## Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple ordination axes

Steven J. Presley · Christopher L. Higgins · Celia López-González · Richard D. Stevens

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Abstract Techniques to evaluate elements of metacommunity structure (EMS; coherence, species turnover and range boundary clumping) have been available for several years. Such approaches are capable of determining which idealized pattern of species distribution best describes distributions in a metacommunity. Nonetheless, this approach rarely is employed and such aspects of metacommunity structure remain poorly understood. We expanded an extant method to better investigate metacommunity structure for systems that respond to multiple environmental gradients. We used data obtained from 26 sites throughout Paraguay as a model system to demonstrate application of this methodology. Using presence-absence data for bats, we evaluated coherence, species turnover and boundary clumping to distinguish among six idealized patterns of species distribution. Analyses were conducted for all bats as well as for each of three feeding ensembles (aerial insectivores, frugivores and molossid insectivores). For each group of bats, analyses were conducted separately for primary and secondary axes of ordination as deWned by reciprocal averaging. The Paraguayan bat metacommunity evinced Clementsian distributions for primary and secondary ordination axes. Patterns of species distribution for aerial insectivores were dependent on ordination axis, showing Gleasonian distributions when ordinated according to the primary axis and Clementsian distributions when ordinated according to the secondary axis. Distribution patterns for frugivores and molossid insectivores were best described as random. Analysis of metacommunities using multiple ordination axes can provide a more complete picture of environmental variables that mold patterns of species distribution. Moreover, analysis of EMS along deWned gradients (e.g., latitude, elevation and depth) or based on alternative ordination techniques may complement insights based on reciprocal averaging because the fundamental questions addressed in analyses are contingent on the ordination technique that is employed.

Keywords Biogeography · Boundary clumping · Coherence · Reciprocal averaging · Species composition