

## RESPONSE TO STEPHENS ET AL. (2020)

A. TOWNSEND PETERSON<sup>1</sup>, JORGE SOBERÓN<sup>1</sup>,  
JANINE M. RAMSEY<sup>2</sup> AND LUIS OSORIO-OLVERA<sup>1,3</sup>

<sup>1</sup>*Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045 USA*

<sup>2</sup>*Instituto Nacional de Salud Pública, Tapachula, Chiapas, México*

<sup>3</sup>*Centro de Cambio Global y Sustentabilidad, CONACyT, Villahermosa, Tabasco, México*

Readers of the contributions to this debate will no doubt be daunted by the length and density of the presentation of the co-occurrences-imply-interactions methodology by Stephens et al. (2020). That is, Stephens et al.'s (2020) presentation of the inspiration, concepts, and justification for the methodology is presented over too many pages, including considerable amounts of text that is lateral, peripheral, and/or extraneous to the main challenge of presenting, justifying, and defending a novel methodology in a debate. The overwhelming length and detail are distracting, and we are concerned that it may obscure certain crucial details (and failings) of the authors' arguments.

The argument for the “co-occurrences-imply-interactions” methodology centers on a rather peculiar set of definitions. That is, “biotic interactions” are accorded a rather holy place in ecology, being the central and defining processes in the entire field of community ecology (e.g., Mittelbach and McGill 2019). These interactions are defined in terms of the precise roles (e.g., predator-prey, pathogen-reservoir), or of relative benefits to each of the interacting species (e.g., symbiosis, mutualism, parasitism, etc.), which are then grouped more broadly based on impact, into positive, neutral, and negative interactions.

Stephens et al. (2020), however, have opted to recycle and redefine this rather important term in ecology, so that it fits with what can be estimated with their methodology. That is, they stated:

*In our methodology, an interaction is defined by quantifying the degree of co-occurrence of variables—biotic or abiotic—relative to that expected in the absence of the interaction.*

They also stated:

*We have defined an interaction as a deviation from an appropriate null hypothesis of the spatial distribution of a taxon conditioned on one or more abiotic and/or biotic variables.*

Clearly, Stephens et al. (2020) are using a definition of “interaction” that is quite distinct from that which is in universal use in ecology. Rather than a definition that responds directly to the biological processes in question, such as one animal eating another (= predation), or an animal pollinating a plant, they have re-defined “interaction” to refer simply to spatial co-occurrence. This empirical and observable definition might be useful were it to be termed “spatial attraction,” or some similar term, but it is quite deceptive and confusing because of its re-definition of such an important term in ecology.

Indeed, Stephens et al. (2020) are aware of the challenges involved in the inferences that they are attempting to make. They stated:

*In ecology, as elsewhere, co-occurrences are a necessary condition for an interaction. For a predation event to occur, the predator and the prey must be in the same place at the same time. Similarly, for pollination, or any other type of ecological micro interaction.*

We concur. Obviously, co-occurrence is necessary for an interaction to occur naturally. Predation or pollination cannot occur if the two species are not ever together in the same place. Still, more information is necessary if one is to be able to make conclusions about the type of interaction—notice that, in the quotation above, both predation and pollination are mentioned, and both require co-occurrence to be positive, and yet one is a negative interaction and the other is a positive interaction. Quite simply, more information is needed before one can make any concrete conclusions about the type, or even the general direction of the interactions between species.

Two recent empirical papers exploring these issues (Sander et al. 2017; Freilich et al. 2018) paint a very different picture, with the authors being careful and specific when reporting and interpreting their results. For instance, Freilich et al. (2018) concluded,

“Thus, as observed in previous empirical and theoretical studies, patterns of interactions in co-occurrence networks must be interpreted with caution.” Similarly, Sander et al. (2017) stated:

*Our findings suggest that although these methods hold some promise for ecological network inference, presence-absence data does not provide enough signal for models to consistently identify interactions, and networks inferred from these data should be interpreted with caution.*

As such, other research groups have arrived at ambiguous and non-conclusive results in their empirical studies as a result of the many factors hindering detection of a proper, actual, biologically-defined interaction. We believe that this non-conclusion is not a function of the simpler need for better software, but rather is illustrative of careful and appropriate caution in interpretation of results.

To summarize, although Stephens et al. (2020) contribute to assembling an interesting and useful analysis tool in the SPECIES site, we disagree strongly with them as regards the interpretation that co-occurrence signals can predict species interactions. Although Stephens et al. (2020) have reinterpreted co-occurrence signals as “interactions,”

co-occurrence alone does not carry sufficient information to permit rigorous interpretation as predictions of actual individual contact or different types of interactions. Rather, co-occurrence should be interpreted as exactly that: co-occurrence that signals geographic distributional coincidence. Interpretation as actual interactions—and determining types of interactions—requires further information that is generally unavailable from simple occurrence data.

#### LITERATURE CITED

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