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## Individual-based modelling: what is the difference?

We agree with several of the points that Uchmański and Grimm raise in their paper, 'individual-based modelling in ecology: what makes the difference?'<sup>1</sup>. Individual-based models (IBMs) are powerful tools for understanding ecological systems, particularly in the examples that the authors state as requiring 'narrowly-defined' IBMs. However, we disagree with the claims that IBMs: (1) are defined by model complexity; (2) differ from classical models in a 'basic' (i.e. qualitative) way; and (3) are necessary to observe non-equilibrium dynamics.

The authors present four criteria that define IBMs: (1) complexity of individual life cycles, (2) explicit resource dynamics, (3) natural number populations, and (4) individual variation. We believe that these criteria are either poorly defined or wrong. In particular, criteria (1) and (4) are unnecessary. Complex life cycles and explicit resource dynamics are properties of *complex* ecological models, and do not differentiate IBMs from other modelling approaches.

We disagree most strongly with the authors' contention that IBMs represent a qualitatively different approach to modelling. Ecological modelling should be approached using a continuum of models. IBMs are simply a type of model along a continuum of complexity<sup>2</sup>. Without natural-number populations (criterion 3), no model can claim to be individual-based; without variation among individuals (criterion 4), all individuals can be lumped together and need not be tracked individually. Differential-equation models, discrete models with few classes, discrete models with many classes representing population variation, and IBMs, are steps along this continuum.

The authors link IBMs with non-equilibrium dynamics in ecological systems. This association is not fundamental to the definition of IBMs nor necessary to embrace complex dynamics in ecology. The authors attempt to isolate IBMs as a separate approach yielding novel dynamics but overlook the fact that, for example, simple-difference equations (e.g. the discrete logistic) can produce non-equilibrium results. Conversely, stochastic IBMs averaged over sufficiently large spatial scales can be indistinguishable from deterministic systems<sup>3</sup>. Thus, IBMs are neither necessary nor sufficient to study non-equilibrium dynamics.

Testing the amount of relevant detail (i.e. the appropriate location along a continuum of models) is one of the fundamental processes of ecological modelling. For example, the individual-based forest simulation model SORTIE<sup>4</sup> meets the criteria of a 'narrowly-defined' IBM. In SORTIE, repeatable forest dynamics emerge as the result of spatially-explicit competition for light among individual trees. The role of local heterogeneity in determining dynamics was tested by comparing the spatially explicit model with a version of the model in which space was removed<sup>5</sup>. This work suggests that spatial heterogeneity at the scale of individuals has a large effect on community-level properties such as forest succession. The observation of significantly different results between IBMs and simpler approaches is taken as evidence that individuals are relevant to a system. Otherwise, we should conclude that the detail of the IBM is unnecessary. Comparing results from models along this continuum allows us to determine which behaviors of natural systems are important to system dynamics<sup>6–8</sup>.

Uchmański and Grimm<sup>1</sup> provide a thought-provoking discussion of the definition and role of IBMs in ecology. While we agree that IBMs are exceptionally useful, we argue that neither the

concept of complexity nor equilibrium dynamics are central to their definition. In addition, separating IBMs from the rest of classical modelling is unnecessary and interferes with the insightful process of comparing models at different levels of detail.

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