bezugssystems für Simulierungen beim Überprüfen von biogeographischen Hypothesen, um den Zusammenhang zwischen Diversität und Verbreitung zu verstehen.

Introduction

Geographic variation in species richness is ultimately determined by the overlap of species' ranges, which is determined by the size, shape and location of those ranges (Gotelli et al. 2009). However, understanding the mechanistic basis of species' ranges and biodiversity gradients remains elusive. Traditionally, species richness gradients have been investigated with correlative approaches relating species richness to climate variables, assuming climatic gradients underlie biodiversity gradients (Field et al. 2009). Likewise, climate is considered a fundamental factor determining the conditions and ecophysiological constraints that restrict population growth at coarse spatial scales, thus delimiting species' geographic distributions (Gaston 2003; Soberón 2007). Recently, niche conservatism, the tendency of species to retain ancestral ecological characteristics, has also been proposed as a potential cause of biodiversity gradients in which the ancestral niche of a clade determines the regions in which the clade can persist and further diversify, and those regions to which it could spread (Wiens & Donoghue 2004).

Current approaches advocate simulation models of species' range construction and placement to assess potential causes of geographic biodiversity gradients (Gotelli et al. 2009). Early studies using simulation models examined the effect of geometric constraints by simulating range placement within homogeneous domains of regular shape (Colwell & Lees 2000) or resembling actual continents (Jetz & Rahbek 2001). Other studies included topographic and climatic gradients in simulating ranges (Rahbek et al. 2007), whereas others modeled range dynamics by simulating evolutionary processes of speciation, extinction, and niche conservatism (Rangel, Diniz-Filho, & Colwell 2007).

Most of these studies used species richness as the sole response variable to assess the predictive power of different models, comparing observed with simulated values. However, these comparisons may be incomplete because similar results can be obtained under different combinations of predictive variables (Dormann et al. 2012); hence, other patterns are also needed to evaluate model performance. For instance, comparing different patterns between observed and modeled data, such as range-size frequency distributions (Rangel et al. 2007) or phylogenetic structure (Stevens, Tello, & Gavilanez 2013) can be used to validate models at different hierarchical levels as done in pattern-oriented modeling (Grimm et al. 2005), thus providing stronger tests of potential mechanisms.

Recently, Arita, Christen, Rodríguez, and Soberón (2008) introduced an alternative approach based on composite response variables simultaneously linking diversity and distributional information in range-diversity (RD) plots. The basic informational unit in biogeography and macroecology is a presence-absence matrix (PAM) in which columns represent sites, rows represent species, and the elements are binary entries showing the occurrence – presence (1) or absence (0) – of a given species in a given site (Arita et al. 2008). Range size values are easily calculated in a PAM as row sums, and, equivalently, species richness values can be calculated as column sums. The use of a "common currency" (the number of occurrences) for site-level (species richness) and species-level (range size) measurements, allows developing response variables that incorporate both diversity and distribution. This inherent relationship between species richness and range size can be visualized and evaluated with RD plots, enabling researchers to investigate such relationship directly when testing biogeographic hypotheses (Borregaard & Rahbek 2010; Villalobos & Arita 2010).

Here we develop stochastic simulation models of species' ranges to assess the roles of climate and niche conservatism, through their effect on range structure and location, on the linked patterns of diversity and distribution for the New World leaf-nosed bats (Phyllostomidae). We used range-diversity plots and incorporated two types of variance-ratio tests to assess model fit to observed patterns of species' geographic coexistence (co-distribution) and similarity among sites (co-diversity). Recent studies have suggested that geographic patterns of phyllostomid diversity are the result of historical processes among which niche conservatism seems to be one of the most important (Stevens 2011; Villalobos, Rangel, & Diniz-Filho 2013). Hence we expect the outcome of niche conservatism to be discernable, and stronger than climate determining range structure, in the co-distribution and co-diversity of phyllostomid species and assemblages.

Materials and methods

Data and analyses

We constructed a database of the continental distribution of 143 phyllostomid bats. We obtained range maps (i.e., extents of occurrence) for these species from data from the primary literature up to 2007 for North American species