Better model transfers require knowledge of mechanisms

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Model transferability is an emerging and important branch of predictive science that has grown primarily from a need to produce ecological forecasts in the face of widespread data deficiency and escalating environmental novelty. In our recent article in TREE [1], we outlined some of the major roadblocks that currently undermine the practice of model transfers in ecology. Radchuk *et al.* [2]'s response to our work stresses the value of considering 'first principles' in projections of ecosystem change [3], and offers insights into outstanding challenges specific to mechanistic (synonym: process-based) models [4].

We strongly agree that improving ecological prediction under novel conditions requires a mechanistic understanding of natural systems [5]. Indeed, several of the research priorities we identified reflect this very idea (see [1] - Box 3 and pp. 795, 799). However, as Radchuk *et al.* [2] point out, the majority of mechanistic models are data-hungry by nature and rely heavily on imposed parameters derived from field observations or empirical relationships [6]. Given the real-world constraints of data availability, obtaining the detailed measurements necessary for robust model calibration and setup is not only time-consuming but also costly [6], such that mechanistic models have only been successfully built for the most charismatic, well-studied, and/or economically valuable species [7]. This limits their utility to support many of the management decisions that model transfers could inform. Data constraints also mean that Radchuk *et al.* [2]'s recommendation to capture what are largely unquantified and dynamic biotic interactions (e.g. competition, facilitation, predation) appears, for now, more aspirational than realistic. Borrowing information from related (and better known) taxa can partially circumvent the problem of data scarcity [7], but often at the cost of accepting unverified assumptions about parameter validity, and with potentially large biases in model outputs introduced by seemingly trivial changes in parameter values and initial conditions [6]. This uncertain behaviour perhaps explains why process-based models have received less attention in the literature to date, and remain less prominent overall in the context of model transfers [1].

While we see tremendous appeal in a process-based view of ecological inquiry, we therefore wish to temper general expectations. Significant advances in data collection are still imperative to pushing the discipline forward [8], and model transfers remain most urgently needed in knowledge-poor contexts [1], where information gaps make correlative descriptions of patterns the only viable pathway to ecological prediction. As a result, ecologists have proven rather slow to embrace mechanistic approaches [9]. For instance, although dynamic vegetation models built on first principles (e.g. physiology, photosynthesis) have been available for a few decades, they are either only applicable at coarse spatial resolutions or need detailed parameterisations to local site conditions [9]. Likewise, animal ecology has only very recently started to consider first principles such as dynamic energy budgets or foraging theory for modelling population dynamics reflecting individual-based processes [9].

Importantly, and as Radchuk *et al.* [2] remind us, mechanistic and correlative models also share many of the same underlying issues (e.g. equifinality, nonstationarity, model misspecification, model complexity) [4]. Rigorous tests of mechanistic models in non-analogue contexts are largely lacking (but see [10, 11]), meaning that external model evaluation should be seen as a critical step in determining their benefits for transferability. Until this is addressed, the relative value of mechanistic models over correlative models will arguably remain equivocal [11], and neither 'correlationists' nor 'mechanists' should thus feel entitled to claim holding the moral high ground [4].

Ultimately, the complexity of conservation challenges in the Anthropocene requires that we invest in finding efficient solutions grounded in an understanding of the inner workings of nature [3]. A modelling philosophy that allows parameters to naturally emerge from first principles could offer exciting opportunities to attain this goal, as long as it is subjected to meticulous testing and that principles can be defined explicitly and consistently [7,12]. Without a common and consistent definition, one ecologist's first principles could easily become another's phenomenologies [12], making transfers strongly dependent on correctly identifying the key processes driving system behaviour in the first place, lest the model fails [7]. Whilst we agree with Radchuk *et al.* [2] that both mechanistic and correlative models are equally valuable, the latter still remain, in many cases, the most utilisable. As a result, we argue that the most immediate advances in transferability will be achieved by encouraging the development of correlative models grounded in well-established mechanisms [1].

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