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Mechanisms matter: Predicting the ecological impacts of global change

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Climate change, the conversion of natural landscapes, anthropogenic exploitation, pollution, and invasive species have caused global declines in biodiversity (Díaz et al., 2019), with the impacts of climate change expected to intensify throughout the 21st century (Urban, 2015). Ecosystems will be hit by a combination of stressors, in many cases experiencing conditions outside those observed in their recent history. A crucial task for ecologists and conservationists is to understand how these novel conditions will impact populations, communities, and ecosystem function. Only with this understanding can society effectively target conservation and management interventions for the protection of biodiversity.

But what capacity does ecology have to anticipate the impacts of future conditions? The standard ecological toolkit of statistical approaches has helped to isolate environmental variables driving the observed dynamics of populations and communities. However, due to a lack of long-term monitoring data and the inherent rarity of extreme environmental events, these relationships are often only understood under a narrow range of environmental conditions and are limited in their predictive ability by known pitfalls of extrapolation. For example, species' responses to novel conditions may be nonlinear, impacted by the timing and duration of stressors, and stressors may be more damaging in combination than a sum of their individual impacts.

Fields with a focus on prediction, such as meteorology and climate science, develop models representing the mechanisms underlying changes in the system. Understanding these mechanisms enables robust prediction of the impacts of changing conditions.

However, these mechanisms are based on a relatively limited number of well-established physical principles, raising the question as to whether such an anchor exists in ecology.

One starting point is physiology, and in this issue, Desforges et al. (2021) provide an example of how this might be applied using an individual-based physiological model to understand the response of muskoxen (*Ovibos moschatus*) to environmental change in the high Arctic. Physiological mechanisms are assumed to have been shaped by natural selection to maximize individual fitness and are thus not expected to change under novel environmental conditions (Sibly et al., 2013). Individual-based models (IBMs) consider population-level dynamics to emerge from individual-level processes and interactions with other individuals and the environment. Individuals are autonomous (each individual pursues its own objectives through fitness-maximizing processes), adaptive (individuals respond or adjust to the current state of the system) and heterogeneous (individuals vary in terms of, e.g. their age, sex, and reproductive state). Central to IBMs including physiology is the acquisition and allocation of energy to life-history processes, including growth, survival, and reproduction. Many impacts of environmental change can then be evaluated as mechanisms directly influencing either energy acquisition, costs of metabolism, or survival.

To demonstrate, while previous statistical analysis found a relationship between muskox calf recruitment and winter severity, the approach taken by Desforges et al. (2021) was able to identify the mechanism underlying this relationship: deeper snow depth limits winter food accessibility, increasing the likelihood that pregnant females will abort and first-year calves struggle to compete for sufficient food. Furthermore, by tracking the changing state of individuals' energy stores, the IBM provided novel insight into muskoxen

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responses to plausible environmental scenarios. Desforges et al. (2021) simulate the impacts of snow depth, timing of snowfall, and their effects over consecutive years, producing a series of predictions about how potential future environmental scenarios will impact muskox demography and population size.

There is a clear value in the use of mechanistic models to predict the impacts of future change. So why then have they not been more widely used in ecological forecasting? We suggest three major obstacles: (1) data requirements, (2) the inherent difficulties in prediction, and (3) the culture of modelling in ecology. Desforges et al. (2021) provide an example upon which to discuss each in turn.

First, mechanistic models are comparatively complex when compared to statistical approaches. With added complexity, more data are required to inform a greater number of parameters. For example, the Dynamic Energy Budget model (DEB) used by Desforges and colleagues to represent muskox physiology required data to parameterize rates of energy acquisition, expenditure and allocation to maintenance, growth, and reproduction across different life stages. Moreover, model validation also required data with which to evaluate key model outputs, such as changes in population size. As a result of heavy data requirements, mechanistic physiological models to date have largely focused on well-studied populations, limiting the application of these models to only a small number of longitudinal demographic studies (e.g. North Atlantic fish stocks, Boyd et al., 2018; the Amboseli elephants, Boulton et al., 2018; the Zackenberg muskoxen, Desforges et al., 2021).

Second, to understand the difficulties in prediction, we can perhaps critically question how successful the model developed by Desforges et al. (2021) is at predicting population changes. The model captured a little less than half of the observed variation in population change—which we consider quite successful. Through several years of mild winters, population dynamics were poorly predicted by the model, suggesting other factors besides food accessibility drive population change. The challenge in capturing all drivers hinders both mechanistic and statistical approaches, but when a model is built from the bottom up, the spectre of a missing process(es) looms larger. This is largely because in focusing on mechanisms, rather than correlations, our ignorance is made transparent. This is probably a positive, but regardless makes developing mechanistic models difficult and means that concerns around bias and uncertainty must be foremost when attempting to communicate or apply model outputs to real-world problems.

Third, when referring to culture, we mean the general aims and strategy of modelling in ecology. An in-depth discussion is beyond the scope of this commentary, and has been raised elsewhere (Dietze et al., 2018), but we have pointed to differences in practice in ecology compared to fields such as meteorology and climate science. These fields focus on a single system (the Earth's physical system), represented by multiple models which are built by large collaborative teams and are subject to iterative development and testing. In ecology, the reverse is true; many discrete systems (e.g. the system controlling muskox population dynamics) are often represented by only a single model (if any at all) built by small, independent teams

and rarely further developed or tested. The practices employed in meteorology and climate science will not directly translate to ecology, but what can ecology do to advance mechanistic modelling?

Considerable efforts to establish standardized approaches for mechanistic models have already provided a platform upon which applied studies, such as that by Desforges et al. (2021), can be undertaken. There have been significant theoretical advances in mechanistic modelling (Grimm & Railsback, 2005) alongside the formation of practical guidance for the development, calibration, and analysis of mechanistic models (Railsback & Grimm, 2012). Targeted tools for the construction of mechanistic models have emerged in the form of NetLogo (<https://ccl.northwestern.edu/netlogo/>) and options for analysis now exist in popular statistical software including Pynetlogo (<https://pynetlogo.readthedocs.io/en/latest/>), NetLogoR (<https://cran.r-project.org/web/packages/NetLogoR/index.html>), and nlrx (<https://cran.r-project.org/web/packages/nlrx/index.html>). Furthermore, the ODD (Grimm et al., 2010) protocol has become established as the standard format for documenting and communicating mechanistic models.

There is still a way to go. We suggest a greater focus on iterative model testing and development, supported by the development of a database of ecological mechanistic models (mimicking the success of large trait databases) so that models can be easily accessed to improve wider collaboration and provide an opportunity to explore generalities between models.

As we move on from the 2020 Aichi Biodiversity Targets and realign our focus to the post-2020 Global Biodiversity Framework, the ability of mechanistic models to extrapolate to novel conditions could position them as the gold standard in understanding the impacts of global change. As the conservation community works to protect biodiversity, scientists and practitioners might capitalize on advances and examples of mechanistic theory to better understand, and plan for, the future of our planet, but exactly how mechanistic models can be used most effectively remains to be determined.

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