Trends in Ecology and Evolution Mechanism, process, and causation in ecological models --Manuscript Draft--

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Dear Paul:

As per our earlier correspondence, please find uploaded our response to the comment on our paper from McGill and Potochnik. We have submitted this as a "letter", and followed the relevant length limits and other formatting requirements for this type of submission. We hope that this was appropriate.

You will see from our response that we think that there may be classes of ecological models that do not satisfy our definitions of "process-based" or "mechanistic", but that share many of the same advantages that we attribute to such models. However, we do not think that this can be said for models grouped broadly under the classification "causal", as proposed by McGill and Potochnik. Nevertheless, we believe that many ecologists hold views very similar to those expressed in their letter, so we welcome the opportunity to, firstly, clarify that the validity of our arguments do not hinge on adherence to a component-based definition of mechanism, and, secondly, specifically explain why we did not define a class of models based on whether or not they incorporated causal relationships.

The only point we did not address was their example of Newton's Law of Gravity. The extent to which physicists' concepts of "mechanism" are relevant to the biological sciences is a significant problem in its own right: the problem is just too big to tackle in correspondence arising. Since we are already on 785 words, we thought we would just let this point go and focus on the broader conceptual issues and the two ecological examples cited by our colleagues.

It is not clear to us whether our response should have its own title, or should be titled as a response to McGill and Potochnik's title, but we have submitted the MS with its own title. We are happy to change it to another format, should you prefer that.

Please note that the corresponding author (Sean) will be on leave from 30 November to 27 December.

We look forward to hearing from you.

Sincerely, Sean, Sally, Rob, and Carsten

Innovative science for sustainable use of coral reefs

Title: Mechanism, process, and causation in ecological models

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We thank McGill and Potochnik (hereafter M&P) for a thoughtful and constructive response to our paper [1]. In our view, there are two main elements to their response. Firstly, they consider our definition of mechanistic model too narrow. Secondly, they argue that the advantages that we attribute to what we term "process-based" and "mechanistic" models (PBMs and MMs) are shared by a broader class of "causal" models, which include, but are not limited to, PBMs and MMs.

In our paper, we noted that some ecologists might consider process-based models (PBMs) to be distinct from mechanistic models (MMs), while others might prefer to consider PBMs and "component-based" models to be sub-classes of MMs [1]. M&P fall into the latter camp. However, for many ecologists, the ecology of lower-level entities (typically individuals) must be explicitly considered in mechanistic explanations (see Box 2 in [1] for examples), a view shared by many philosophers of science [2-4]. We aimed to make a case for the advantages of PBMs (component-based or not) that could be embraced by ecologists regardless of the restrictiveness or expansiveness of their concept of mechanism. Thus, we defined an overlapping but not identical class of models that we hoped would be agreeable to ecologists favoring the more restrictive view. M&P instead define mechanism "...to include the processes responsible for some natural phenomenon." If these processes must be explicitly represented in a model for it to be considered mechanistic, then such models would satisfy our definition of PBMs, and thus would be accounted for already in our framework.

M&P argue that there is a broader class of "causal models" that have the benefits we describe in our paper, but that are neither PBMs nor component-based mechanistic models (hereafter CBMs). We agree with M&P that PBMs and CBMs are not the only forms of causal models, and we are open to the possibility that other classes of models represent causal structure in a way, or to a degree, that allows them to be used in many of these same ways. However, the representation of causal relationships alone is insufficient to meet this criterion. Consider a regression model fitted to observations of environmental temperature and species richness or metabolic rate. Ecologists typically use such analyses because they believe that there is a causal link between the explanatory and response variables. However, few, if any, ecologists, would claim that such models could be employed in the range of ways described in our paper for PBMs and CBMs (e.g., theoretical or virtual worlds modeling). Whether it is possible to distinguish between causal models that can and cannot be employed in such ways (for instance, by operationalizing the term "causal structure") is an open and interesting question.

M&P use the example of thermal niches to illustrate problems with a component-based conceptualization of mechanism. They note that some factors likely to be included in a model of the phenomenon, such as air temperature, are problematic if conceptualized as components. Our Interactive Question 1 presents a closely analogous example (Supplementary Information in [1]). However, not everything in a mechanistic model needs to be a component of the mechanism. For a physiologically-based model of distribution or abundance, we think most ecologists would consider the individuals to be the components, and air temperature to be an external factor influencing individuals' physiological states. If the states of individuals were explicitly characterized in such a model, it would satisfy our definition of an MM. Regardless, however, if the model of the thermal

niche characterizes "responses of proteins...protein denaturation...[and] enzyme kinematics", then the model should satisfy our definition of a PBM, since these are physiological processes.

In a second example, M&P note that body size distributions are often explained by applying the Central Limit Theorem to ontogenetic growth. If we assume that the model implied here is a product of a large number of arbitrarily-distributed random variables representing growth in a given year, then we concur with M&P that it is neither PBM nor CBM. However, it also lacks the advantages of such models that our paper highlighted. We do not think one would undertake theoretical analysis of such a model, or seek to independently estimate its parameters, for example. Moreover, we question whether "it would be absurd to search deeper for a causal explanation" for such phenomena. For instance, species-abundance distributions can be explained by reference to the Central Limit Theorem. However, theoretical analysis of process-based community dynamics models has revealed ways of using time series of species-abundance distributions to move beyond the shape and estimate the amount of variance in species abundances explained by species traits, environmental fluctuations, and demographic stochasticity [5]. In other words, they can yield insights that invocation of the Central Limit Theorem cannot.

References

1. Connolly, S.R. et al. (2017) Process, mechanism, and modeling in macroecology. Trends in Ecology & Evolution 32 (11), 835-844.

2. Paslaru, V. (2017) Mechanisms in ecology. In The Rutledge Handbook of Mechanisms and Mechanical Philosophy (Glennan, S. and Illari, P. eds), pp. 348-361, Taylor and Francis.

3. Glennan, S. (2017) The New Mechanical Philosophy, Oxford University Press.

4. Craver, C. and Tabery, J. (2017) Mechanisms in science. In The Stanford Encyclopedia of Philosophy (Zalta, E.N. ed.), Metaphysics Research Lab, Stanford University.

5. Engen, S. et al. (2011) Disentangling the effects of heterogeneity, stochastic dynamics and sampling in a community of aquatic insects. Ecological Modelling 222 (8), 1387-1393.