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Short note

A framework for assessing the scale of influence of environmental factors on ecological patterns

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ABSTRACT

The distribution of living organisms, habitats and ecosystems is primarily driven by abiotic environmental factors that are spatially structured. Assessing the spatial structure of environmental factors, e.g., through spatial autocorrelation analyses (SAC), can thus help us understand their scale of influence on the distribution of organisms, habitats, and ecosystems. Yet SAC analyses of environmental factors are still rarely performed in biogeographic studies. Here, we describe a novel framework that combines SAC and statistical clustering to identify scales of spatial patterning of environmental factors, which can then be interpreted as the scales at which those factors influence the geographic distribution of biological and ecological features. We illustrate this new framework with datasets at different spatial or thematic resolutions. This framework is conceptually and statistically robust, providing a valuable approach to tackle a wide range of issues in ecological and environmental research and particularly when building predictors for ecological models. The new framework can significantly promote fundamental research on all spatially-structured ecological patterns. It can also foster research and application in such fields as global change ecology, conservation planning, and landscape management.

1. Spatial scale and ecological models

1.1. Why is scale important when predicting the potential distribution of species, biodiversity, habitats and ecosystems?

The modern global biodiversity crisis has promoted the development and application of ecological models (Pereira et al., 2010; Guisan and Thuiller, 2005), ranging from conservation planning (Hannah et al., 2007) to the adaptive management of alien invasive species and their impacts (Giljohann et al., 2011; Vicente et al., 2011). However, accurately predicting species distributions and range dynamics is not an easy task since environmental, historical and human factors, as well as stochastic events jointly contribute to shape them (Soberon and Nakamura, 2009). These many factors influence the occurrence, abundance and the patterns of ecological diversity with different intensities and at distinct spatial and temporal scales (de Knegt et al., 2010; Dorman, 2007; Levin, 1992; McGill, 2010). Climate can well explain ecological patterns at the continental scale (Araujo and Pearson, 2005), whereas topography, human land use or biotic interactions are more important at regional and local scales (Dirnböck et al., 2003; Guisan and Thuiller, 2005).

Ongoing environmental changes are also acting at different spatial scales, and many ecosystems are predicted to be impacted by those changes (Pereira et al., 2010). Shifts in environmental conditions occurring at multiple scales could affect biodiversity, habitats and ecosystems independently (Hannah et al., 2007; Pereira et al., 2010). However, in most cases, they may interact and produce either enhanced responses due to synergistic effects, or

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minor responses due to compensation effects (Kalnay and Cai, 2003). For example, global climate warming may promote regionally agricultural intensification in colder areas thus acting synergistically with land-use change on species distributions, whereas agricultural abandonment may compensate for increased drought stress related to climate change by promoting forest encroachment. Species range shifts under climatic change may be hampered by local conditions such as soils (e.g., alkaline soils at higher altitudes may prevent the upward movement of acid-ophilous species; Theurillat et al., 1998) and land-use (see Bradley and Mustard, 2006; Davis et al., 1998), not only for native biodiversity but also for invasive species (Bradley et al., 2010; Vicente et al., 2011). Thus, it becomes urgent to develop new approaches that explicitly consider the effects of such environmental factors on ecological processes at the appropriate scales. Such approaches may be more informative and/or more accurate when forecasting biodiversity dynamics (Bradley et al., 2010; Vicente et al., 2011).

1.2. How can we explicitly include the effects of spatial scale in ecological models?

Although different levels of causality and proximality can be found in the relation between biodiversity patterns and environmental factors (as inferred from ecological theory; Austin, 2002), predictive variables are usually generated at a same grain size and geographic extent, without specific consideration for their intrinsic scale of influence on the biological features they are related to. This "traditional" approach to ecological modeling has been applied so far to a multitude of species and ecological contexts with variable success. However, efficiently tackling the multiple drivers of change and loss of biodiversity and the scales at which they act will require novel or improved modeling frameworks (Pereira et al., 2010). Such multi-scale approaches may capture dimensions that have been ignored by approaches conducted at single scales (Pearson et al., 2004). Classifications of environmental factors can be applied with fixed extent and grain size, or with different extents and grain sizes ("multi-scale approach" Milbau et al., 2009; Pearson et al., 2004; Vicente et al., 2011). Two types of approaches based on a priori classification according to spatial scale have been used so far in ecological models: (i) fitting one model and performing a posterior analysis of the relative importance of each environmental factor (or group/type of factors) which vary at different scales (e.g., by using variation partitioning Borcard et al., 1992); or (ii) combining multiple models, each fitted with subsets of environmental factors varying at a given spatial scale (e.g., Vicente et al., 2011). Both approaches require an a priori classification or grouping of environmental factors according to their scale of patterning. Spatial scale of variation (e.g., regional vs. local) is generally supported by ecological theory, but theoretical foundations should be supported by (geo-) statistics for additional robustness and objectivity of predictor classifications (Vicente et al., 2011).

2. Toward a conceptual framework for assessing scale of patterning, and classification of environmental factors

2.1. Developing the framework

Improvements in the analysis of spatial distribution of biological data could be achieved through the classification of environmental factors according to their expected scale of influence, which calls for a synthesis between ecological theory and spatial statistics (Austin, 2002; Pearson et al., 2004). If the environmental factors used to analyze and predict biological features are structured in space in a way that can be captured by SAC indicators, and if spatial models that relate biological features (typically species occurrences) to these environmental factors can be fitted fairly accurately, then SAC of environmental predictors may be used by ecological modelers to infer their scale of influence on the modeled biotic response variables.

Here we present such a novel framework (Fig. 1) to classify environmental factors according to their scale of spatial structure based on the estimation of their spatial autocorrelation (Moran's *I* and Geary *C* measures; Cliff and Ord, 1981; Legendre and Legendre, 1998 for more details see Supplementary data 1 and 2).

The classification of environmental factors is performed in order to discriminate between classes of scale, for instance between locally and regionally structured environmental factors. For example in Vicente et al. (2011) environmental factors were classified a priori as regional or local based on a theoretical framework supported by ecological theory, namely concepts from landscape ecology, (meta) community ecology, phytosociology, and biogeography. The underlying rationale was that the distribution of species is driven by processes linked to several levels of ecological complexity, and therefore expressed at different spatial scales. This type of classification is based on: (i) their scale of spatial patterning, i.e., the scale at which SAC is detected, and (ii) the ecological and environmental scale/context in which they are theoretically hypothesized to influence spatial patterns of biodiversity and other biological features (i.e., a maximum covariance between an environmental factor and a biological feature). This approach has been used by ecologists seeking a better understanding of how patterns of environmental heterogeneity influence ecological processes (Law et al., 2009) but, to our knowledge, this has never been applied to classify environmental factors in the context of distribution modeling. We illustrate this novel framework by distinguishing "regional" from "local" predictors and use them in a complementary way to predict species distributions. The terms regional and local are used here in a flexible sense and may not directly relate to formal spatial scales since they are inherently dependent of the actual spatial extent of analysis.

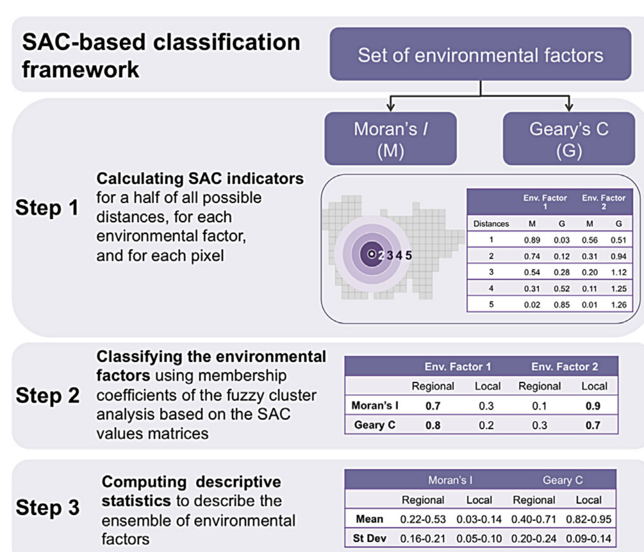

Fig. 1. Using a set of environmental factors, Moran's *I* and Geary *C* indicators were calculated for each environmental factor. (Step 1). Then, the calculated SAC values were used to perform a fuzzy cluster analysis, obtaining a membership coefficient of each environmental factor to each group/scale (Step 2). Finally, from the values of Moran's *I* and Geary *C* descriptive statistics were computed to describe the range of possible values of the ensembleof regional and local environmental factors. "Mean" refer to the range of means, and "St. Dev." corresponds to the range of values for standard deviation (Step 3).