



Capitalizing on a wealth of spatial information: Improving biogeographic regionalization through the use of spatial clustering

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ARTICLE INFO

Keywords:

Biogeographic regionalization
Angola
Mammals
Spatially constrained clustering

ABSTRACT

Biogeographic regionalization, the categorization of geographical areas on the basis of their biotas, provides a valuable approach for understanding biogeographical and ecological patterns and processes and serves as a valuable tool in conservation management practices. Contemporary, quantitative approaches for delineating and mapping biogeographic regions that make use of increasingly available species occurrence data have typically been conducted using clustering methods that do not consider spatial information of sample sites during the aggregation processes. This shortcoming has led to challenges in identifying spatial patterns and interpreting the underlying ecological factors responsible for these patterns. To address the shortcomings of non-spatial clustering methods and to highlight the value of utilizing spatial information during regionalization, we conducted biogeographic regionalization on a dataset of observed mammalian species locations in Angola using a non-spatial clustering method (Ward's clustering) and a spatial clustering method (Regionalization with Dynamically Constrained Agglomerative Clustering and Partitioning). When compared to results from the non-spatial method, biogeographic regions delineated by the spatial clustering method were more closely associated with distinct climatic conditions, had greater concurrence to accepted ecoregions, and were more strongly associated with species assemblages within these regions. We argue that the spatial clustering method makes regions more meaningful and interpretable; as a result, biogeographic regions identified by our approach could facilitate prioritizing conservation plans, developing natural resources management strategies, and reducing data complexity for spatial representation and ecological interpretation of species distribution.

1. Introduction

Biogeographers have long been interested in identifying and mapping regions that are distinct with respect to biotic structure or composition as a means for exploring and better understanding the factors responsible for shaping species distributions (Ficetola, Mazel, & Thuiller, 2017). Various tools and approaches associated with geographical regionalization have since provided analytical frameworks for a range of biogeographical, ecological, and environmental applications. For example, biogeographic regionalization has been used at scales ranging from the entire globe down to geographic regions, nations, and landscapes to prioritize conservation plans and options (Kier et al., 2005; Olson et al., 2001) and to aid in identifying areas in which similar or specific natural resources management strategies could be applied (Bernert, Eilers, Sullivan, Freemark, & Ribic, 1997; Hobbs & McIntyre, 2005). Regionalization is also a powerful tool that can be used to reduce data complexity for spatial representation and facilitate ecological interpretation (Kupfer, Gao, & Guo, 2012; Long, Nelson, & Wulder, 2010).

The practice of mapping biogeographic regions based on aspects of species composition or physiognomy dates back more than a century (Huggett, 2002; Wallace, 1876). Earlier approaches, based largely on researchers' knowledge of species distributions, were generally subjective and non-replicable, sometimes leading to disagreement among different parties (e.g., African biogeographic regions: Chapin, 1923; Cox, 2001; Dasmann, 1972; Diamond & Hamilton, 1980; Williams, de Klerk, & Crowe, 1999). Recently, the importance of quantitative, replicable and transparent regionalization methods has been recognized (Mackey, Berry, & Brown, 2008), and biogeographers have begun actively exploring and utilizing a variety of quantitative techniques to solve regionalization-related problems (e.g., Hattab et al., 2015).

Morrone (2018) has provided a useful overview of important concepts and methods involved in biogeographic regionalization. Generally speaking, one set of approaches to regionalizing biogeographic data is rooted in principles associated with biogeographic homology and seeks to identify spatial-temporal elements with a mutual biogeographic history (Morrone, 2001). An underlying assumption is that the resultant

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biogeographic regions are ‘natural’ or monophyletic, that is, the included biota possess a shared historical relationship or evolutionary history (Ebach & Parenti, 2015; Escalante, 2017). Such approaches are rooted in traditions associated with evolutionary biogeography, which emphasizes taxonomic groups and the importance of past biogeographic events such as dispersal, evolution and vicariance, and extinction. In terms of biogeographic regionalization, approaches focused on homology emphasize the identification of areas of endemism, commonly beginning with an analysis of the geographic distribution of individual species and leading to the hierarchical categorization of geographical areas with distinct sets of endemic taxa (Escalante, Morrone, & Rodriguez-Tapia, 2013; Morrone, 2018).

Other approaches, such as the ones used in this paper, seek instead to identify regions containing sets (communities) of species characteristic of that region and distinct from sets of species in other regions. Grounded in concepts from the field of ecological biogeography and utilizing tools common to multivariate ecological analysis (e.g., clustering), such approaches emphasize more contemporary time scales and ecological constraints on species patterns. The assumption is that clusters of species with similar niches form groups with similar morphological and physiological characteristics and shared common ecological roles (Crisci, Sala, Katinas, & Posadas, 2006); the goal of regionalization is thus to identify spatial units that effectively capture those groups based on a stated criterion such as within-vs. between-region species similarity. Biogeographic regions from this perspective are more akin to ecoregions, but with an explicit focus solely on biotic elements (e.g., species occurrences). Kreft and Jetz (2010) demonstrated the usefulness of these types of quantitative regionalization methods by evaluating the performance of nine clustering methods used to delineate regions based on the global distribution of mammalian fauna.

As Crisci et al. (2006) note, biogeographic approaches associated with historical- and ecological biogeography employ different concepts that are frequently explored in the literature but are rarely integrated. In this paper, we utilize clustering-based techniques because such approaches are more familiar to many applied biogeographers and ecologists and because our interests center on contemporary management applications that emphasize an understanding of community-level species patterns.

Despite the range of regionalization applications and concerted efforts aimed at exploring, utilizing, developing, and testing regionalization techniques, the important role of spatial adjacency or proximity has not been adequately considered in biogeographic regionalization procedures, even though spatial relationships can greatly influence ecological processes that shape biogeographic patterns and thus are of interest in designing effective networks of protected areas (e.g., Delmelle, Desjardins, & Deng, 2017; Gao, Kupfer, Guo, & Lei, 2013). Prevailing regionalization methods adopted by biogeographers, including *k*-means (e.g., Heikinheimo, Fortelius, Eronen, & Mannila, 2007; Mateo, Vanderpoorten, Munoz, Laenen, & Desamore, 2013; Razavi & Coulibaly, 2013; Xu et al., 2014), unweighted pair-group method using arithmetic averages algorithm/Average Linkage clustering (UPGMA/ALK) (e.g., Bradshaw, Colville, & Linder, 2015; Dapporto, Ciolli, Dennis, Fox, & Shreeve, 2015; Hattab et al., 2015; Kreft & Jetz, 2010), principal component analysis (e.g., Zhang, Wu, Wang, Yuan, & Zhao, 2011), and Ward’s clustering (e.g., Rodrigues, Figueira, Vaz Pinto, Araújo, & Beja, 2015; Wohlgemuth, 1996), are all clustering or dimension reduction methods that do not consider spatial information during the aggregation processes. We use the term ‘non-spatial’ for such methods.

Though non-spatial techniques can be used for the purpose of regionalization by aggregating spatial units without using spatial information, they do not strictly follow the principles of regionalization (Huang, Fan, Li, & Wang, 2013), and the use of non-spatial approaches may impose challenges on interpreting spatial patterns and hinder the understanding of underlying ecological processes. Conversely, Andrew,

Wulder, and Coops (2011) found that regionalization methods that consider spatial constraints outperformed non-spatial methods in capturing patterns of butterfly community composition and species affinities that are strongly structured by space. Rickbeil et al. (2014) similarly found that spatially contiguous regionalization methods were superior to non-contiguous ones for delineating bird communities. Incorporating spatial contiguity into non-spatial clustering methods such as ALK also facilitated characterizing forest patterns and interpreting underlying ecological processes in different regions of the continental United States (Kupfer et al., 2012). In contrast, non-spatial clustering methods failed to distinguish small-scale forest formations and resulted in increased similarities of grid cells across borders of various animal regions in the regionalization of European biota (Rueda, Rodriguez, & Hawkins, 2010).

Biogeographic regionalization of species patterns employs data on species presence or abundance that are often collected from a limited number of accessible sites due to economic and logistical constraints. Sample sites also often have spatial bias because of (in)accessibility to potential sample locations. Given the inadequate consideration of spatial information in the procedure of biogeographic regionalization, approaches to utilizing spatial information from *discrete* and usually *unevenly distributed* samples when conducting regionalization on species distribution is even more underexplored. For instance, Rodrigues et al. (2015) had to compromise on the optimal number of regions when they interpreted the regionalization patterns of Angolan mammals because regions delineated by their non-spatial clustering method lost spatial coherence. To address the shortcomings of non-spatial clustering methods and to highlight the value of utilizing spatial information during regionalization, we present a regionalization method that incorporates spatial information from species sample points and compare results from our method against those obtained using non-spatial clustering methods.

2. Materials and methods

2.1. Study areas and species datasets

We used the same dataset of mammalian occurrences that was analyzed by Rodrigues et al. (2015) using a non-spatial clustering method to produce a biogeographical regionalization of Angola. The Republic of Angola is located in subtropical southern Africa and covers an area of ca. 1,246,700 km², with elevations that range from 0 to 2,620 m above sea level. Topography ranges from the arid coastal lowland, which is characterized by low plains and terraces, to hills and mountains that rise from the coast into a great inland escarpment, to a large area of high plains of dry savanna extending east from the escarpment, to rain forest in the north (Hance, 1975; Rodrigues et al., 2015). Generally, the climate includes a dry and hot season from May to October, a transitional season with some rain from November to January, and a rainy season from February to April, with coastal areas being affected by the cool Benguela Current. The Angolan terrestrial mammalian fauna includes ca. 275 species, including a number of species of conservation interest (Kuedikuenda & Xavier, 2009; Rodrigues et al., 2015).

The dataset included 9,880 occurrence records for 140 rodent, ungulate, and carnivore species that were collected from the literature of Crawford-Cabral (1989), Crawford-Cabral (1998), Crawford-Cabral and Simoes (1988), and Crawford-Cabral and Veríssimo (2005). The sampled points were aggregated to grids at a resolution of ¼ degree (approximately 25*25 km). The northwestern enclave of Cabinda was not included in the analyses, because it is discontinuous with the rest of Angola, and aquatic species were excluded. Grid cells that contained records for fewer than five species were excluded to avoid potential bias (Rodrigues et al., 2015), resulting in a total of 457 grid cells.

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