

REFLECTIONS ON THE CHALLENGE OF INFERRING ECOLOGICAL INTERACTIONS FROM SPATIAL DATA

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PREAMBLE

Dr. Luis Escobar asked me to provide a joint review of the submissions by Stephens et al. (2019, this issue) and Peterson et al. (2019, this issue) to this debate. I pulled thoughts together, but by the time I sent them, he had received other reviews and made an editorial decision. However, he felt my perspective might nevertheless warrant publishing as a commentary alongside these two pieces. My review was of the original submissions, which are now appearing with minor, mainly cosmetic changes. I have edited the text of my review only lightly, and added a few additional thoughts and pertinent references. Neither group of authors has seen my commentary, and so I am responsible for any omissions or lapses in interpretation.

INTRODUCTION

The basic bone of contention between the two contributions, by Stephens et al. and Peterson et al., is whether or not one can make inferences about interactions among species based on spatial patterns of co-occurrence (or not). This is of course a long-standing issue in ecology, going back at least to the ‘assembly rule and null model debate’ that raged in the 1970s and 80s (e.g., Diamond 1975, Connor and Simberloff 1983; see Sanderson and Pimm 2015, for a review of this debate). In this commentary, I first briefly summarize the central points of the two papers, and then note points on which I disagree with each of them. I note at the outset that I respect all the authors.

Stephens et al.

Stephens et al.’s paper has a grandeur about it, as it deals with issues such as the meaning of ‘interactions,’ not just in ecology and biogeography, but more generally across the sciences. They make particular reference to physics and the four fundamental forces of nature, and define an interaction to exist if the spatial positions of two objects of study differ from a null expectation, across an ensemble of observations. They reflect briefly on the relationship

between niche concepts and interactions, and touch on the issue of direct vs. indirect interactions. The bulk of the paper is devoted to developing a metric of co-occurrence, called epsilon, with a focus on binary information (presence/absence), and a Bayesian framework for making inferences about interactions.

They champion the use of a software platform (SPECIES), and present intriguing examples. One of these is for the bobcat (*Lynx rufus*) in Mexico, in which they argue that including information about other mammals greatly increased the predictive power of a distributional model. They then summarize previous work they have done on zoonoses, where the problem is to identify vectors and hosts associated with a particular pathogen. I read the manuscript with interest, and found their approach and examples intriguing, if not entirely convincing, for reasons laid out below.

Peterson et al.

Peterson et al. argue that patterns of co-occurrence shed no light at all on underlying process. They point out that large and poorly understood sampling biases exist in the kind of biodiversity data that Stephens et al. use. They provide some specific critiques of the metrics and the notation used by Stephens et al. They then examine the example of co-occurrences of trogons and scarab beetles across Mexico, using the methodology of Stephens et al., and find examples of tight co-occurrence (or non-co-occurrence). Still, nothing in the natural history of these taxa suggests either strong mutualisms or competition. They likewise examine two taxa for which independent evidence of interactions exists – desert rodents, and felid cats. In the former case, the epsilon of Stephens et al. indicates positive interactions, yet experiments show negative interactions. In the latter case, different results emerge from different databases. Finally, Peterson et al. walk through some examples from epidemiology, suggesting caution in the inference of interaction from co-occurrence data, as assessed by the Stephen et al. epsilon metric.

DISCUSSION

Stephens et al. *define* interactions in terms of co-occurrence, and then try to identify interactions from data on spatial distributions. They use an analogy with physics to understand ecology (in their Box 1), and state that fundamental interactions in physics are ‘direct’, whereas other interactions are ‘indirect’. They note that the fundamental data of physics are not just positions, but rather changes in positions over time, e.g., orbits in astronomy. Spatiotemporal data—i.e., trajectories—provide much stronger information about presumptive causes of physical phenomena, than just spatial pattern data. The classical celestial mechanics of Isaac Newton focused on planetary orbits, i.e., spatiotemporal data, not the static patterns of the stars. In Newtonian mechanics, if the initial conditions of non-interacting particles happened to have them arranged in some spatially correlated pattern with equal velocities and trajectories pointing in the same direction, with equal forces acting on them, as time goes on, the spatial correlation structure will remain unchanged. In other words, static measures of co-occurrence in a snapshot could reflect the imprint of history and shared responses of the particles to their physical environments, not ongoing interactive processes. This general issue is recognized by the authors, I think, but ends up somewhat lost in the flow of the paper, which focuses on analyses of static spatial patterns, not dynamical spatiotemporal patterns. All of these remarks have analogues in ecology. When available, spatiotemporal data provide much more powerful insights into processes than do static spatial data.

Moreover, interactions in particle physics do not consist just of changes in spatial position. The weak force for instance can flip the ‘flavor’ of quarks—important in processes such as beta nuclear decay, in which a neutron is converted to a proton. This is not a trivial process—it powers the stars. In other words, interactions in physics change *state variables*, not just spatial positions. Again, this point holds in ecology, as well.

Stephens et al. include a paragraph touching on population genetics. Their use of terms like ‘epistasis’ and ‘linkage’ unfortunately deviates from accepted usage of population genetics. However, leaving this terminological issue aside, it is worth noting that there are protocols in molecular population genetics that do analyze static patterns to infer a process—in particular, natural selection (e.g., the

McDonald-Kreitman test for detecting the presence of selection on amino acid sequences, see Ch. 6 in Charlesworth and Charlesworth 2010) The authors also refer to text-mining protocols in linguistics, such as inferences about syntax or semantics from positions of words in sentences. Deciphering ancient languages requires interpreting ‘interactions’ among script elements arranged in a linear spatial pattern. These analogies with other disciplines do suggest that useful information about causal processes may be buried in static ecological patterns. However, such inferences rely not just on pattern analysis, but also on prior knowledge about processes (e.g., how living languages work).

There are challenges in executing the Stephens et al. approach in ecology, beyond those mentioned by Peterson et al. Unlike physical forces, ecological interactions are often context dependent. For instance, the qualitative sign of an indirect interaction of two prey species via a shared predator depends on (among other factors) whether or not that predator is constrained in its numerical response by higher-order predators. Such constraints could prevent the occurrence of apparent competition (Holt and Bonsall 2017), and turn the indirect interaction from (-,-) to (+,+). Quantitatively, even without a change in interaction sign, the impact of species A on species B depends on the abundance of species A, so mere co-occurrence is at best a crude assay of the strength of their interaction. In addition, interactions depend upon abiotic conditions (Dunson and Travis 1991) and networks of interactions can vary along environmental gradients (Pellissier et al. 2018). Hence, considerable contingencies likely exist in the strength and even signs of interspecific interactions, implying spatial and temporal variability in interactions among many species. The protocol of Stephens et al., however, seems to assume that interactions are fixed (if I understand it correctly).

Ecologists by and large recognize the inherent difficulty in inferring interactions from descriptive data, and many authors are actively engaged in developing methods to do so, while recognizing the difficulties (e.g., Cazellas et al. 2015; Sander et al. 2017). Stephens et al., however, do not engage with that literature, nor do they attempt to relate their proposed measure or definition of interaction to other metrics of interaction strength that are used widely in the ecological literature (see, e.g., Novak et al. 2016). This linkage might be a goal in future developments

of their methodology. Metrics of interactions should be linked to basic population dynamics—what is the effect of individuals of species A on *per capita* birth, death, movement, and stage transition rates of individuals of species B? This information might lead to changes in spatial relationships, but not always. A well-mixed chemostat for instance by definition rapidly destroys any spatial structure of the populations it contains, but there can be (for example) strong resource competition among algal species because one competitor reduces the mean-field abundance of a shared resource needed by another. Under a giant canopy tree, spatial locations of each individual in a cluster of understory herbs may be driven by microenvironmental germination requirements, but the rate of their individual growth and ultimate seed production may be governed by light competition with that tree. This point matters at larger spatial scales, because seed production and dispersal are required by the herb for colonization of empty sites. Nonetheless, the interspecific interaction need not be reflected in local spatial patterns under the dominant light competitor at all; instead, the interaction alters the internal states of the herbs.

One issue largely ignored by Stephens et al. is the importance of background spatial structure in the environment, and spatial autocorrelation. Imagine two species that do not interact but that have distinct responses across a gradient, with one species more prevalent at one end, and the other species at the other. Using the metric of Stephens et al. one would (I think) conclude there was a negative interaction at play—but this conclusion would be incorrect. There needs to be attention paid to spatial autocorrelation and related issues. Bar-Massada and Belmaker (2017) showed for tree species in the United States that co-occurrence varied across gradients, and conclude that pairwise analyses of co-occurrence (and thus, interactions) are scale-dependent.

Peterson et al. crisply lay out several problems in the Stephens et al. protocol. However, I do think some of their categorical claims need to be qualified. One point about ‘inference’ is that inference is not ‘either/or.’ One can have a tentative inference, a weak inference, a reasonably convincing inference, and even a strong and nearly irrefutable inference. Clearly, the latter is best, but that does not mean the former are worthless. So when Peterson et al. state “... patterns of co-incidence and non-co-incidence are no indication of the processes causing them” (cit-

ing Bell 2005), I think that that is too strong a conclusion. In conjunction with other information about a system (e.g., natural history), such patterns can provide some indication that something is going on.

Scientific inferences should when possible draw on a wide array of evidence, not just single sources, which sometimes can be quite convincing. Both sets of authors refer to the celebrated dispute back in the 1970s between Jared Diamond on the one hand, and individuals like Dan Simberloff and Ed Connor, on the other, about inferring competition between species based on distributional patterns. Neither paper refers, however, to the recent, incisive book by Sanderson and Pimm, *Patterns in Nature* (2015), which reviews that entire debate, and lays out more sophisticated versions of null models than were used in the past. Sanderson and Pimm provide a reasonably convincing case that some classic examples of checkerboard distributions of related species, and distributions along gradients, indeed reflect competition. The precise specification and analysis of appropriate null models is crucial—and non-trivial.

If one could not use patterns of co-occurrence over time to make tentative inferences about causal processes, most of paleoecology would become an intellectually derelict discipline. Wisz et al. (2013) cite many examples in which biotic interactions have large-scale, biogeographic consequences, many of which they drew from the paleontological record. The spread of *Homo sapiens* across the globe, along with our (alas) symbionts such as rats, have had huge consequences for the persistence and geographic ranges of (for instance) large-bodied and highly edible vertebrates, and particularly for flightless birds. Cases like this one of course involve not just patterns in spatial data, but spatiotemporal data (e.g., piles of moa bones in prehistoric sites of human habitation in New Zealand).

One issue missing in this interchange is a thorough consideration of time scales. A tight mutualism or asymmetric facilitation implies that species A cannot be present over even a single generation without species B. This effect should be manifested in ongoing interactions matching current distributions. By contrast, competition and predation can lead to elimination of species co-occurrences—the interactions may all be in the past, not in the present (dubbed “the ghost of competition past” by Connell 1980). The point is that current distributions reflect not just current interactions, but *past* interactions. Inferring in-

teractions from current distributions requires paying attention to ecological memory, as well as drawing on other avenues of ecological understanding.

There are known strong positive associations between species that surely have distributional consequences. For instance, many epiphytic orchids cannot germinate and survive as seedlings without specific mycorrhizal fungal symbionts. There are ecological niche models for orchids in the literature, which successfully predict the distribution of orchid species based on climatic variables (along with bark and other habitat factors). However, it is a leap of faith to conclude that those models portray merely direct ecophysiological responses of the orchid to those specific abiotic factors—they could equally well involve responses of the orchid’s required symbiont. One problem in conservation of endangered orchids is that getting them to germinate and grow can be quite tricky, which apparently reflects problems in getting conditions ‘just right’ for the symbionts, as well as ensuring they are present in the first place. In this sense, a beautifully verified ecological niche model that uses only abiotic variables, might well have an underlying causal dynamic involving strong interspecific interactions. The protocol developed by Stephens et al. could potentially provide a valuable tool helping to sort among initial hypotheses about potential mutualist partners in a community, I think (given some prior natural history or trait data).

The exercise by Peterson et al. relating distributional data on trogons to scarabs is, at best, underwhelming. One always has background hypotheses at play (e.g., the debate between Diamond and Simberloff focused on biogeographically relevant and phylogenetically related bird taxa, which have similar diets and likely share parasites, and so arguably might compete), but nothing is presented here to warrant this exercise. Looking at enough taxa, across enough situations, will surely reveal some ‘significant’ associations. We all know that correlation need not imply causation, but certainly correlations can help to generate hypotheses. With respect to the bobcat, Stephens et al. provide a reasonably convincing exposition that their protocol improves understanding the determinants of the distribution of this generalist predator. It would have been instructive for Peterson et al. to focus on that case study.

Peterson et al. then present as a case study two desert rodents, a *Dipodomys* and a *Perognathus*, and show they have positive epsilon values. However,

prior experiments by Lemen and Freeman (1983, 1986) had demonstrated (according to Peterson et al.) strong competition. This outcome would seem to be a clear indication that the Stephens et al. protocol is grossly misleading. However, I looked at these papers and note that Lemen and Freeman (1986, p. 390) in fact stated that “interference competition was present but weak,” and cited studies by other authors, at other sites, *not* showing competition, or with variable results among sites. Lemen and Freeman also noted that there is a “great deal of overlap in food habitats and habitat preferences” (p. 395). So it is not surprising that at larger spatial scales, there might a positive association in the spatial distributions of these two species.

The final set of case studies examined by Peterson et al. involve epidemiology. The Stephens et al. protocol seems to overpredict host-vector-pathogen interactions. This is an important criticism. However, the epsilon metric might still help refine the pool of possibilities for identifying likely suspects; whether or not such is the case is not clear from this critique. This is the sort of system in which the gold standard of demonstrating unequivocally interspecific interactions—manipulative experiments—are likely either unfeasible or unethical. Still, it is important to reach sensible conclusions about what potential suite of vectors should be monitored by public health agencies, and any tool that can help refine our Bayesian priors about this matter should be tried repeatedly until it is found to be wanting. A quote from a forthcoming book by Ovaskainen and Abrego (in press) is apt here, however, with respect to inferring interactions from such exercises: “The results from species association analyses should always be interpreted with caution, and in light of ecological knowledge on the study system.”

I want to make a final conceptual point, relevant to both species distribution models (SDMs) in general, and the challenge of inferring interactions from static spatial data specifically. As Stephens et al. note, many authors use SDMs (correlative statistical models) to make inferences about species abiotic niches with no mention of biotic interactions, which in effect sweeps causal reasoning under the rug. Consider a thought experiment. A prey species has an intrinsic growth rate r that is a function of abiotic environmental conditions e , formally described by $r(e)$, and these conditions vary across a biogeographic region. The fundamental niche is that set of e for which

$r(e) > 0$. A generalist predator has uniform density P across that region and invariant *per capita* attack rates a ; thus, the predator is not affected by our focal prey (i.e., that prey species suffers “incidental predation,” Schmidt 2004). When rare, the prey *per capita* growth rate is $(1/N)dN/dt = r(e) - aP$. The range of the prey will include those locations for which $r(e) > aP$. However, locations outside that range include not just sites with negative $r(e)$, but also sites for which $0 < r(e) < aP$. A correlative SDM might be constructed that does a perfect job of predicting the range, based solely on abiotic variables. However, it would be incorrect to conclude that only physiological factors *cause* the range limits, as removing predators in some locations would permit persistence otherwise impossible.

Conversely, given that P is invariant, no correlation can exist with the presence or absence of the prey species. From a statistical point of view, the predator is uninformative in ‘explaining’ the distribution of this prey species. In other words, one could not reveal this important interaction based purely on co-occurrence data, along the lines of the Stephens et al. protocol. In short, my point is that “the absence of a correlation need not imply an absence of causation.”

CONCLUSIONS

It can be useful to have provocative papers published, even if flawed, and even if we disagree with them. Both of these papers are provocative. All the points I made above about physics carry over to distributional ecology. (i) The distinction between ‘direct’ and ‘indirect’ interactions depends on the fineness of resolution of information about causality. Interference competition between terrestrial plants due to allelopathy, for instance, can be represented as a direct interaction (e.g., in a Lotka-Volterra model), or as an indirect interaction mediated by the concentration of an allelopathic compound. (ii) For inferring interactions, spatiotemporal data are much more insightful than purely spatial data. (iii) Patterns of co-occurrence reflect many factors such as initial conditions (*viz.*, history) and responses to external (and possibly unmeasured) environmental factors, and interactions can occur that will not be reflected in co-occurrence data. (iv) Interactions should be expressed not just in spatial position, but in terms of all the state variables needed to capture the ‘forces’ driving dynamics of a system. Advances in remote sensing are leading to terabytes of data on the physiological states of plants

across environments (Cavender-Bares et al. 2017), and such data should be mined by distributional ecologists addressing range limits, and community ecologists teasing out interactions. It also would be valuable for metrics such as the epsilon of Stephens et al. to be evaluated with ‘virtual ecologist’ approaches (see, e.g., Zurell et al. 2010, Ovaskainen and Abrego, in press), in which one creates virtual, spatially explicit communities and ecosystems, and then beats the hell out of them with reference to assessing the utility of proposed metrics or data analytic methods. These two papers contribute to the evolving dialogue about how best to link community ecology and distributional ecology.

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CONFLICT OF INTEREST

None

REFERENCES

- Bar-Massada, A. and J. Belmaker. 2017. Non-stationarity in the co-occurrence patterns of species across environmental gradients. *J. Ecol.* 105:391-399.
- Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. *Ecology* 86:1757-1770.
- Cavender-Bares, J., J.A. Gannon, S.E. Hobbie, M.D. Madritch, J.E. Meireles, A.K. Schweiger, and P. A. Townsend. 2017. Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales. *Amer. J. Botany* 104:966-969.
- Cazelles, K., M.B. Araujo, N. Mouquet, D. Gravel. 2015. A theory for species co-occurrence in interaction networks. *Theor. Ecol.* 9:39-48.
- Charlesworth, B. and D. Charlesworth. 2010. *Elements of Evolutionary Genetics*. Roberts and Company Publishers, Greenwood Village, Colorado.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131-138.
- Connor, E.F. and D. Simberloff. 1983. Interspecific competition and species co-occurrence patterns on islands: Null models and the evaluation of evidence. *Oikos* 41:455-465.
- Diamond, J.M. 1975. Assembly of species communities. Pp. 342-444 in *Ecology and Evolution of Communi-*

- ties, eds. M.L. Cody and J.M. Diamond. Harvard University Press, Cambridge.
- Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. *Amer. Nat.* 138:1067-1091.
- Holt, R.D. and M.B. Bonsall. 2017. Apparent competition. *Ann. Rev. Ecol., Evol. Syst.* 48: 447-471.
- Lemen, C. and P.W. Freeman. 1983. Quantification of competition among coexisting heteromyids in the Southwest. *Southw. Nat.* 28:41-46.
- Lemen, C.A. and P.W. Freeman. 1986. Interference competition in a heteromyid community in the Great Basin of Nevada, USA. *Oikos* 46:399-396.
- Novak, M., J.D. Yeakel, A.E. Noble, D.F. Doak, M. Emmerston, J.A. Estes, U. Jacov, M.T. Tinker, and J.T. Wootton. 2016. Characterizing species interactions to understand press perturbations: What is the community matrix? *Ann. Rev. Ecol., Evol. Syst.* 47:409-432.
- Ovaskainen, O. and N. Abrego. In press. *Joint Species Distribution Modeling with Applications in R*. Cambridge University Press.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E. & Gravel, D. 2018. Comparing species interaction networks along environmental gradients. *Biol. Rev.* 93: 785-800.
- Peterson, A.T., J. Soberon, J.M. Ramsey, and L. Osorio. 2019. Co-occurrence networks do not support identification of biotic interactions. *Biodiv. Inf.* 17:1-10.
- Sander, E.L., J.T. Wootton and S. Allesina. 2017. Ecological network inference from long-term presence-absence data. *Sci. Rep.* 7:7154.
- Sanderson, J.G. and S.L. Pimm. 2015. *Patterns in Nature: The Analysis of Species Co-occurrences*. University of Chicago Press, Chicago.
- Schmidt, K.E. 2004. Incidental predation, enemy-free space, and the coexistence of incidental prey. *Oikos* 106:353-343.
- Stephens, C.R., C. Gonzalez-Salazar, M. Vaillalobos, and P.A. Marquet. 2019. Can ecological interactions be inferred from spatial data? *Biodiv. Inf.* 17:11-54.
- Wisn, M.S. et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling *Biol. Rev.* 99:15-33.
- Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nana Pagel, N.J., Reineking, B., Schröder, B., and Grimm, V. (2010). The virtual ecologist approach: Simulating data and observers. *Oikos*, 119(4), 622-635.