

Do simple models lead to generality in ecology?

Matthew R. Evans^{1*}, Volker Grimm^{2*}, Karin Johst², Tarja Knuuttila³, Rogier de Langhe⁴, Catherine M. Lessells⁵, Martina Merz⁶, Maureen A. O'Malley^{7*}, Steve H. Orzack⁸, Michael Weisberg^{9*}, Darren J. Wilkinson¹⁰, Olaf Wolkenhauer¹¹, and Tim G. Benton^{12*}

¹ School of Biological and Chemical Sciences, Queen Mary, University of London, Mile End Road, London, E1 4NS, UK

² Department of Ecological Modelling, Helmholtz Center for Environmental Research – UFZ, Permoserstrasse 15, D-04318 Leipzig, Germany

³ Department of Philosophy, History, Culture, and Art Studies, University of Helsinki, Helsinki, FIN-00014, Finland

⁴ Center for Logic and Philosophy of Science, Tilburg University, PO Box 90153, 5000 LE Tilburg, The Netherlands

⁵ Nederlands Instituut voor Ecologie, PO Box 50, 6700 AB Wageningen, The Netherlands

⁶ Department of Sociology, University of Lucerne, Frohburgstrasse 3, PO Box 4466, CH-6002 Lucerne, Switzerland

⁷ Department of Philosophy, School of Philosophical and Historical Inquiry, Quadrangle A14, University of Sydney, NSW 2006, Australia

⁸ The Fresh Pond Research Institute, 173 Harvey Street, Cambridge, MA 02140, USA

⁹ Department of Philosophy, University of Pennsylvania, 433 Cohen Hall, Philadelphia, PA 19104, USA

¹⁰ School of Mathematics and Statistics, Newcastle University, Newcastle Upon Tyne, NE1 7RU, UK

¹¹ Department of Systems Biology and Bioinformatics, Faculty of Computer Science and Electrical Engineering, University of Rostock, Ulmenstrasse 69, 18057 Rostock, Germany

¹² Institute of Integrative and Comparative Biology, University of Leeds, Leeds, LS2 9JT, UK

Modellers of biological, ecological, and environmental systems cannot take for granted the maxim ‘simple means general means good’. We argue here that viewing simple models as the main way to achieve generality may be an obstacle to the progress of ecological research. We show how complex models can be both desirable and general, and how simple and complex models can be linked together to produce broad-scale and predictive understanding of biological systems.

Background: model strategies and purposes

An oft-repeated maxim of ecological modelling is that to achieve general insights, ecologists should favour simple models. This belief is rooted in the methodological precept known as Occam’s razor, and in the success of theoretical physics, where it is often the case that simple models, expressed in a few equations, are able to provide a coherent framework for a wide range of phenomena while simultaneously making testable predictions (e.g., Maxwell’s equations for electromagnetism). Holling [1] was the first to propound this argument in ecology when he made a distinction between strategic models, which are as simple as possible to reveal potential explanatory generalities, and tactical models, which are more complex because they are designed to predict the dynamics of specific systems (Box 1). May echoed this with his plea for a strategic modelling

approach that ‘sacrifices precision in an effort to grasp at general principles. . .to provide a conceptual framework for the discussion of broad classes of phenomena’ [2]. As well as inspiring a whole generation of ecological modellers, May’s heuristic has often been interpreted as ‘simple means general means good’ and, accordingly, complex models have been interpreted to be of little use when attempting to obtain general insights. Consequently, work based on complex models has been, and still remains, hard to publish and fund.

Model strategies

The general principles on which Holling’s and May’s strategic models rely are not first principles or mechanisms (such as natural selection or the law of conservation of energy). Their use of the term ‘general principles’ refers to concepts or phenomenological descriptions of processes and interactions. In these cases, a strategic model better fits what Crick refers to as a demonstration [3] of certain concepts, or what Roughgarden calls a minimal model for ideas [4], rather than an attempt to represent any specific ecological system (Figure 1, Box 1). Because of this confusion, we think that the term ‘strategic model’ should be best reserved for those that are based on general principles, such as natural selection, whereas ‘demonstration’ is more appropriate for models based on phenomenological descriptions (Figure 1).

Demonstration models are useful because they provide a toolkit for developing ecological theory. However, one must realise that they only provide elements of possible explanations of real systems. Demonstration models, at best, show that the modelled principles are sufficient to produce the phenomenon of interest; they do not help

Corresponding authors: Evans, M.R. (m.evans@qmul.ac.uk); Grimm, V. (Volker.grimm@ufz.de); O'Malley, M.A. (maureen.omalley@sydney.edu.au); Weisberg, M. (Weisberg@phil.upenn.edu)

* These authors are the first authors on this paper.

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Box 1. Modelling strategies: definitions and sources

- **Strategic models:** models made to be as simple as possible to reveal general explanations. First labelled by Holling in 1966 [1] and emphasised by May in 1973 [2]. We restrict the use of 'strategic model' to one that genuinely encompasses general principles, such as natural selection or conservation of energy (Figure 1, main text).
- **Tactical models:** complex models constructed ('merely') to predict specific system dynamics. These form part of Holling's 1966 model typology [1].
- **Demonstration model:** models in which the so-called 'general principles' are in fact concepts or phenomenological descriptions of processes; first labelled by Crick in 1988 [3].
- **Minimal model for ideas:** similar to Crick's demonstration and part of Roughgarden *et al.*'s 1996 model typology [4].
- **Minimal model for a system:** models designed to explain only certain aspects of a system, with the justification that these might be the most important ones. Such models form part of Roughgarden *et al.*'s 1996 model typology [4]. We include this modelling strategy within demonstration models but recognise that they are more likely to be linked to an individual system (see Figure 1 in main text).
- **Synthetic model for a system:** tactical models that aim to explain system dynamics and provide testable predictions; first labelled by Roughgarden *et al.* [4].

decide whether they are necessary. Demonstrations do not need to be tested against specific data because they represent concepts rather than systems. However, confusion arises when demonstration models, which are not designed to explain specific systems, are nevertheless compared with data from specific systems, as if they are making predictions for these systems. In 1925, Volterra made explicit reference ([5] p. 559) to the similarity between the observed changes in the fish community of the Adriatic after the cessation of fishing during World War I and the results of his simple model. Likewise, May and Anderson in 1979 [6] compared the output of their model with data from real populations exposed to diseases. They found that 'some of the theoretical conclusions can be pleasingly supported by hard data, while others remain more speculative' ([6] p. 460). This confusion of model purposes gives the false impression that simple demonstration models can provide actual explanations of specific systems. This is one of the main reasons why the notion 'simple means general means good' has been so dominant in ecology over the past few decades.

However, tactical models aim not only to explain system dynamics, but also to provide testable predictions. Roughgarden *et al.* [4] called this sort of model a 'synthetic model for a system' (Box 1, Figure 1). Such models contain details about particular systems and are especially important for making predictions about the future behaviour of those systems. Many models of this type are simulation models, such as individual-based models of forests [7], stream fish [8], and regional vegetation models [9].

Model purposes

When a model is being developed, the first task is to define its purpose [10]. This determines what is included in a model, and what needs to be represented in detail or in a more aggregated way. The distinction that Holling made between strategic and tactical models emphasised two different purposes: (i) understanding and identifying general principles, which requires simple, abstract models free

of system-specific details; versus (ii) predicting the dynamics of specific systems, which requires models that include specific factors (e.g., the type of disturbance or environmental stochasticity, and the parameter ranges for the class of systems under consideration) [1].

Here, we argue that the adage that 'simple means general' needs to be treated with caution. Viewing simple models as the primary route to generality can obstruct progress in ecological research. The generality of simple models is often superficial because they only demonstrate possible explanations rather than provide actual instances of explanation (Figure 1). We believe that the implied necessity of sacrificing predictive ability to achieve generality is overblown and hinders progress in ecology [11]. Retaining complexity in a model does not necessarily mean that irrelevant detail has been included, and including detail is often a necessary step towards a general understanding of ecological systems.

In the following sections, we discuss how some modelling strategies can bring both explanatory power and (relative) simplicity to the science. However, we also think that it is important to keep in mind that models are constructed for specific purposes, and a single model will rarely, if ever, be optimal for all the desired criteria. First, however, we should be clear about what we mean by 'simple' and 'general'.

What is meant by simplicity and by generality?

Although it might seem that the definitions of the terms 'simple' and 'general' are self-evident and unambiguous, even a cursory examination of how scientists use these words shows that this is not the case.

Simplicity

Models vary in the number and complexity of processes included to describe the system, the way the processes are described mathematically, and the ease with which the model can be analysed. This leads to three conceptions of model simplicity: (i) the number and complexity of entities and processes represented in a model: a simpler model has fewer entities characterised by fewer variables, and fewer and simpler processes; (ii) the brevity of the mathematical or computational description of the model: a simpler model has fewer and shorter terms, equations, parameters, and state variables, and includes fewer stochastic elements; and (iii) the effort needed to analyse and understand a model: a simple model is usually easier to understand because it includes fewer confounding factors and, thus, can often be fully analysed, which enables greater comprehension of its behaviour under all circumstances (however, see [12]). By contrast, more complex models may require simulation to provide solutions for specific parameter combinations. Comprehensive solutions can be gained by many simulations of different parameter values, but generally do not provide a complete analysis of the model because doing so would require simulation of the entire parameter space.

These three types of simplicity are often positively correlated, but need not be. For example, a model with a small number of differential equations may be hard to analyse and require further simplifying assumptions

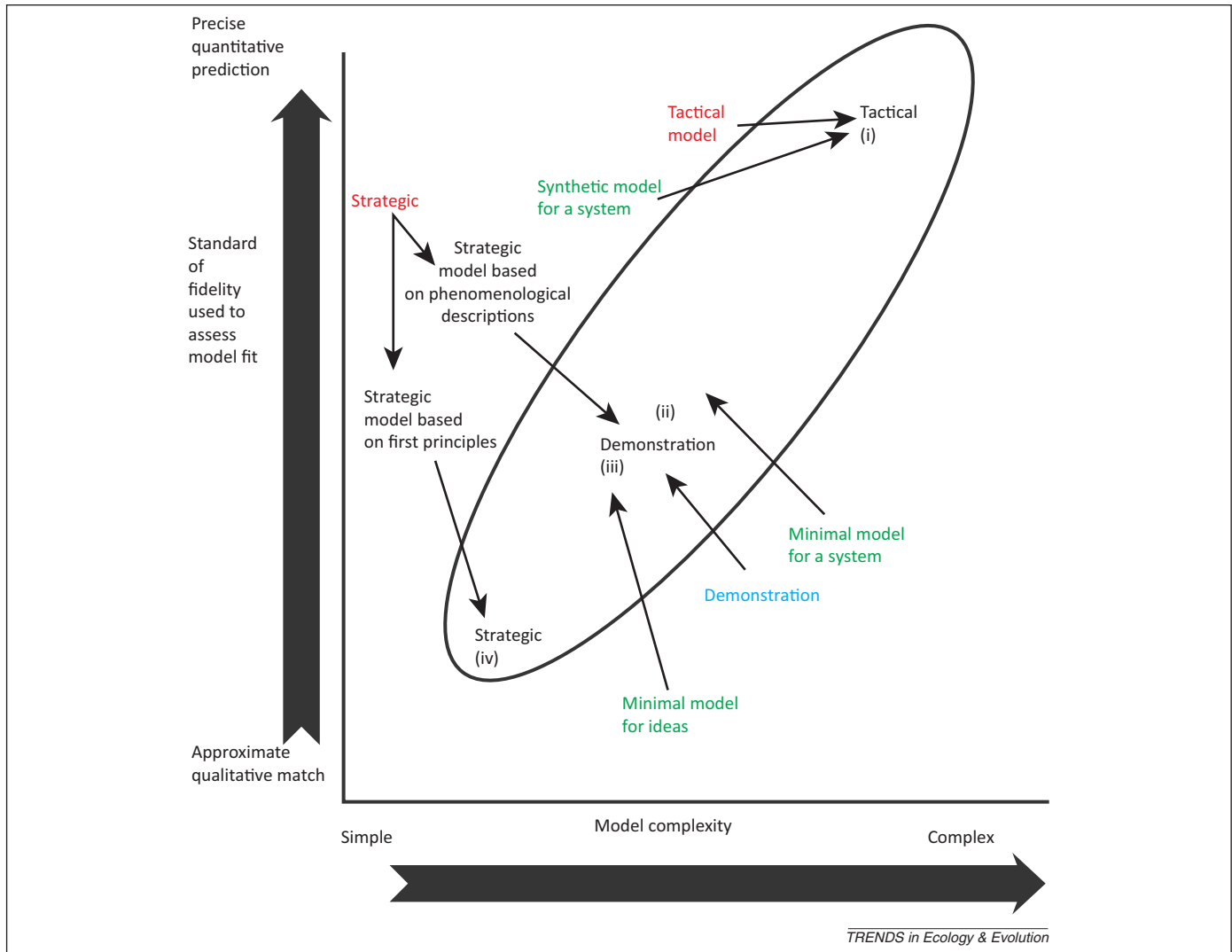


Figure 1. Modelling strategies can be represented as the production of models that vary in complexity but which also aim for different levels of fidelity when compared with the real world. Here, we display a typology of alternative terminologies on these axes (Holling's nomenclature is shown in red, Roughgarden *et al.*'s in green, and Crick's in blue). We suggest that modelling strategies mainly lie in the region defined by the ellipse and we place our terminology within it. Examples of models that fit at different regions of this parameter space (indicated by roman numerals) include: (i) forest-gap models, stream fish models, and regional vegetation models [7–9]; (ii) Andersson and May host–parasite models and most ecological models [6]; (iii) Lotka–Volterra, Levins' metapopulation model, and community matrix models [2,5,33]; and (iv) natural selection and conservation of energy.

and simulation to achieve a numerical solution (e.g., [13]). By contrast, a simulation model, described by thousands of lines of code, may be causally very simple: the dynamics of an entire forest may be driven by vertical competition among individual trees for light (e.g., [7]). Moreover, the classifications 'simple' and 'complex' can usually only be evaluated in comparison with other systems, which means that categorical judgements about whether a particular model is simple or complex cannot usually be made.

Generality

Just as there is a range of notions of simplicity and its converse, complexity, there are several conceptions of generality. Most ecologists view the generality of a model as being proportional to the number of biological systems (such as species or environmental conditions) that a model can capture or to which its conclusions can be applied. As with simplicity, generality is best understood as a comparative notion. In most cases, all one can claim is that one model is more (or less) general than another model [14]

and then only if one uses the same standards for comparing model output to data. This is how we approach generality below.

Are simple models always more general?

An ecologist in search of models to explain broad ecological phenomena may wish to model just a few fundamental processes, ones that are likely to be found in many systems. This seems to be the original (strategic) interpretation of the 'simple means general' argument, and what May [2] had in mind (Figure 1). Of course, such simplicity comes at a cost. Very general models with only one or two causal factors will not have an especially good fit to any particular system [15]. Thus, the generality of strategic models is of a particular sort: they potentially inform about phenomena that exist in many systems, but may not necessarily make good predictions about any individual system. For example, consider a standard model that demonstrates density-dependent growth: the logistic equation. This is a single difference map that represents the negative feedback

between population growth rate and population size. Investigation of this model reveals the existence of a range of attractors in phase space, which could correspond to the resilience of the modelled population to disturbances. Such attractors could perhaps be found in many ecological systems. However, subsequent analysis may reveal that, although this insight holds for many systems, the extent to which it describes real populations depends on the standards of fidelity for the model. Environmental change and variability, spatial heterogeneities, and demographic differences between individuals will lead to quantitatively or qualitatively different dynamics from those suggested by the simple model [16]. Simple, strategic, or demonstration models illustrate how phenomena could be produced; they may inform biologists about many systems, but will not apply to any particular system with a high degree of fidelity. They will not be useful at predicting the behaviour of specific systems and, thus, cannot be empirically tested against data from a particular system.

The other consideration in any discussion of whether simplicity begets generality concerns the assumptions that are made to create a model. All models are only as good as their underlying assumptions, and both simple and complex models can be based on unrealistic assumptions. However, in many cases, simple models require higher levels of idealisation than do complex models and, thus, are more likely to be biologically unrealistic [17]. As a result, simple models may lead to theory that cannot apply to any real biological system.

Simple–general trade-off

If it were always true that simple models were more general than were complex models, a preference for simple models might be justified. However, we argue that there is usually a trade-off between simplicity and generality, such that simpler models are, all other things being equal, less general than are complex models. For example, a nonlinear population growth equation such as $dN/dt = \alpha N + \beta N^{1+a}$ represents a large family of models, the members of which correspond to the constant parameters α and β being set to particular values (whereas a can take any value). If β is set to zero, we obtain a simpler linear equation, $dN/dt = \alpha N$. Obviously, the nonlinear equation includes the linear one as a special case. Thus, the more complex equation represents a larger family of models than the linear ones and, therefore, is more general. It can pick out all the real systems that are described by the linear equation plus a range of others. This is an illustration of the observation that, when dealing with related equations lacking numerically quantified parameters (called ‘uninstantiated’ models by [14]), simplicity decreases generality.

We suggest that ecologists should be concerned about the simplicity versus generality trade-off that results in simple models being less general than complex models. However, despite its existence, many ecologists believe that simple models really are more general. One reason why this adage is believed to be true is because, in ecology, simple models are often assumed to be strategic (*sensu* Holling [1], Figure 1) without their purpose being critically examined. As soon as models move away from the examination of general principles towards making predictions for

specific systems, then increasing complexity will usually increase generality.

In summary, our discussion so far shows that the widespread acceptance of the maxim that simple models are always more general is at best misleading and may often be untrue, especially when attempts are made to relate models to systems to make predictions, including those involved in model validation. Unlike in physics, where general models have to make testable predictions, ecology has embraced an approach where models claiming generality are untestable in any real system. It made sense during the 1960s for Holling and others to foster the development of simple models to achieve more generality, because complex models were then not very tractable due to their structural, conceptual, and computational limitations. However, these limitations no longer apply after half a century of scientific and technological development, and there is a danger that progress in ecology is being impaired by the rejection of more complex forms of models that can be related to real systems. We now turn to some of these newer developments.

Explanatory focus

A key decision that modellers face is to determine which aspects of the dynamics of real systems should be explained, and which ignored or ‘built in’. There are no hard and fast rules about how such decisions are made, but a common strategy is to identify the background processes that are not known in detail or are not of theoretical interest for current purposes, and to impose these on the model with parameters. Thus, attention can be focused on the ecological processes that are deemed to be of more interest. Mortality, for example, can be modelled as a mixture of a constant background mortality and mortality emerging from processes such as starvation, predation, or disturbances [10].

The ‘simple means general’ heuristic can lead to an overemphasis on the imposition and abstraction of particular structures that are believed to be important. For example, including a density-dependence term in an ecological model, on the assumption that this process has a role in population dynamics, gives the theorist no understanding of the mechanisms underlying density dependence. By contrast, representing the resources of the environment, and the ways that organisms use those resources, can show how density dependence arises. Such cases illustrate that simple models often lack realism, or require especially complex justifications to reconcile these models with reality [18].

Simple models may demonstrate that particular processes could influence dynamics and may apply generally, but still may not strongly inform any real biological system. For example, dynamical chaos can arise in simple deterministic systems and could be an explanation of many complex population dynamical patterns. Yet, despite being a strong focus of research in population biology for 25 years, good examples of chaotic population dynamical systems are rare and often still controversial. Explanations of ‘chaotic’ population dynamics now usually invoke stochastic processes interacting with deterministic dynamics [16]. In these cases, a simple model (chaos arising from

purely deterministic processes) has been supplanted in favour of a more complex model (stochasticity interacting with deterministic processes). This may be an example of where biologically unreasonable assumptions led to the development of simple models that proved to be unhelpful guides to the way the world operates.

Because of the cost of simplicity, and the difficulties associated with constructing hyper-realistic models, many contemporary ecological models adopt a middle ground [19], attempting to explain phenomena in some detail, while ignoring many characteristics of the real system in the hope they are not essential (e.g., [20,21]). Models of this type are close to what Roughgarden *et al.* [4] refer to as minimal models for a system. These models are less purely demonstrations than are minimal models for ideas but are more abstracted than tactical models (Figure 1). Thus, in our view, Roughgarden *et al.*'s minimal models can be regarded as different types of demonstration model, useful for elucidating or illustrating ideas but not helpful in generating testable predictions.

Roads to generality

Complex models have been fruitfully developed for both theoretical and practical ecological problems (e.g., see overviews in [22–26], Box 2). Crucially, such complex models can, if they encompass relevant mechanisms, make predictions for new conditions and represent the properties of highly variable phenomena, as is needed when studying the effects of changes to the environment [27]. Therefore, they can help to solve practical ecological problems, such as those in conservation biology and resource management [24,25,27] (Box 2).

Simulation experiments as exemplars

The price for complexity is that such models usually need to be tied to data from specific systems. We are still left with the problem of how to generate general insights from models that are tied to specific systems. A key strategy currently used to solve this problem is the use of simulation experiments [28,29]. Such experiments are performed on models, but parallel the kinds of experiment performed on laboratory systems. Techniques include analysing confounding factors, such as heterogeneities and stochasticity, changing the number of types of entity and process considered in the system [30], and systematically varying the parameters and variables of the model to determine whether its predictions are strongly or weakly influenced by changing values and, thus, which processes are more or less important dynamically. Utilising such simulation experiments requires the systematic consideration of possible (but not actually occurring) scenarios to understand the scope and limits of the model in question [31]. An approach that might be usefully applied here is numerical bifurcation theory, which is a powerful approach to model analysis that does not require analytical solutions but can yield results that are more robust than those obtained by simulation.

This sort of analysis might help to extract key ecological processes, or even principles as discussed above, that strongly influence certain ecological phenomena or patterns. Processes that have been excluded in the course of

Box 2. Rabies and the economic and social costs of relying on simple models

Practical applications of modelling include guiding the development of large-scale, long-term projects, such as disease control and conservation strategies. The amount of system-specific detail incorporated in such models can affect the conclusions drawn from the models and, thus, impact substantially on the outcome of the projects.

An example of this is the control of rabies, a serious disease that kills tens of thousands of humans a year. Substantial amounts of money are spent annually on rabies prevention (e.g., in the USA approximately US\$300 million per annum [33]). Since the early 1980s, large-scale oral vaccination campaigns have been used in Europe to immunise red foxes (*Vulpes vulpes*) against rabies. The critical question is 'what level of immunisation needs to be achieved to eradicate the disease?' Anderson *et al.* [34] produced 'a simple mathematical model for the overall dynamics of the interaction between fox populations and rabies'. It suggested that, at fox densities typical of central Europe, a vaccination rate of 70% of the fox population needed to be achieved to eradicate rabies successfully, and the rabies eradication programmes over Europe over the past 30 years have been designed to achieve this level of vaccination.

However, data from some populations in which rabies had been successfully eradicated suggested that the percentage of immunised animals was as low as 50% [35,36]. To re-examine the issue, Eisinger and Thulke [37] created a complex, spatially explicit individual-based model [38]. In this model, infected foxes mostly infect other individuals in their own or neighbouring social groups, whereas in the Anderson *et al.* [34] model, an infected fox can potentially infect any susceptible fox in the population however distantly separated.

Eisinger and Thulke's [37] model suggested that rabies would be eradicated from the population if 60% (rather than 70%) of the foxes were immunised. If they changed local transmission to global transmission, and removed spatial heterogeneity in vaccination, the predictions of the modified model matched the 70% figure of the Anderson *et al.* [34] model.

This revised model has economic consequences [37]. To achieve 70% immunisation requires 20 baits per km², whereas to achieve 60% requires approximately one-third fewer. This would generate substantial cost reductions, estimated in multinational regions as ca. €15 million annually for bait alone. Thus, the results of a simple, unrealistic model led to considerably higher costs for the rabies eradication programme.

analysis can be understood as less important, or only important for a few specific systems. In some cases, simplification may result in the creation of an analytically tractable model, but this is not an absolute requirement. This dynamic of modelling captures important aspects of the interplay between simple and complex models.

Concluding remarks

The maxim 'simple models are more general than complex models' often misleads modellers. The statement may be true for those strategic models that are based on first principles (Figure 1), but such models are rare in ecology. In other instances, simple models can help identify broad-scale and widespread phenomena. We have called these instances 'demonstration models'. We recognise that simple models have great utility both in acting as demonstrations of particular phenomena and in acting as submodels of more complex models. However, in most cases, models must be relatively complex to make predictions about real ecological systems. These are the models we have labelled 'tactical' (Figure 1, Box 1).

By depending on an approach that detaches prediction from generality, ecology has developed in a way that is distinctly different from the physical sciences. Complex, system-specific models are needed to provide the ability to predict the current and future behaviour of systems. These models need to incorporate all relevant processes and then be tested, perhaps by simulation, to assess which processes most influence the predictions of the model; those that are less influential can be removed [32]. A dynamic approach to ecological modelling emphasises the separate and combined roles that simple models and complex models have in ecological explanation. We do not propose a new adage to replace ‘simple means general’. Instead, we have outlined guidelines for ecological modelling that will make future efforts to manage the complexity of ecological systems more comprehensive, predictive, and useful.

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