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A multi-species co-occurrence index to avoid Type II errors in null model testing

Pairwise species co-occurrence metrics along with community matrix randomization algorithms have been widely used in null model testing to detect significant signals of species association or dissociation and infer different types of biotic interactions between species (e.g. facilitative or antagonistic). However, these tests ignore co-occurrence patterns involving multiple species simultaneously, which could reflect functional guilds or motifs composed of multiple species within the community. Null model tests without considering multi-species co-occurrence could lead to false negatives (Type II error) in detecting non-random forces at play. Here, we present a new, multi-species co-occurrence index that quantifies the joint occupancy of two or more species simultaneously in a community. We derive the mean and variance of the proposed joint occupancy index to facilitate testing for statistical significance in observed co-occurrence patterns. Using this joint occupancy index along with standard randomization algorithms in null model testing, we identify nine possible archetypes of multi-species co-occurrence. The application of the index to a large database of 289 species-by-site community matrices reveals that some archetypes are more frequent than others, four archetypes not being observed. We show that null model testing using pairwise co-occurrence metrics could indeed lead to severe Type II errors in two specific archetypes. As such, we recommend and advocate for the use of the proposed joint occupancy index for null-model-based inference of species association and biotic interactions.