

- 10 James, J.C., Grace, J. and Hoad, S.P. (1994) **Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland**, *J. Ecol.* 82, 297–306
- 11 Van Gardingen, P., Grace, J. and Jeffree, C.E. (1991) **Abrasive damage by wind to the needle surfaces of *Picea sitchensis* (Bong) Carr and *Pinus sylvestris* L.**, *Plant Cell Environ.* 14, 185–193
- 12 Telewski, F.W. (1995) **Wind-induced physiological and developmental responses in trees**, in *Wind and Trees* (Coutts, M.P. and Grace, J., eds), pp. 237–263, Cambridge University Press
- 13 Niklas, K.J. (1996) **Differences between *Acer saccharum* leaves from open and wind-protected sites**, *Ann. Bot.* 78, 61–66
- 14 Mattheck, C. (1991) *Trees: the Mechanical Design*, Springer-Verlag
- 15 Ennos, A.R. **Flexible structures in biology**, *Comm. Theor. Biol.* (in press)
- 16 Vogel, S. (1995) **Twist-to-bend ratios of woody structures**, *J. Exp. Bot.* 46, 981–985
- 17 Stokes, A., Fitter, A.H. and Coutts, M.P. (1995) **Responses of young trees to wind and shading: effects on root architecture**, *J. Exp. Bot.* 46, 1139–1146
- 18 Vogel, S. (1978) *Life in Moving Fluids*, Princeton University Press
- 19 Mayhead, G.J. (1973) **Some drag coefficients for British trees derived from wind tunnel studies**, *Agric. Meteorol.* 12, 123–130
- 20 Roodbaraky, H.J. *et al.* (1994) **Experimental observations of the aerodynamic characteristics of urban trees**, *J. Wind. Eng. Ind. Aerodyn.* 52, 171–184
- 21 Vogel, S. (1989) **Drag and reconfiguration of broad leaves in high winds**, *J. Exp. Bot.* 40, 941–948
- 22 King, D. and Loucks, O.L. (1978) **The theory of tree bole and branch form**, *Radiat. Environ. Biophys.* 15, 141–165
- 23 Bertram, J.E.A. (1989) **Size-dependent differential scaling in branches: the mechanical design of trees revisited**, *Trees* 4, 241–253
- 24 Blackburn, P., Petty, J.A. and Miller, K.F. (1988) **An assessment of the static and dynamic factors involved in windthrow**, *Forestry* 61, 29–43
- 25 Baker, C.J. (1995) **The development of a theoretical model for the windthrow of plants**, *J. Theor. Biol.* 175, 355–372
- 26 Wood, C.J. (1995) **Understanding wind forces on trees**, in *Wind and Trees* (Coutts, M.P. and Grace, J., eds), pp. 133–164, Cambridge University Press
- 27 Nielsen, C.C.N. (1995) **Recommendations for stabilisation of Norway spruce subjected to snow and wind damage**, in *Wind and Trees* (Coutts, M.P. and Grace, J., eds), pp. 424–435, Cambridge University Press
- 28 Whitmore, T.C. (1984) *Tropical Rainforests of the Far East*, (2nd edn), Clarendon Press
- 29 Gardiner, B.A. (1995) **The interactions of wind and tree movement in forest canopies**, in *Wind and Trees* (Coutts, M.P. and Grace, J., eds), pp. 41–59, Cambridge University Press
- 30 Ennos, A.R. (1995) **Development of buttresses in rainforest trees: the influence of mechanical stress**, in *Wind and Trees* (Coutts, M.P. and Grace, J., eds), pp. 293–301, Cambridge University Press

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?'¹. 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 complexity². 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 systems³. 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 SORTIE⁴ 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 removed⁵. 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^{6–8}.

Uchmański and Grimm¹ 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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References

- 1 Uchmański, J. and Grimm, V. (1996) *Trends Ecol. Evol.* 11, 437–441
- 2 Caswell, H. and John, A.M. (1992) in *Individual-based Models and Approaches in Ecology* (DeAngelis, D.L. and Gross, L.J., eds), pp. 36–66, Chapman & Hall
- 3 Rand, D.A. and Wilson, H.B. (1995) *Proc. R. Soc. London Ser. B* 259, 111–117
- 4 Pacala, S.W., Canham, C.D. and Silander, J.A.J. (1993) *Can. J. For. Res.* 23, 1980–1988
- 5 Pacala, S.W. and Deutschman, D.H. (1995) *Oikos* 74, 357–365
- 6 Jarvis, P.G. (1993) in *Scaling Physiological Processes: Leaf to Globe* (Ehleringer, J.R. and Field, C.B., eds), pp. 115–126, Academic Press
- 7 Durrett, R. and Levin, S. (1994) *Theor. Popul. Biol.* 46, 363–394
- 8 Levin, S.A. (1991) in *Differential Equations – Models in Biology, Epidemiology and Ecology* (Busenberg, S. and Martelli, M., eds), pp. 9–15, Springer-Verlag