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Letter

Transferability of Mechanistic Ecological Models Is About Emergence

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Because of the lack of time, data, and resources and the need for urgent actions, ecologists often transfer models developed for one study system to a different context. Such transfers imply multiple challenges, which are identified by Yates and colleagues [1]. Although being insightful and elaborate, their review primarily focuses on correlative species distribution models (SDMs) whereas in their title they refer to 'ecological models', which would also include mechanistic models.

Some of the issues in transferring correlative and mechanistic models overlap, as pointed out by Yates and colleagues [1] in their Box 3, but some are also unique to mechanistic models and have been identified only over the past 10 years or so. As Yates *et al*. write in their Box 3, traditionally also many mechanistic models were entirely based on empirical (i.e., correlative) relationships, but modellers are increasingly replacing imposed, empirical relationships with models in which behaviours emerge from the adaptive decision making of individual organisms or similar first principles. Thus, one main challenge for the transferability of mechanistic models is estimating the degree to which processes can be imposed versus should be modelled as emerging property from underlying first principles.

Mechanistic ecological models have been transferred on multiple occasions [2,3] but so far the success is mixed [4,5]. A main limitation is the legacy of 'demographic thinking', which fails to make the distinction between imposed and emergent mechanisms. Demographic rates – for example, mortality – are often used as parameters in population dynamics models and parameterized via, for example, mark–recapture studies. In this way mortality is imposed, so that the model reflects the conditions under which the underlying data were collected (Figure 1). Simply extrapolating the model to new conditions can be highly misleading, as has been shown with a model addressing winter mortality of shorebirds [6]. SDMs are facing the same challenge, as pointed out by Yates *et al*. [1].

To allow transfer to new conditions, any aggregated parameters, such as demographic rates or parameters describing species presence–environment relationships, must emerge from what the building blocks of ecological systems, the organisms, are doing (Figure 1). In other words, the behaviour of the organisms should emerge from first principles such as energy budgets, stoichiometry, photosynthesis, resource uptake, or, more generally, fitness seeking [7]. A further requirement is to generically capture the interactions among individuals, in particular competition, facilitation, and trophic relationships. Examples of this 'next-generation' type of ecological models [7] that allow transfer to new conditions include models of tropical forest growth and dynamics based on photosynthesis and allometric relationships [8] and models of invertebrate population dynamics based on Dynamic Energy Budget theory [9].

Consequently, these challenges were not identified for correlative SDMs [1], as relations in such models are exclusively imposed. Further, some of the challenges identified by Yates *et al*. [1] for correlative SDMs are irrelevant for mechanistic models. For example, the issue of what response variables make a model transferable [1] does not apply to mechanistic models, because what is a response variable in a correlative SDM (abundance or presence–absence) usually emerges from lower-level processes in mechanistic models. Also, the issue of incorporating species interactions in model transfers, identified by Yates *et al*. [1], is rather naturally dealt with in the context of mechanistic models using the individual as the lowest entity.

We concur with Yates and colleagues [1] that solving the issues of model transferability requires establishing standards for assessing transferability and investigating the determinants of ecological predictability. We submit that an indispensable way to address some of the transferability issues is by using next-generation mechanistic ecological models that are ideally based on first principles. Such models are more generally applicable (i.e., across systems and closely related species) and thus more transferable. Moreover, mechanistic models may alleviate some of the transferability issues of the correlative models by generating range dynamics as a property emerging from the underlying population-level processes (as in Dynamic Range Models *sensu* [10]). Ecology needs both correlative and mechanistic models and neither one is more important than the other; thus, both must be considered.

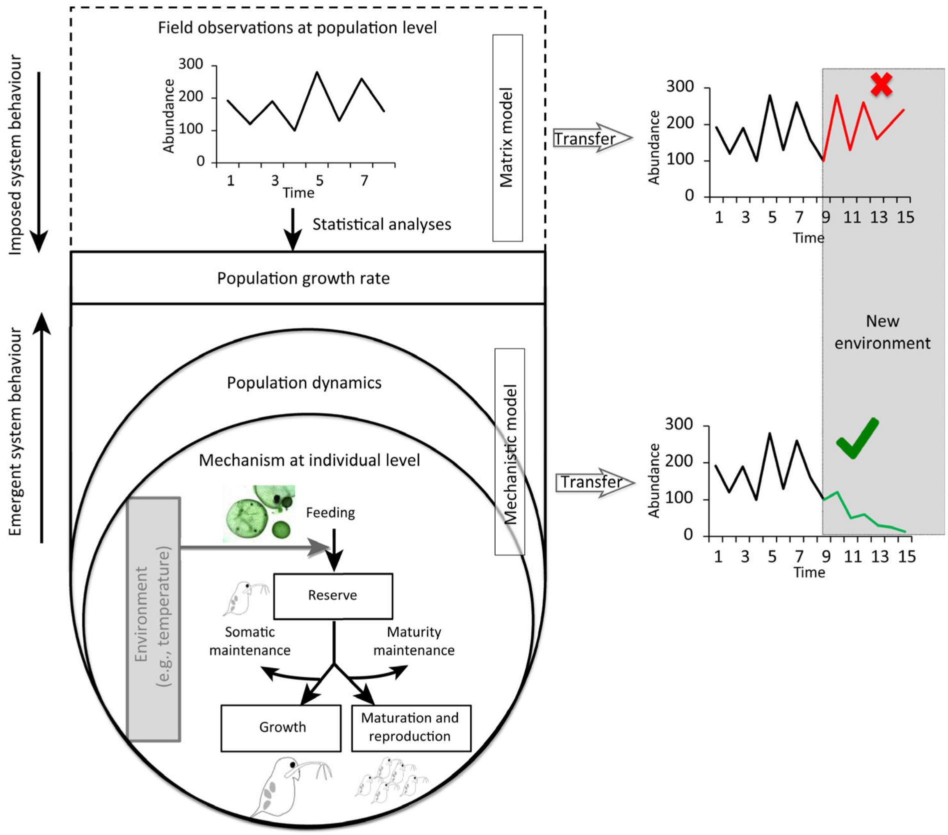

Figure 1. The System Behaviour (i.e., Here, Population Dynamics) May Be Imposed by Using Demographic Parameters Obtained from Statistical Analyses of Empirical Data (e.g., with Capture–Recapture and Survival Analyses). This is often done, for example, in population projection matrix models. However, the system behaviour in dynamic ecological models emerges from lower-level mechanisms at the individual level. The imposed and emergent system behaviours are indicated by a down- and an upward arrow, respectively, shown at the left of the scheme. The models with imposed system behaviour fail to capture the underlying mechanisms and therefore often fail when transferred to new conditions, as shown with the projections of population abundance on the right (incorrectly projected population dynamics in red). By contrast, the transfers using dynamic mechanistic models are expected to be successful (population dynamics in green; see Figure 4 in [6] as an example).

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