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Appendix 1

Quantifying trait importance in the prediction of species relative abundances using a Maxent model

Shipley et al. (2006) recently developed a maximum entropy (maxent) model that can predict the relative abundances of all species occurring in a regional pool within a local community. This model gives the Bayesian probability (i.e. the predicted relative abundance) of a randomly chosen individual in a local community belonging to each of the species from the species pool as a function of its traits; it is possible to include binary or multistate qualitative traits in the maxent model by appropriate factor coding. These probabilities will change across plots because the environmental conditions in each plot create different selective pressures, which select for different trait combinations.

Formally the relative abundance distribution (for a given local community) is obtained in two steps. First, one determines all those relative abundance distributions (the feasible set) that agree with the measured constraints. One then chooses from this feasible set of distributions the one that has the maximum entropy and that therefore does not implicitly imply any additional constraints (Shipley 2009, 2010). The constraints corresponded to the community-level trait composition as measured by community weighed means (*CWM*, Eq. 1, (Diaz et al. 2007)).

$$CWM_{jk} = \bar{t}_{jk} = \sum_{i=1}^S o_{ik} t_{ij} \quad (1)$$

Where o_{ik} is the observed relative abundances of species i in plot k , t_{ij} is the value of trait j for species i and \bar{t}_{jk} is the observed community-weighted mean value of trait j in community k . This was done after standardizing each trait j to unit variance in order to quantify trait variation in common units of standard deviations. One then chooses predicted relative abundance values (p_{ik}), i.e. Bayesian probabilities, that both agree with the observed constraints, thus $\bar{t}_{jk} = \sum_{i=1}^S p_{ik} t_{ij}$

and that maximizes the entropy: $H_k = -\sum_{i=1}^S p_{ik} \ln p_{ik}$.

The solution is a generalized exponential equation (Eq. 2) that gives the predicted relative abundance of each species i in local community k : (p_{ik}) as a function of its $j=1, \dots, T$ traits (t_{ij}) and a series of constants (λ_{jk}) (Lagrange multipliers) that are estimated during the entropy maximisation process. Each Lagrange multiplier quantifies by how much a unit change in a particular trait j is associated with a proportional change in the predicted relative abundance (p_{ik}) in local community k when all other traits are kept constant.

$$p_{ik} = \frac{e^{(\lambda_{0k} + \sum_{j=1}^T \lambda_{jk} t_{ij})}}{\sum_{i=1}^S e^{(\lambda_{0k} + \sum_{j=1}^T \lambda_{jk} t_{ij})}} \quad (2)$$

Formally this is defined as: $\partial p_{ik} / \partial t_{ij} = \lambda_{jk} p_{ik} (1 - p_{ik})$. A positive λ means that species with larger values for the trait are more abundant when holding all other traits constant, $\lambda < 0$ means that species with larger values will become less abundant when holding all other traits constant and $\lambda = 0$ value means that there is no directional selection on the trait and variation in the trait does not change abundance. Therefore lambda values inform us both about the direction and the force of selection occurring during community assembly and quantify the expected proportional change in relative abundance associated with a unit change in the trait. Moreover, since traits are standardized to unit variance prior to analysis, it is possible to rank traits according to their

relative importance by looking at the absolute value of lambda. The lambda values that solve Eq. 2 were obtained using the improved iterative scaling algorithm of Della Pietra et al. (1999) and implemented in the `maxent()` function of the FD Library of R (Laliberté and Shipley 2010). These lambda values are those that maximize simultaneously the (relative) entropy and the likelihood of Eq. 2.

References

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