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A graphical causal model for resolving species identity effects and biodiversity–ecosystem function correlations: comment

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In a recent paper, Schoolmaster, Zirbel, and Cronin (SZC) (2020) claim "Formal causal analysis show[s] that biodiversity–ecosystem function (BEF) correlations are non-causal associations." If this conclusion is accepted as true, it suggests a reconsideration of much of our current understanding of how biodiversity relates to the functioning of ecosystems. On the surface, it is easy to spot clear signs of something problematic with SZC's presentation. They claim, for example, that (1) species richness is incapable of having a causal effect on ecosystem functioning on theoretical grounds, and (2) that trait diversity cannot be causally influenced by species diversity. These remarkable claims are counter to existing thought and evidence. We point to logical errors that lead them to a misapply causal analysis and produce erroneous conclusions.

SZC's Argument

We start with an overview of the four key elements of their logical arguments that lead them to reject existing theory (the Standard Model; e.g., Loreau 2000, Loreau et al. 2001) and to propose an alternative model (SZC's Model) for understanding BEF. We follow this with our critique of SZC's logical arguments and of their use of graphical causal modeling. We offer alternative causal diagrams that omit inappropriate components and use these to provide support for the Standard Model. Fig. 1 provides a storyboard for our examination of SZC.

Element 1: The Standard Model

SZC summarize the current biodiversity–ecosystem function (BEF) literature via a causal diagram for the "Standard Model," $B \rightarrow Q \rightarrow F$, where B is biodiversity, Q refers to functional trait diversity, and F represents ecosystem functions (Fig. 1A). In their words, "if environmental variation [E] is accounted for, then variation in species diversity causes variation in functional traits and, subsequently, ecosystem function."

Element 2: SZC's first criticism of the Standard Model

SZC state that to evaluate the causal claims in Fig. 1A, "it is necessary to recognize that… species diversity and functional trait diversity are calculated…" They go on to present a diagram (Fig. 1B) that is meant to reflect the process they might use to calculate species biodiversity (B) and trait diversity (Q) from the vectors of species abundances (**C**, indicated by boxes $s_1 \ldots s_n$) and species traits (**T**, indicated by boxes $t_1 \ldots t_n$). They claim that by representing the computation process in a diagram, it exposes a logical error in the Standard Model.

Element 3: SZC's second criticism of the Standard Model

SZC go on to say the hierarchical representation of the Standard Model (Fig. 1B) is itself fatally flawed. They state that the diagram, "makes the claim that in order to calculate trait diversity, some measure of species diversity can be first calculated and then subsequently used to calculate trait diversity, or alternatively, that measures of trait diversity can be rewritten in terms of B. This claim is simply not true for any definition of trait diversity currently used." Here they are claiming that trait diversity (Q) cannot be computed from species diversity (B) and, therefore, species diversity cannot possibly have a causal effect on trait diversity and ecosystem function.

Element 4: SZC propose an alternative to the Standard Model, which we refer to as SZC's Model

Fig. 1C represents SZC's diagram for an alternative to the Standard Model. They argue that, "In Fig. 1B, species diversity is a cause of ecosystem function via causal chain, whereas in Fig. 1C, species diversity is correlated with ecosystem function due to their joint

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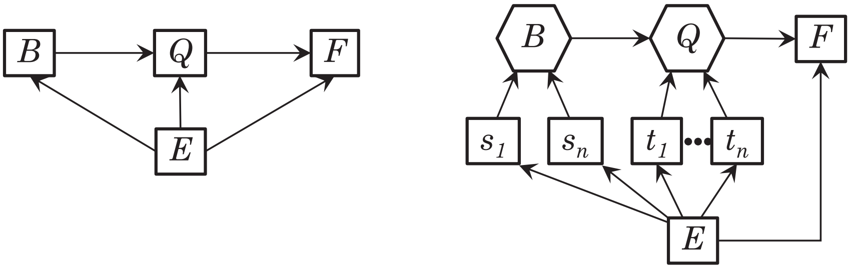
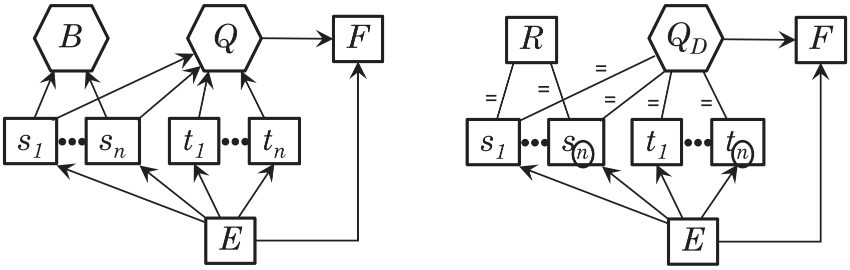
(A) SZC's single-level causal diagram for the Standard Model

(B) SZC's hierarchical diagram for the Standard Model



(C) SZC's proposed hierarchical diagram

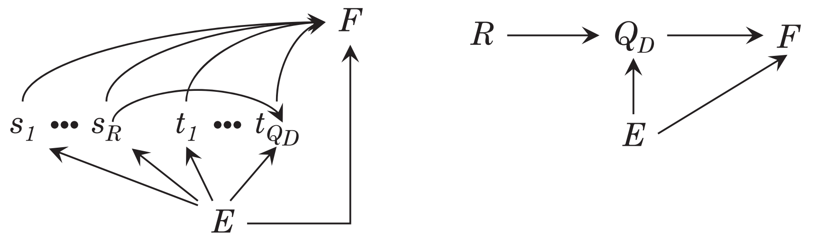
(D) SZC's diagram modified and annotated for discussion



R, richness, = the number of nonzero elements in the vector of species abundances in a sample.

(E) Hierarchical causal diagram for Standard Model

(F) Single-level causal diagram for BEF experiment, Standard Model



R is number of species in a sample.
Q_D is number of traits in a sample.

FIG. 1. (A) SZC's representation of a single-level causal diagram for the Standard Model ($B \to Q \to F$). B = a set of possible expressions of species diversity {species richness, Simpson's Index, Shannon's Index}, F = any of a set of possible ecosystem functions, Q = composite index of a functional trait vector that predicts F (e.g., $F = f(s, t)$). (B) SZC's representation of a hierarchical diagram for the Standard Model. E = environmental gradient, n = number of species encountered in a study, s_i = abundance of species i, t_i = traits of species i. (C) SZC's Model, which removes the directed arrow from B to Q in Fig. 1B. (D) Version of SZC's Model that we have modified and annotated by replacing B with R, species richness, and Q with Q_D, the number of distinct functional traits. We annotate the graph using the = sign to draw attention to arrows that actually represent noncausal, reversible computations as if they were irreversible causal effects. We further remove the heads of those arrows to correct the misrepresentation. We also circle the subscript *n*s SZC use to index the total numbers of species and traits across all samples to draw attention to the fact that those represent study-wide information rather than sample plot-level information. (E) Our representation of a valid hierarchical causal diagram for the Standard Model. Here we (a) remove computational elements, including both the computational arrows and computed quantities, (b) index species abundances (s_i) to show that the number of species in a sample = R; (c) index traits (t_i) to show that the number of traits in a sample = Q_D; (d) include a causal arrow to show that the number of traits in a sample depends on the number of species; (e) remove variable outlines to conform to the standard format for causal diagrams. (F) Single-level causal diagram for a BEF experiment assuming the Standard Model. We remove the arrow $E \to R$, reflecting the fact that R is exogenous when randomly assigned. Note hierarchical diagrams (B–E) do not reflect species interactions, the main cause of biodiversity effects in experiments.

dependence on the abundances of the species in the community." Based on this, they conclude that Fig. 1C is a valid diagram for causal analysis and Fig. 1A, B are not valid causal diagrams.

A Brief Introduction to Causal Diagrams

In order to aid our discussion of causal diagrams, we give a brief statement of their formal properties here. A more complete description of causal diagrams as well as causal calculus (the procedures used to assess causal logic) can be found in Pearl (2009) and Elwert (2013). Causal diagrams are based on directed acyclic graphs (DAGs) and represent hypotheses about the data-generating processes related to a problem of interest. Causal diagrams comprise a set of nodes representing variables, and directed arrows connecting those nodes representing hypothesized causal processes (e.g., $X \rightarrow Y$). The "directed" requirement for causal diagrams means that all one-headed arrows represent unidirectional, irreversible cause–effect relationships. Thus, we can test the logic represented by any given arrow in Fig. 1 to see if it meets the irreversibility requirement by asking the question, "If we were to manipulate the variable at the tip of the arrow (e.g., Y), would there be a potential for a response by the variable at the base of the arrow (X)?" For true causal arrows, the answer is "no" for the most fundamental reason that you cannot change conditions in the past (parent or ancestor variables) by making changes in the present. SZC include in their diagrams arrows that represent reversible relationships (noncausal calculations), but argue (in their Appendix S1) that arrows in causal diagrams do not need to represent irreversible relationships. We critique their diagram and their defense of it in detail in our Appendix S1. To be clear, we wish to emphasize that causal diagrams, when used properly, permit researchers to state their assumptions about causal structures explicitly and transparently. This can be of great benefit by allowing other researchers to examine those causal assumptions and subsequent interpretations critically, as is done in this comment.

Our Synoptic Reactions to the Four Elements of SZC's Argument

Reaction 1: The Standard Model

We do not disagree with SZC's single-level representation (Fig. 1A) of a causal diagram for the Standard Model.

Reaction 2: SZC's first criticism of the Standard Model

SZC argue that a hierarchical representation (Fig. 1B) is required to evaluate the causal claims made by the Standard Model properly. They claim this is so because it makes explicit that diversity is computed from the nonzero elements in the vector of species abundances. We do not agree with their argument. Rather, we see this as their first fundamental error, because it introduces noncausal relationships into what is supposed to be a causal diagram. We address this point in detail in Appendix S1, but essentially their decision to include species vectors and community-level properties in the diagram in the way they do, and to treat species diversity as if it is not an inherent property of the community, invalidates their diagrams as suitable for causal calculus. The reasons for this become clear when we discuss Fig. 1E, our alternative representation of a valid causal diagram.

Reaction 3: SZC's second criticism of the Standard Model

SZC argue that the hierarchical representation of the Standard Model (Fig. 1B) is invalid because it implies, "that measures of trait diversity (Q) can be rewritten in terms of B (species diversity), which is not true." We disagree with their statement for reasons given in the section entitled "Critique 1" and directly dispute it in Appendix S2.

Reaction 4: SZC's Model

Fig. 1C represents SZC's attempt to address their second criticism of the Standard Model. In this diagram, they represent the relationship among key quantities as $B \leftarrow \{\mathbf{C},\mathbf{T}\} \rightarrow Q \rightarrow F$, where **C** and **T** are the vectors of species abundances $\{s_{1..n}\}$ and traits $\{t_{1..n}\}$ across the entire study. This representation becomes the basis for the claims made in their paper, particularly for the claim that species diversity (B) is not a cause of either trait diversity (Q) or ecosystem function (F). It is also the basis for their claims that BEF experiments, "do not actually manipulate biodiversity." These claims are direct consequences of their diagram, because there is no direct ($B \rightarrow Q$) or indirect ($B \rightarrow Q \rightarrow F$) path from B to F. SZC spend a significant portion of their paper illustrating the use of causal calculus to express the empirical expectations that arise from their assumptions. This logic is carried over into their presentation of an empirical example as well as their simulation studies. We argue that their diagram (1) is not a valid causal diagram, (2) is not appropriate for their application of causal calculus, (3) does not justify their theoretical and empirical claims against the Standard Model, and (4) does not support their claim that BEF experiments are incapable of showing that diversity has a causal effect on function.

Critique 1: SZC's Model is not a Valid Causal Diagram and is not suitable for the Analyses they Perform

We use Fig. 1D to facilitate discussion of the problems we see with SZC's Model. In that figure, we annotate and relabel SZC's diagram to simplify discussion, draw attention to SZC's misuse of directed arrows for noncausal computations, and highlight other problems with their diagram. First, we replace the label *B*, which SZC use to refer to a suite of possible measures of species diversity, with *R*, which refers to species richness, the most elemental measure from their set and the one widely used in BEF experiments. We also replace *Q*, which SZC define as "functional trait composites" with Q_D, which refers to trait diversity, specifically the number of unique traits in a sample. Second, we use the "=" operator to indicate noncausal computations that are misrepresented by SZC as causal operations through their use of the "→" symbol and remove the tips of those arrows to correct the notation (see more on this in Appendix S1).

There are multiple problems with SZC's diagram. The most serious is the inclusion of noncausal hierarchical relations as if these are cause–effect relationships. Hierarchical relationships are embedded in their model by including both community-level summary properties (*B* and *Q*) and underlying species-level information (**C** and **T**). As they have drawn it in Fig. 1C, the elements of the community (**C** and **T**) are represented as causes of the properties of the community (*B* and *Q*). More specifically, SZC point unidirectional arrows, which represent causal effects by convention, from the community elements to the community properties (Fig 1C). However, community elements are not causes of community properties; rather, the two levels of information are simultaneous descriptions at different levels of detail. To illustrate this critical point further, imagine we have a warehouse filled with items and hold in our hands a ledger that accurately and instantaneously reflects the total number of items and the number of distinct types of items in that warehouse. If there are 10 types of items in the warehouse, the information about how many types of items there are exists simultaneously in the warehouse and on the ledger. The warehouse does not cause there to be 10 types of items, rather, the ledger simply reflects how many types there are, which is a quantitative property of the assemblage of items in the warehouse. We show specifically how their diagram corresponds to this analogy in Appendix S2: Fig. S1. SZC actually recognize there is a problem with their representation when they say, "Because biodiversity is a calculated variable, setting its value independently of the species abundances is impossible." What we would say instead is, "Because biodiversity is represented as a noncausal calculation in the diagram, Fig. 1C is not a valid causal diagram." Despite their recognition that the relationship between **C** and *B* in their model (shown as $\mathbf{C} \rightarrow B$) fails to represent a true causal effect, they go on to perform causal analysis using conditional independence tests as if all the arrows were true causal arrows.

The key subset of relationships in SZC's diagram (Fig. 1C) we wish to draw attention to is $B \leftarrow \mathbf{S} \rightarrow Q \rightarrow F$. This sequence presents **S** as a common cause for both *B* and *F* (through *Q*). If this were a true and complete representation, we would describe the associations between *B* and *Q* and between *B* and *F* as inherently spurious because of a common cause. As SZC put it (referring here to our figure numbers), "In Fig. [1B (Standard Model)], species diversity is a cause of ecosystem function via causal chain, whereas in Fig. [1C (SZC Model)], species diversity is correlated with ecosystem function due to their joint dependence on the abundances of the species in the community." This interpretation lies at the heart of SZC's entire paper and leads to their claim that the relationship between *B* and *F* is noncausal. However, their logic hinges on treating the directional arrows from **S** to *B* as irreversible causal effects in their conditional independence tests. Their conclusions that (1) species richness has no causal effect on ecosystem functioning and (2) trait diversity is not causally influenced by species diversity, emerge from this logic.

Aside from the misuse of arrows, there are other features of their diagram that obscure symptoms of the flaws in their approach. A critical point SZC fail to emphasize is that the number of nonzero elements in the vector **C** that are found in a sample is, in fact, species richness (*R*). SZC have chosen to represent the vectors for all species found across all samples in their diagram (i.e., *n* in their diagram is gamma diversity). This choice obscures the fact that *R* is an implicit property of samples/plots. When that is recognized, we can see that richness is actually represented twice in their diagram, once as a distinct variable *R* at the community level and again as the number of nonzero abundances within each sample plot at the species level (this is shown explicitly in Appendix S1: Fig. S2). It is this duplication of information that leads SZC to claim that *R* is unnecessary for computations of causal effects once we have used the information contained in **C**.

In Fig. 1E, we remove the inappropriate noncausal calculations from SZC's diagram. We further modify the diagram to conform to the standard format by removing box outlines for the variables, a practice designed to avoid confusing causal diagrams with structural models (see Grace and Irvine 2020). We make other changes as well. We index the vector of species abundances so as to show that the number of species in a sample = *R* and we index the vector of traits so as to show that the number of traits = Q_D. As a result of this reconfiguration, we avoid representing richness twice in the diagram, which is a key hidden flaw in their diagram. Another important change is to include a directed arrow from *R* to Q_D to show that the number of traits in a sample depends on the number of species in a sample. The result of these various changes is to make clear that even in a hierarchical diagram, it is possible to provide a valid representation of the hypothesis $R \rightarrow Q_D \rightarrow F$ (the Standard Model). Appendix S2 provides simulation results that support the representation in Fig. 1E and show how an effect of diversity emerges through the filling of niche space as one sums the contributions of species with distinct traits. It is possible and even appropriate to develop a corresponding single-level diagram (Fig. 1F), and in fact the entire literature on causal diagrams is based on single-level representations. In summary, our causal diagrams provide support for the Standard Model. Further, our critique of SZC's diagram leads us to reject their diagram because of its double inclusion of species diversity, both as an attribute of the community sample and as if it were an additional piece of information.

Critique 2: SZC Do Not Show that Biodiversity Has No Effect on Ecosystem Function. Rather, they Build the Assumption of No Effect into Their Graph

SZC subject their diagram to causal analysis using formal procedures. The results from those analyses are completely dependent on their diagram (Fig. 1C), as SZC freely admit. In their diagram they provide no pathway that points directly or indirectly from B to F. Therefore, their diagram encodes the *assumption* that biodiversity is not a cause of community structure. The tests of conditional independence presented by SZC follow from that assumption, but do not test it. SZC indicate that they recognize that their conclusions follow directly from their assumptions when they say, "Using the DAG in Fig. [1C], we will derive the statistical model required to measure a biodiversity effect … Fig. [1C] makes clear that the value of this effect is zero [as] there are no causal arrows emitted from the biodiversity node." Thus, their analyses provide no test of their model. This same criticism applies to their simulation study and analysis of field data. For this reason, we do not consider further those elements of SZC's presentation.

Critique 3: Biodiversity Experiments Illustrate Conditional Causation, not Noncausal Associations—Structural Invariance is not a requirement

SZC state, "Because the effect of the manipulation on ecosystem function will depend on trait distribution of the set of species present and not the number of species recognized under current taxonomy (i.e., it is not structurally invariant; Pearl 2009), attempting to estimate a 'biodiversity effect' on particular ecosystem functions will never find consistent results and will not be improved by multisite studies, multiscale studies or meta-analysis..." It is not true that structural invariance is a requirement for the estimation of an average causal effect (ACE) of R on F. An invariant causal mechanism is one that expresses itself to the same degree for all members of a population and under all conditions. When the ACE for a subpopulation depends on covariates of any sort (which is typical in biological systems), it is a case of conditional causation (VanderWeele 2015:57). In this particular example, there are expected to be variations in F among replicate mixtures for any given R. This in no way invalidates the estimation of a valid ACE for the biodiversity effect. More to the critical point, conditional causation is still causation and would not justify declaring $R \rightarrow F$ a spurious relationship. For practical reasons, as long as we lack important measures for Q in the sequence $R \rightarrow Q \rightarrow F$, we will have to include paths for $R \rightarrow F$ for causal modeling and prediction (Appendix S2).

Critique 4: SZC's "Actual-Cause" Arguments are Fallacious

Although SZC's arguments arise from a literal interpretation of their diagram, the authors rely heavily on verbal arguments in their paper. Most notably, they rely on so-called "actual-cause" arguments. First, they say that species richness is not an actual cause of community function; rather, it is the constituent species that are the actual cause. Second, they say BEF experiments do not actually involve manipulations of diversity, but instead manipulations of the constituent species. More specifically, they state, "… it is impossible to manipulate biodiversity directly in an experiment. So-called biodiversity manipulation experiments are *actually* manipulations of community structure." [italics added for emphasis]

Actual-cause arguments are common in human argumentation. They represent a family of fallacious arguments known as "half-truths." In this case, SZC imply that if species composition contributes to variations in F, then somehow species richness is prohibited from contributing to variations in F. Expressed more explicitly, they imply "The number of species in a community does not affect function, it is the species themselves." The reason this statement is a half-truth is because the second half of the statement is true, but the first half of the sentence is false. The reason half-truth fallacies are effective in argumentation is that the human mind tends to focus on the part of a sentence that follows a comma and dismiss the part that comes before.

A related type of half-truth found in common discussions of causes is when variables exist in a causal chain and someone argues one of the variables in that chain is the "actual" cause. In truth, all variables in a directed causal chain are causes, it is just that some are more distal to the terminal end of the chain and others are more proximal. So, if manipulating richness produces a change in the number of traits, which subsequently leads to changes in function, then richness is one of the causes in the chain of events. We argue that a more appropriate conclusion to draw regarding causal influences on ecosystem function is, "The evidence suggests that species diversity influences community function, *and* that the characteristics of the individual species in a community contribute to variations in function." This represents the form of a "whole-truth" argument.

SUMMARY

Schoolmaster et al. (2020) claim that species diversity cannot have a causal influence on ecosystem functions in natural systems or in experiments because the relationship between the two is noncausal (specifically, spurious). They reach this conclusion despite demonstrations that ecosystem functions often respond to manipulations of species richness in experimental studies, as well as other evidence. SZC further claim that they are able to prove their claim using the principles and tools of causal analysis. We draw attention to critical errors in their diagram and analyses that invalidate their conclusions. We provide background on this methodology for the reader and offer alternative diagrams with valid structures, which support the conventional understanding that species diversity can influence ecosystem function indirectly through influences on trait diversity.

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