

1 Better model transfers require knowledge of mechanisms

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

16 We strongly agree that improving ecological prediction under novel conditions requires a
17 mechanistic understanding of natural systems [5]. Indeed, several of the research priorities
18 we identified reflect this very idea (see [1] - Box 3 and pp. 795, 799). However, as Radchuk *et al.* [2]
19 point out, the majority of mechanistic models are data-hungry by nature and rely heavily
20 on imposed parameters derived from field observations or empirical relationships [6]. Given
21 the real-world constraints of data availability, obtaining the detailed measurements necessary
22 for robust model calibration and setup is not only time-consuming but also costly [6], such that
23 mechanistic models have only been successfully built for the most charismatic, well-studied,
24 and/or economically valuable species [7]. This limits their utility to support many of the
25 management decisions that model transfers could inform. Data constraints also mean that
26 Radchuk *et al.* [2]'s recommendation to capture what are largely unquantified and dynamic
27 biotic interactions (e.g. competition, facilitation, predation) appears, for now, more aspirational
28 than realistic. Borrowing information from related (and better known) taxa can partially
29 circumvent the problem of data scarcity [7], but often at the cost of accepting unverified
30 assumptions about parameter validity, and with potentially large biases in model outputs
31 introduced by seemingly trivial changes in parameter values and initial conditions [6]. This
32 uncertain behaviour perhaps explains why process-based models have received less attention
33 in the literature to date, and remain less prominent overall in the context of model transfers
34 [1].

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

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

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

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