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ECo: A new measure evaluating the degree of consistency between environmental factors and spatial arrangement of species assemblages

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ABSTRACT

We introduce a measure of Environmental Consistency (ECo), which assesses the probability of reducing homogeneity in the environmental factors within a species' distribution by randomly displacing its occurrences. ECo is computed by applying null model analysis to a species incidence matrix where each locality is associated with a set of environmental values. Environmental homogeneity is measured, for each species, as the average multiparametric distance between any pair of localities where the species occurs. ECo can account for the effect of species interactions and resource availability by using different null models that permit or forbid occurrence displacements altering species local abundance or species prevalence. ECo provides researchers with a flexible statistical framework to address a wide range of ecological and biogeographical issues. We investigated in depth the properties and the potentialities of ECo, showing how it integrates the concepts of Eltonian and Grinnelian niches. We demonstrate that a close relationship exists between niche breadth at species level and environmental consistency of species assemblages. In addition, we provide evidence that ecological consistency is closely related to species range. A software to compute ECo is freely available at http://forest.jrc.ec.europa.eu/download/software/eco.

1. Introduction

Investigating the causes of species distribution is a primary goal in ecology, because it has many applications in both theoretical and applicative fields (Cox and Moore, 2004). Current distributions are determined by the interaction among historical (paleogeographical and paleoecological) causes, inter-specific relationships, and species' environmental needs (Woodward, 1987; Huntley, 1999).

The influence of history on species biogeography can be investigated by searching for non-random patterns in species per site matrices. Nestedness and modularity are typical examples of patterns originating from historical processes (Fortuna et al., 2010). Similarly, significantly high or low species co-occurrence values in species per site matrices may indicate, respectively, positive or negative inter-specific interactions (Stone and Roberts, 1990; Bertness and Callaway, 1994; Gotelli, 2000; Hausdorf and Hennig, 2007).

When environmental variables can be measured at sites of a species' occurrence, Ecological Niche Modelling (ENM) can be used to estimate dimensions of the species' fundamental ecological niche. Then, these estimates can be used to reconstruct species distribution by area suitability (Soberón and Peterson, 2005; Guo and Liu, 2010). The two approaches, i.e. the examination of species per site matrices and ENM are somehow complementary. Yet, the conceptual integration of species/locality analyses and ENM is not straightforward.

Here we describe a new ecological measure that aims at this purpose by providing information about the influence of environmental variables on the spatial arrangement of species assemblages. We called this index ECo, which is the acronym for 'Environmental Consistency', as it measures, in practice, how consistent are the environmental/climatic characteristics of the localities where each species of a species assemblage occurs. This is achieved by combining the valuable information provided by species/locality matrices with environmental/climatic data. Using different null models, ECo makes it possible to discriminate between the effect of environmental factors, and the constraints related to the spatial

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structure of species distribution (i.e. local species richness, and species prevalence).

ECo can find applications in various ecological fields. For example, as we will show in our case studies, it makes it possible to investigate general ecological patterns such as the potential relationships between ecological specialization and species range size, or how much individual species' niche breadth affect the overall environmental consistency of a species assemblage. Thanks to this latter ability, ECo might be also useful to investigate the relative importance of environmental filtering and species interactions in determining community assembly rules. Moreover, the degree each species contributes to the overall environmental consistency of an assemblage constitutes also a robust measure of how much environmental/climatic variables affect the distribution of that species, and thus can be used to orient and/or justify the use of ecological niche modelling approaches.

ECo may also be useful in conservation biology. For instance, assessing how much environmental/climatic characteristics affect the spatial structure a species assemblage can help identifying species assemblages and localities most susceptible to habitat degradation and climate change.

2. Description of the ECo algorithm

The basic functioning of the ECo algorithm is described in Fig. 1. Species occurrences are first used to compile a matrix of presence/absence of species (rows) per areas (columns). A set of desired environmental (for example, values of elevation, soil pH, salinity, etc.) and/or climatic variables (for example air temperature, precipitation, etc.) is then associated with each area. Each species occurrence (presence in a row) is therefore linked to the values of each variable in the areas (column) in which the species is found. These variables are used to compute distances (for example Euclidean) between any possible pair of occurrence of a given species. Finally, these pairwise values are used to compute an overall (average) distance among all the species occurrences in a given row. If all occurrences are placed in areas (columns) that have identical values for all measured environmental variables, the average distance between species occurrences will be 0, i.e. the ecological consistency for that species (row) will be maximum. Otherwise, the average distance will be higher than 0. Increasing average distances indicate decreasing consistency between the distribution of the considered species (row) and the variables associated with the areas (columns).

We may now imagine to randomly modify the matrix by adding or removing the presence of a species in a given area, i.e. by replacing a 0 in the matrix with a 1 or vice versa (in the following, we will refer to this kind of replacement simply as a "shift"). This may increase, decrease or leave unaltered the average distance computed between the occupied cells of the row (i.e. of the species) involved in the shift. In a matrix where occurrences are placed with a strong consistency with respect to environmental variables, a random shift will tend to increase the average distance. By contrast, in a matrix where the placement of occurrences in columns (i.e. of species in localities) is not or weakly in agreement with the corresponding environmental variables, a random shift would have the same probability of decreasing, increasing or leaving unaltered the overall ecological distance for the row. Thus, we define the

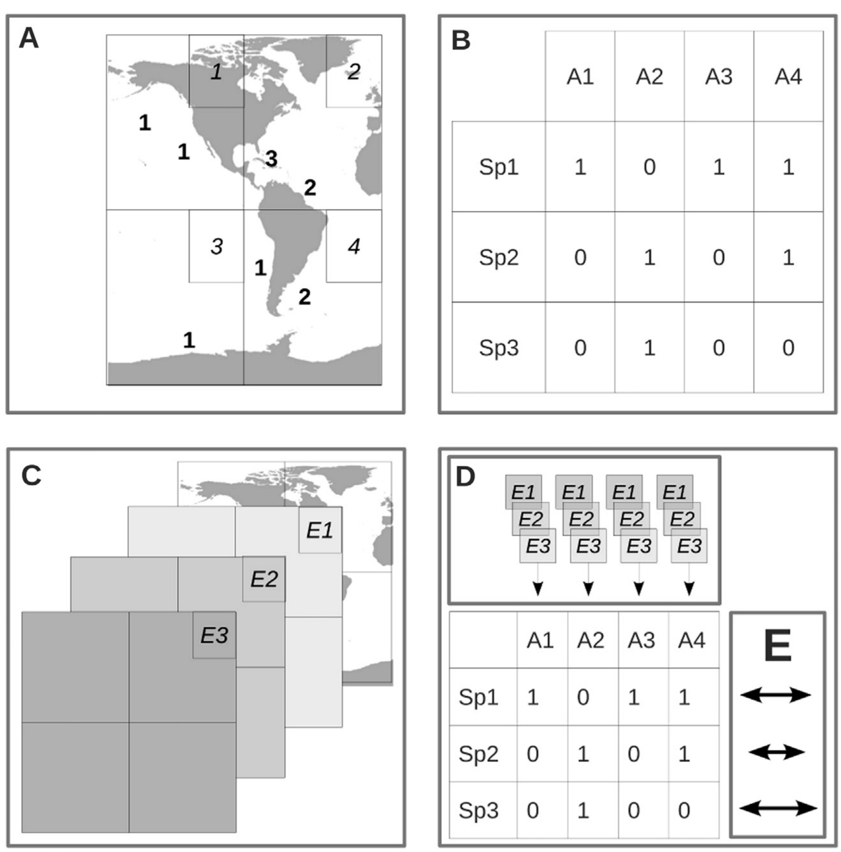

Fig. 1. Functioning of ECo algorithm. Species occurrences (A: species 1–3 are identified by numbers in roman, areas 1–4 are identified by numbers in italic) are used to compile a binary species (rows) per areas (columns) matrix (B). A set of desired environmental variables is associated with each area (C: layers E1, E2, and E3). Each species occurrence (presence in a row) is therefore linked to the corresponding environmental variables of the areas (column) from which the species is known (D). Using these variables it is possible to compute a distance (for example Euclidean) between any possible pair of occurrences in a row, and to use these pairwise values to compute an overall (average) distance (E) among all the species occurrences in a given row.