COMMENTARY

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'Null model analyses are not adequate to summarise strong associations: Rebuttal to Ulrich et al. (2022)' by Mainali & Slud (2023)

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Mainali et al. (2022) proposed a metric of association in pairwise co-occurrence data (termed affinity) based on a probabilistic approach previously developed by Veech (2013). Ulrich et al. (2022) commented on this proposed metric, concluding that it (1) does not advance over Veech (2013), (2) performs equivalently to common metrics of co-occurrence used in combination with a null model that randomises the matrix of species occurrences with fixed row and equiprobable column totals (the FE model of Gotelli, 2000) and (3) might only work reliably on matrices of limited species richness.

In their rebuttal, Mainali and Slud (2023) repeat their claim that traditional indices have fundamental flaws while their affinity metric based on a hypergeometric probability distribution provides a better estimate of deviation from expected co-occurrences. However, they admit that affinity and Veech (2013) probabilities are nearly identical except for very low (significant) or very high probabilities ($p < 0.05$ or $p > 0.95$). Their figures 1c and S1 indicate that even at these low probabilities both approaches return equivalent results. Consequently, we conclude that affinity inherits the potential shortcomings of null models that do not constrain column totals (or equivalent probabilistic approaches). Because these models assume that species richness is equiprobable in all sites, results covary with numbers of species, sites and occurrence totals (Ulrich et al., 2018).

More importantly, Mainali and Slud (2023) admit that affinity cannot be calculated for tied and fully nested ranks, but they downplay this problem as being a 'small sample phenomenon requiring care in reporting'. Given that ecologists and biogeographers always take care, the issue is not trivial. In fact, this is a major problem because empirical matrices typically contain many species pairs with tied and nested ranks, effectively excluding the use of affinity for larger matrices. For example, in their own analysis of the popular set of matrices compiled by Atmar and Patterson (1995), Mainali and Slud (2023) reported that tied and nested ranks occurred in 83% of the species pairs. This means that affinity was properly computed only for 17% of species pairs. For the remainder, the index was set to an arbitrary value of $\pm \log(2N^2)$ (the purple and red clusters of points in Mainali & Slud, 2023; figure 1a). How can Mainali and Slud (2023) claim that their index is more 'novel' or 'informative' than available methods, when it cannot even be computed for the large majority of real-world cases?

Finally, we reiterate that 'true' probabilities as defined by Mainali and Slud (2023) are based on a single null distribution that assumes species occurrences are fixed, but that species richness per site can vary equiprobably (despite well-known constrains such as those imposed by species-area relationships). The interpretation of metric values and co-occurrence probabilities always depend on explicit assumptions about row and column constraints and filling algorithms that define a particular null model (Gotelli, 2000; Strona et al., 2018). Identical co-occurrence patterns might be probable or improbable depending on the constraints imposed to define a particular null model. We emphasise that any metric that is associated with a fixed null assumption and that allows for a single interpretation only, might miss important aspects of community assembly.

AUTHOR CONTRIBUTIONS

Werner Ulrich wrote the first draft, Giovanni Strona performed analyses and all authors contributed to the final version.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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