

in terms of component parts. If the atmosphere is a component part, how much of it is a component – 10 cm out, 20 cm? Then, do we need to include the air temperature in the burrow or of the entire home range? There is no way to draw such lines in a motivated way. It is thus forced, to the point of inaccuracy, to consider temperature and natural selection to be components of the lizard thermoregulation system. As with Newton's law of gravity, the system's context is causally central (we denote these as 'embedded causal models').

To take another simple example, the distribution of body sizes over a large taxonomic span of organisms is typically lognormal [3] (although scientists quibble over some of the precise details). Almost nobody rejects the idea that this distribution is produced by a simple application of the central limit theorem applied to a multiplicative process (ontogenetic growth). This is neither a MM nor a PBM. Yet it would be absurd to search deeper for a causal explanation.

In light of these cases and many others like them, we suggest that the explicit representation of causal structure is accomplished by a much broader class of models than just MMs and PBMs. Better, then, to focus on the general class of causal models.

A related point is that we question restricting the designation of mechanistic models to what CKCR define as a MM ('a characterization of the state of a system as explicit functions of component parts and their associated actions and interactions'). As CKCR note, there has been significant attention on mechanism in recent philosophy of science, and CKCR's description of MMs accords with prominent recent philosophical conceptions of mechanism (e.g. [4]). But other philosophers who focus on mechanism

have questioned whether nature is always decomposable and hierarchically organized [5]. This suggests that it may not always be possible to identify the contribution of component parts. We believe that most ecologists define mechanisms more broadly, to include the processes responsible for some natural phenomenon. This deviates substantially from CKCR's much more limited MM. We thus propose renaming the latter 'component-based models' (CBMs), which certainly is an important subclass of mechanistic and of causal models. This, then, leaves the word mechanism to retain its usual meaning to ecologists and avoids confusion.

By limiting mechanistic models to what we have termed CBMs and by advocating CBMs and PBMs to the exclusion of all other approaches, CKCR could be read to imply that CBMs and PBMs are the only forms of legitimate causal model. We propose supplementing the CKCR framing with three additions, shown in Figure 1 with broken lines and underlined text. Causal models should be viewed as an important subset of models containing but not limited to CBMs and PBMs. We do not provide an exhaustive list of types of causal models (and we doubt whether this could be done). But the figure does include two additional types of causal model beyond CBMs and PBMs, corresponding to the examples developed above, to illustrate the existence of other approaches.

We believe this amended view has the potential to be a consensus-based and constructive account of model-based practices in general ecology and macroecology in particular. It also applies more generally to fields investigating other complex biological systems, such as cognitive science [6].

<sup>1</sup>School of Biology and Ecology and Mitchell Center for Sustainability Solutions, University of Maine, Orono, ME 04469, USA

<sup>2</sup>Department of Philosophy, University of Cincinnati, Cincinnati, OH 45221-0374, USA

\*Correspondence: [mail@brianmcgill.org](mailto:mail@brianmcgill.org) (B.J. McGill).

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## Letter

### Mechanism, Process, and Causation in Ecological Models: A Reply to McGill and Potochnik

Sean R. Connolly,<sup>1,\*</sup>  
Sally A. Keith,<sup>2,3</sup>  
Robert K. Colwell,<sup>2,4,5</sup> and  
Carsten Rahbek<sup>2,6</sup>

We thank McGill and Potochnik (hereafter M&P) for a thoughtful and constructive response [1] to our paper [2]. In our view, there are two main elements to their response. First, they consider that our definition of a mechanistic model is too narrow. Second, they argue that the advantages that we attribute to what we term 'process-based' and 'mechanistic' models (PBMs and MMs, respectively) 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 PBMs to be distinct from MMs, while others might prefer to

consider PBMs and ‘component-based’ models to be subclasses of MMs [2]. 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 [2] for examples), a view shared by many philosophers of science [3–5]. In our original paper [2], 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’ [1]. 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 [1] 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 MMs (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 used 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 used 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 [1]. 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 (in the supplemental information online in [2]). 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 that most ecologists would consider the individuals to be the components, and air temperature to be an external factor influencing the physiological states of individuals. 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’ [1], 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 [1]. 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’ [1] 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 [6]. In other words, they can yield insights that invocation of the Central Limit Theorem cannot.

<sup>1</sup>Marine Biology and Aquaculture, College of Science & Engineering, and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

<sup>2</sup>Center for Macroecology, Evolution, and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

<sup>3</sup>Lancaster Environment Centre, Lancaster University, Lancaster, UK

<sup>4</sup>Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

<sup>5</sup>University of Colorado Museum of Natural History, Boulder, CO, USA

<sup>6</sup>Department of Life Sciences, Imperial College London, Ascot, UK

\*Correspondence:

sean.connolly@jcu.edu.au (S.R. Connolly).

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