

Research

Making predictive ecology more relevant to policy makers and practitioners

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One of the aims of ecology is to aid policy makers and practitioners through the development of testable predictions of relevance to society. Here, we argue that this capacity can be improved in three ways. Firstly, by thinking more clearly about the priority issues using a range of methods including horizon scanning, identifying policy gaps, identifying priority questions and using evidence-based conservation to identify knowledge gaps. Secondly, by linking ecological models with models of other systems, such as economic and social models. Thirdly, by considering alternative approaches to generate and model data that use, for example, discrete or categorical states to model ecological systems. We particularly highlight that models are essential for making predictions. However, a key to the limitation in their use is the degree to which ecologists are able to communicate results to policy makers in a clear, useful and timely fashion.

Keywords: evidence-based conservation; horizon scanning; policy; practice; density-structured models; genetically modified organisms

1. INTRODUCTION

One main function of ecology is to understand how the natural world operates; one function of models is to aid the testing of this understanding by converting verbal concepts into testable predictions. The process of theory development, creation of predictions, testing and then subsequent reassessment of theory in response to the results is, of course, the basis of all science, including ecology [1,2]. In informing management and policy, models can be used to explore different options, make predictions, as well as form the basis for subsequent experiments.

One example of the iterative interplay between models and practice concerns the use of genetically modified herbicide-tolerant (GMHT) crops. Theoretical models using empirical observations and data showed that these could have a marked impact upon weed seed density and thus granivorous birds [3]. In response, it was suggested that these crops could actually benefit biodiversity by allowing the delaying of spraying weeds to grow that would otherwise be controlled; a field test of delayed spraying [4] showed that delaying spraying did benefit weeds and the associated arthropods. Freckleton *et al.* [5] combined a review of weed phenologies with a population model to show that few species will be able to set seed before spraying and thus that any benefits would be short-lived. The analysis of Freckleton *et al.* [5] suggested that if spraying can be ceased earlier in the season, then a viable population of late-emerging weeds could be maintained. May *et al.* [6] carried out

field trials and showed that, as predicted, early spraying can enhance weed seed banks and provide benefits to invertebrates but, significantly, did not reduce yield.

The development and the uptake of policy that affects ecological systems are influenced by numerous factors, and in this paper, we explore several of these. We begin by highlighting that ecologists need to be aware of the issues that are most relevant to the development of policy; conversely, policy makers need to ensure that the questions that are most important for policy development have been clearly articulated and formulated in a manner that can be addressed by scientists [7]. Moreover, given the inevitable lag between beginning a project to address a new research question and providing an answer, it is desirable that possible issues and research priorities are identified as early as possible. Below, we describe the development of one approach to do this based on horizon-scanning, as well as collaboratively identifying key questions, the options for management and policy and their effectiveness.

Once a question has been identified, the possible options explored and best course of management decided upon, the next stage is to implement recommendations. The next important issue we highlight is that the uptake of any recommendation from scientists is dependent on the political and social background. Continuing the example of GM crops (see also below), GMHT crops offer undoubted agronomic benefits [8]. However, they are not grown in the UK at present, largely because of the attitudes of the public [9]. Arguably, this is because the research conducted on their use only focused on agronomy and did not consider social reactions or the wider environmental impacts from the outset, specifically the suggestions that these crops could harm

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biodiversity [3,10]. Public outcry, followed up with limited ecological impact analysis [11,12], did not change this view. The lesson is that applied scientists cannot ignore the wider social impacts or perceptions of their technology. We highlight that in developing predictive ecology, interdisciplinary projects are crucial.

Horizon scanning and social integration can identify problems, pitfalls and possible solutions. However, models are required in order to determine the magnitude of the problems and its impact in different locations. Similarly, solutions can be suggested and research can show that these can be successful, but again research is needed to determine the level of interventions needed at different locations to achieve a given objective. The final point we highlight relates to providing such prediction. The models developed by ecologists are frequently very intricate, and modellers are now capable of developing extremely complex simulations and analytical models, incorporating a wide range of processes. Complex models of this sort have been extremely successful, for example, in climate change modelling [13], forest models [14,15] and in understanding the ecology and evolution of disease outbreaks, e.g. Grenfell *et al.* [16]. It is no coincidence that these are all systems for which there are enormous amounts of data, and that have been studied extensively for many years. If extensive data are not available, then it is not possible to parametrize complex models; however, models can still be developed and predictions generated, e.g. Taylor & Hastings [17]. Our final point is to highlight that policy-relevant models have been developed over relatively short periods, but by using simpler formulations that sacrifice detail for ease of development: where feasible, and for systems, where large amounts of data are available.

There are greater calls for the closer integration of science and policy. In this paper, we will examine these three ways in which this process could be improved: exploring means of identifying the research issues of greatest utility to policy makers and practitioners (hereafter 'policy makers'), integrating ecological models with social science models including those of economics and, finally, exploring means of improving the speed of model development and the transparency of model presentation.

2. MEANS OF IDENTIFYING PRIORITY ECOLOGICAL ISSUES FOR POLICY MAKERS AND PRACTITIONERS

Although much of the justification for conducting scientific research is that the information gained can be used by policy makers and practitioners, in practice, many decisions are made without the use of the scientific literature [18]. An alternative approach is to collaborate with policy makers to identify key issues and priorities. These methods are described in Sutherland *et al.* [19]. Thus, each of the methods described below acts to set another component of the possible research agenda.

(a) *Horizon scanning*

For predictive models to be useful, the information has to be available at the appropriate time in the process of decision making. In some cases, such as the

response to the decision to extend the use of biofuels, much of the critical research was completed well after the key decisions were made [20,21]. A review identified the general problem that the policy process tends not to involve science sufficiently early [22]. A solution is horizon scanning, the systematic search for incipient trends, opportunities and risks that may affect the probability of achieving management goals and objectives [23]. Horizon scanning has been used by business to identify forthcoming opportunities [24], the military [25] who aim to identify useful technologies and threats at as early a stage as possible and medicine to identify possible beneficial technologies [26].

This approach has subsequently been used for identifying issues relevant to conservation in the UK [27]. Following the success of that exercise, the decision was made to establish a global team to carry out an annual exercise of horizon scanning [28,29]. This comprises professional horizon scanners, experts in particular topics, such as coral reefs, wetlands, diseases and invasives, representatives from large conservation organizations, such as the Nature Conservancy, Wildlife Conservation Society and Birdlife International, with wide concerns in different subjects and regions, plus some academics with wide interests. That exercise examines changes in technology, attitudes, spread of invasive species and the rise of diseases. A gap was a comprehensive examination of legislative changes that may impact upon ecology and conservation, so an additional annual exercise was established that examined the forthcoming or possible legislation in the UK, in the European parliament and global measures [30].

(b) *Identifying priority questions*

Although one of the practical applications of ecology is to answer questions of importance to society, it is remarkable that policy makers have rarely been consulted in suggesting priority areas for research. Perhaps, the best approach is to express this as the research questions that policy makers would most likely answer. The first attempt was to identify the 100 ecological questions of greatest interest to UK policy makers [7].

This approach has been widely used. The methods are broadly similar, but have evolved especially with the objectives of making them more rigorous and more transparent. The completed exercises include an assessment of the 100 questions of greatest importance to the conservation of global biological diversity [31], the top 40 priorities for science to inform conservation and management policy in the United States [32], the top questions of importance to the future of global agriculture [33], UK forestry [34] and Canada [35], identifying the big ecological questions inhibiting effective environmental management in Australia [36], identifying the major conservation policy issues that need to be informed by conservation science [37] and identifying the ecological research needs of business [38]. While the outputs of such exercises are dependent on the people involved, methods have been developed to try to ensure the process is democratic and transparent, so reducing the risk of undue influence of particular individuals.

There has been a call for others exercises to identify priority questions such as to enhance fisheries and aquatic conservation, policy, management and research [39], and a number of similar exercises have been completed, are being planned or are being discussed.

(c) *Identifying policy options*

Whether research will have an impact partly depends on the policy context, so that identifying options for policy development can help identify options for making research relevant. Thus, a group of policy makers, policy informers and academics identified the options for the development of policy within the UK [40]. This included habitat banking, which is being developed by the current government, and measures to develop and maintain ecologically coherent networks, which became a major theme of a review of conservation strategy [41], and is a key component of the UK government's white paper on the environment.

(d) *Option scanning*

For science to have an impact upon society requires that interventions are implemented. A possible initial stage is to list the possible range of interventions. Of course, this is less satisfactory than an assessment of the effectiveness of each intervention, but is enormously cheaper, and thus we suggest it as a good starting position. Jacquet *et al.* [42] used this approach to attempt a comprehensive list of all the interventions related to the major marine problems.

(e) *Evidence-based conservation*

Medicine has been revolutionized by the collation and analysis of the effectiveness of interventions. Sutherland *et al.* [18] suggested that the same changes could be made to conservation practice. The bee synopsis book [43] (also available for free on the conservation evidence.com website) outlines the evidence for the effectiveness of all the different known options for enhancing and maintaining bee populations. This is equivalent to the book *Clinical evidence* that has greatly improved the access to medical knowledge. Such a synopsis can also be used to identify the areas where knowledge is weakest.

3. COMBINING ECOLOGICAL MODELS WITH SOCIAL AND ECONOMIC MODELS

Answering many applied problems requires incorporating social or economic components. For example, Watkinson *et al.* [3] provided a model of the likely impact of GM crops on the abundance within fields of overwintering skylarks. This considered the likely impact of GMHT crops on the weed populations and the aggregative numerical response of the skylarks in relation to seed density. However, this model showed that the critical unknown relationship was between the uptake of GM technology and seed density. There are two contradictory forces: farmers with numerous seeds could be those in greatest need of the technology and so most likely to use it or, alternatively, those with high weed abundance may have different social or ethical considerations (for example, they may reluctant to adopt new technologies or be

organic farmers) and thus least likely to adopt the technology. As seed abundances are highly skewed across fields, and the aggregative response is such that field use by skylarks is particularly high where seeds are abundant [44], the pattern of uptake by farmers is critical; however, this key aspect is unknown [3].

Cooke *et al.* [45] examined how social and ecological concepts were integrated within models by reviewing all the published integrated models from 2003 to 2008 in 27 journals that publish agricultural modelling research. This found 36 papers that integrated social and ecological concepts in a quantitative model. All these papers used one of four different approaches to integration. *Private profit* models are pure profit models at the single landholder level aiming to maximize profit from the use of natural resources, such as the impact of forestry decisions [46] or rangeland management [47]. In *private conservation* models, there are two components to utility: from profits and from ecological benefits, although the latter are typically beneficial to the society and typically an externality to the farmer [48]. *Collective management* models typically determine the consequences to individuals of a change in the configuration of the landscape or of a change in policy with landscape consequences. These models do not consider the individual behaviour of landholders. In *constrained policy* models, the decisions of landholders are influenced by policy and these either consider different land-use patterns resulting from different policies [49] or optimal policy decisions, such as the payment levels necessary to optimize the benefits from different subsidies to delay mowing [50].

The review of Cooke *et al.* [45] showed that there is a huge literature on the ecological or social aspects of land use, but there are far fewer models that integrate them. In an example of how it is possible to integrate economic, social and ecological models to study the ecological and social responses to changes in agriculture, Cooke *et al.* (I. R. Cooke, E. H. A. Mattison, E. Audsley, A. P. Bailey, R. P. Freckleton, A. R. Graves, J. Morris, S. A. Queenborough, D. L. Sandars, G. M. Siriwardena, P. Trawick, A. R. Watkinson & W. J. Sutherland 2011, unpublished data) adopted the strategy shown in figure 1. The whole farm model [51] uses mixed integer programming to determine the profit-maximizing agricultural decisions given the constraints of farm size, soil type and climate, as well as the existing regulations, and the prices of commodities, inputs and staff costs.

From interviews, literature review and a focus group, it was possible to identify 16 farm-management objectives followed by interviews with utility of each assessed using multi-criteria decision analysis [52]. Satisfaction curves gave the relationship between utility and objectives, such as their liking of profit, and their dislike of risk and crop complexity. This allowed the derivation of the optimal solution for farmers allowing for their responses and showing how attitude to, say, risk changes the farming decisions made.

The impact of crop type and landscape features upon breeding birds was determined using transect data of over two thousand 1 km² areas and relating to landscape compositions, field boundary features and crop type [53]. While landscape was the most important

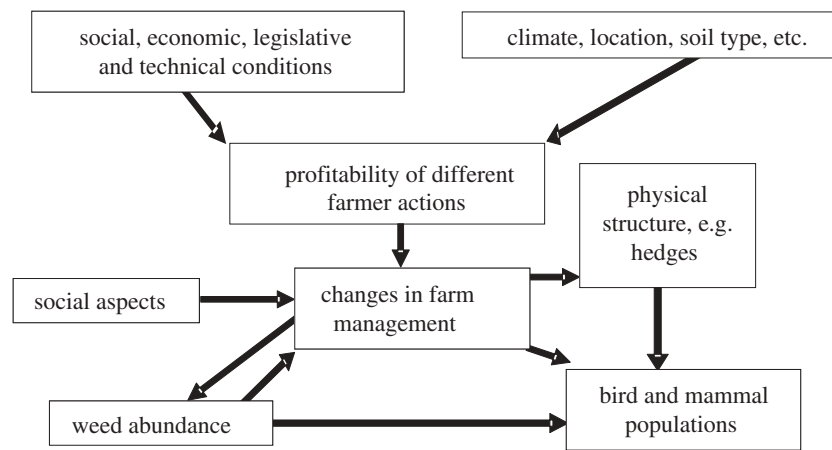


Figure 1. The links between components of the models to describe the agricultural system.

determinant, crop type had an influence in most species, which allows the impact of crop type on bird abundance to be quantified. This example shows that it is possible to integrate social, economic and ecological models; such an approach is likely to be increasingly important.

4. STATE-STRUCTURED MODELS

(a) *Problems with detailed process-driven models*

As our understanding of a system improves, or with the development of new modelling tools, it is possible, and indeed desirable, to create more sophisticated predictive models [54]. Sophisticated models are often necessary: for example, in predicting how a change in climate will impact upon bird populations where there may be impacts on sea level, predators, prey and parasites, the model would need to be relatively complex [55]. However in developing such models, there are several problems, the most important of which are:

- (i) In terms of policy, the most important problem is that results are frequently required very quickly, if they are to be of immediate use. If data are lacking, then it is not possible to parametrize models and the consequence is that key parameters have to be guessed, inferred from the literature or sensitivity analysis used to explore a range of parameter values. These latter approaches are commonly used, the drawback being that when this is done, it is usually not possible to generate a true estimate of model precision.
- (ii) The populations being studied in policy-relevant applications are frequently pests, pathogens or species of conservation relevance. The regions of parameter space that are of greatest interest are usually those that relate to an eradication or extinction threshold, i.e. at low density. For species with high rates of population increase, models can be extremely unstable in such regions of parameter space as at low densities, the effects of stabilizing mechanisms (e.g. density-dependence) are typically weak [56]. These problems can be extreme: for example, a single plant of the weed *Chenopodium album* can produce 250 000 seeds [57]; if a population is to be

stable, then the total lifetime survivorship must be $1/250\,000 = 4 \times 10^{-6}$. In this species, survivorship has to be estimated to at least the sixth decimal place in order for a model to be accurate, and small errors in estimates of parameters can yield enormous impacts on predictions of population size. As the number of parameters in a model increases, the effect becomes multiplicative unless the new parameters are used to model new stabilizing processes [56].

- (iii) The accuracy of the model is limited by both our understanding of the biology of the system, together with our ability to model populations. Prevailing paradigms for modelling can be important in determining how models are structured. As an example, it is only over the past decade that the importance of Allee effects has been recognized [58–60]. In formulating models, it is now routine to consider the likelihood of this, as well as other processes, such as density-dependence. However, prior to the realization that Allee effects are important—a significant component of population dynamics—this effect may well have been ignored in detailed mechanistic models. One way to deal with this is to use purely empirical approaches: phenomenological models fitted to data [61,62] can characterize population dynamics and make fewer assumptions about the underlying processes. However, these obviously lack a mechanistic basis, and of course rely on large amounts of high-quality data. Although, it is possible with such models to predict outside the bounds of observation (as we frequently need to do with models), the downside is that without a mechanistic basis, the confidence we might have in the robustness of those predictions could be low.

To a great degree, these problems arise from a focus on classic demographic measures as state variables in many ecological models, as well as trying to include more processes than the data can accommodate. The typical state variable in an ecological model would be a continuous measure, such as the numbers of individuals in a population, the mass of individuals or the cover of a species. The underlying models are then either difference or differential equations.

(b) Empirically driven models

One solution is to simplify the system, so that instead of aiming for exact parameter estimates or exact outputs (such as the population abundance of a weed or the change in coastal communities), there are just a limited set of states (different levels of weed abundance or different areas of saltmarsh) and the model output is the likelihood of ending in that state.

In this spirit, Taylor & Hastings [17] introduced a density-structured approach for modelling the population dynamics of an invasive grass, *Spartina alterniflora*. The state variable in this model was a discrete density variable: juveniles, low-density individual clones and high-density meadows. The justification for doing this was that the behaviour of populations in these states is qualitatively different: for example, individuals in low-density populations suffer reduced fitness owing to pollen limitation, whereas in high-density populations, space limitation is important. Although density is a continuous variable, the coarse difference in process and dynamics between high- and low-density populations means that this distinction is effective in characterizing the population. Given this basic formulation, it is then possible to phenomenologically model a suite of processes that include both Allee effects, and density-dependent control efficacy.

Being phenomenological, this is not a fully process-driven model. Although some processes are modelled explicitly (e.g. effects of management on different stages), much of the detail is simplified and measured as simple transitions, with the densities being simplified to coarse states. Because the scale of the variables considered is relatively large (whole populations are in one of three density states), a considerable number of processes are not modelled explicitly and averaged over. While sacrificing detail, the approach does permit ready parametrization and analysis, compared with what would be required to parametrize a demographic model.

This model is a particularly relevant example for illustrating how population models can link to policy: the objective of the modelling in Taylor & Hastings [17] was to predict optimal strategies for removal and control of *Spartina*. The population modelling was linked to an economic model and then a genetic algorithm used to find the optimal solution (in the sense of optimizing combined objectives in terms of economics and ultimate plant density). The outputs included the optimal strategy as well as costs and riskiness. Similarly, Hanson *et al.* [63] formulated a model for coastal erosion in which the options for management and their outcomes were modelled as discrete states. The model then estimated transitions probabilities between these states. Figure 2 gives an example of how an ecological demographic model can be framed as a state-structured model.

There are a number of advantages to the approach of considering categories for data or outputs:

- Although this approach seems less precise, model precision is often spurious and the exact result can be taken too seriously. This is particularly the case if estimates of model uncertainty are not given. Using categories can then be more honest,

accurate and realistic. With usual models, the assumptions or parameter estimates may change and it is then necessary to reconsider the consequences of the model output with, say a 45.2 per cent rather than a 58.1 per cent change in weed abundance or coastal habitat. If the output is in broad categories then, as the responses are to the state they remain the same. Thus, they may be a suite of consequences related to high levels of loss of intertidal habitat and this change then says that it is more likely that these will be realized.

- Another advantage is that these models may be more transparent in that they largely consist of the probability of moving between states. This is probably easier to understand, communicate and question than a full mechanistic model. If the processes influencing rates of transition are understood, even only qualitatively, the effects of changing different management options can be explored. Taylor & Hastings [17], for example, were able to do this to model how different management strategies would influence rates of transitions between density states.
- Data collection can be very much more straightforward for such models. In the case of arable weeds, Queenborough *et al.* [65], for example, show that this method can be used to characterize farm scale weed distributions accurately and repeatedly, whereas to do this using conventional detailed demographic counting would be prohibitively labour intensive or time consuming.
- Such models are not an approximation or second rate alternative. For example, Freckleton *et al.* [66] show that it is possible to take a continuous, fully stochastic population model and convert it to a density-structured model without loss of accuracy (as in figure 2). Indeed, it is also possible to go the other way and convert models for discrete data into continuous parameters [66]. The assumptions underlying these models are no more restrictive than those made for other state-structured models in ecology (e.g. age and stage-structured models; [64]).
- State-structured models are numerically stable and require no assumptions about the underlying functional forms of many processes. The density-structured models explored in Freckleton *et al.* [66] yield a stable density-state distribution, and can accommodate a wide range of forms of density-dependence. In these models, the form of density-dependence is determined empirically rather than assumed.

As with any method, there will obviously be limitations to using such approaches. The key issue is that in state-structured models, the underlying processes are not explicitly modelled. As noted above, this is advantageous in that the form of some functions does not have to be assumed, but is determined empirically. However, the models lack explicit parameters driving specific processes: instead the effects of new conditions or management are included by modifying transitions between states. However in some cases, the only knowledge we have is qualitative, and more explicit parametrization may not be possible. For example,

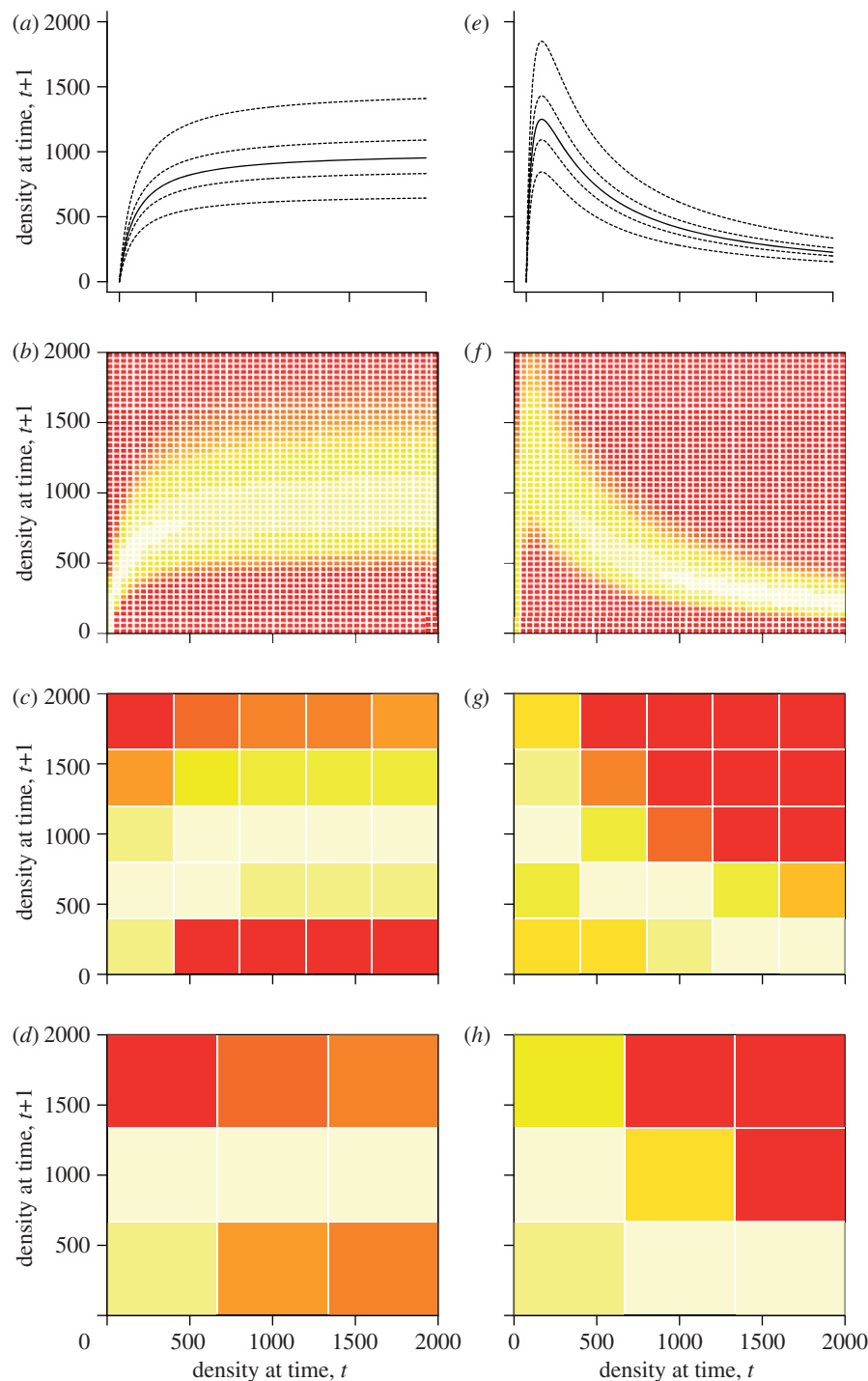


Figure 2. Density-structured models as an example of using a state-structured approach to summarize population dynamics (following Caswell [64]). (a,e) Examples of continuous-density, stochastic population models. The solid line is the mean relationship between density in successive years, the dashed lines indicate 25% and 75% quartiles, representing stochastic variation around the mean response. (b,f) These population models represented as state-structured models in which the model has 50 discrete density states, and in which the model is based on a matrix of transitions between density states. The matrices are shown as heatmaps (red = low probability, yellow = high probability). (c,d) The models represented by five states, and (d,h) The models summarized into three states.

we may know that one form of management may increase the likelihood that a population will move from a low density to a high one, whereas another might have no impact. Even if we do not have a mechanistic model, the effects of this increase can be explored by simply modifying probabilities of growth transitions in the model, and without having to explicitly model the effect of management at the individual or population level.

Although state-structured models are relatively infrequently used in applied ecology, the theory for such models, particularly stage-structured models, which are closely related, is well developed and used frequently [64,67]. Stage-structured models are an approximation to population dynamics in which individuals are grouped according to size categories, and these are a long-established tool in population modelling. Markovian state models are used in

models of succession, for example, vegetation or in marine rocky coast communities [68–70]; however, these approaches could certainly be adapted for a wider range of applications.

5. CONCLUDING REMARKS

The first two issues we have highlighted are important elements in prediction, although they do not directly concern models or predictive tools. The important point is that ecologist's predictions will not be influential unless they are tailored to address the issues that are policy relevant. This requires ecologists to communicate with policy makers in order to identify key questions, as well as requiring policy makers to frame questions in a form that are tractable. For example, in the exercise reported in Sutherland *et al.* [7] over 1000 questions of possible policy relevance were reduced to 100. Many of the initial 1000 questions had already been answered, and throughout the process there was a tension between generic and specific questions. Policy makers often required generic answers, whereas ecologists are often better equipped to answer specific ones.

Although the Discussion Meeting has focused on models as tools for predictions, and how better models can be developed, it is worth noting that predictions can be made in a range of forms, and generic predictions are useful and influential. Although it is natural to think of predictions in terms of quantitative models for specific systems or populations, it is possible to use very general models to generate principles that can be used in informing policy. A good example of this is metapopulation theory, which became influential during the 1990s. Although there are good examples of where fully parametrized metapopulation models have been used to guide conservation, such as the spotted owl in North America [71], arguably the main impact of this model has been in promoting the realization that populations do not exist in isolation but are linked: for instance, the need for linkage was a major component of the Lawton review of biodiversity [41] and the conclusions of that review were incorporated in the UK government's white paper on the environment. In this example, a general lesson or prediction of theory has influenced policy recommendations, but not through a specific modelling exercise.

Predictive ecology will only succeed in influencing policy if its creators realize that there is a wider social and economic context. Scientists who ignore wider context are likely to have little impact. The lesson from the debate surrounding GMHT crops is that although the scientific case may be reasonably straightforward, poor communication of the risks and options can lead to the science being overwhelmed by other agendas.

We have suggested that simple-structured models may be useful tools in predictive modelling. In doing so, we do not wish to imply that sophisticated process-based simulations are not desirable or useful. We believe, however, that simply formulated models can be used to model otherwise extremely complex systems. The examples we have given include a

landscape-scale model for an invasive grass, which includes different management options and economic consequences [17] and a geomorphological model including management and mitigation options at a regional scale [63]. It is worth noting that global circulation models (GCMs), in many ways the 'flagships' for predictive modelling, are usually reliant on 'box models'. These are simplifications in which the box is assumed to be an area in which all processes are homogeneous. The analogy relevant to ecology is that GCMs do not try to model every drop of rain, or even every rainfall event, in order to make useful predictions, so ecological models may not require the fate of every individual in a population, or every process operating, to be considered.

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REFERENCES

- 1 Peters, R. H. 1991 *A critique for ecology*. Cambridge, UK: Cambridge University Press.
- 2 Sutherland, W. J. 2006 Predicting the ecological consequences of environmental change: a review of the methods. *J. Appl. Ecol.* **43**, 599–616. (doi:10.1111/j.1365-2664.2006.01182.x)
- 3 Watkinson, A. R., Freckleton, R. P., Robinson, R. A. & Sutherland 2000 Predictions of biodiversity response to genetically modified herbicide-tolerant crops. *Science* **289**, 1554–1557. (doi:10.1126/science.289.5484.1554)
- 4 Dewar, A. M., May, M. J., Woiwod, I. P., Haylock, L. A., Champion, G. T., Garner, B. H., Sands, R. J. N., Qi, A. M. & Pidgeon, J. D. 2003 A novel approach to the use of genetically modified herbicide tolerant crops for environmental benefit. *Proc. R. Soc. Lond. B* **270**, 335–340. (doi:10.1098/rspb.2002.2248)
- 5 Freckleton, R. P., Stephens, P. A., Sutherland, W. J. & Watkinson, A. R. 2004 Amelioration of biodiversity impacts of genetically modified crops: predicting transient versus long-term effects. *Proc. R. Soc. Lond. B* **271**, 325–331. (doi:10.1098/rspb.2003.2603)
- 6 May, M. J., Champion, G. T., Dewar, A. M., Qi, A. M. & Pidgeon, J. D. 2005 Management of genetically modified herbicide-tolerant sugar beet for spring and autumn environmental benefit. *Proc. R. Soc. B* **272**, 111–119. (doi:10.1098/rspb.2004.2948)
- 7 Sutherland, W. J. *et al.* 2006 The identification of one hundred ecological questions of high policy relevance in the UK. *J. Appl. Ecol.* **43**, 617–627. (doi:10.1111/j.1365-2664.2006.01188.x)
- 8 Royal Society 2009 *Reaping the benefits: towards sustainable intensification of global agriculture*. London, UK: Royal Society.
- 9 Prime Minister's Strategy Unit 2003 *Field work: weighing up the costs and benefits of GM crops*. London, UK: Cabinet Office.
- 10 King, D. *et al.* 2003 GM Science Review. First Report. London, UK: Department of Trade and Industry.

- 11 Firbank, L. G. *et al.* 2003 An introduction to the farm-scale evaluations of genetically modified herbicide-tolerant crops. *J. Appl. Ecol.* **40**, 2–16. (doi:10.1046/j.1365-2664.2003.00787.x)
- 12 Freckleton, R. P., Sutherland, W. J. & Watkinson, A. R. 2004 The fate of GM crops in Europe. *Science* **304**, 954–956.
- 13 Randall, D. A. *et al.* 2007 Climate models and their evaluation. In *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller). Cambridge, UK: Cambridge University Press.
- 14 Clark, J. S., Bell, D. M., Kwit, M., Stine, A., Vierra, B. & Zhu, K. 2012 Individual-scale inference to anticipate climate-change vulnerability of biodiversity. *Phil. Trans. R. Soc. B* **367**, 236–246. (doi:10.1098/rstb.2011.0183)
- 15 Grimm, V. & Railsback, S. F. 2012 Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. *Phil. Trans. R. Soc. B* **367**, 298–310. (doi:10.1098/rstb.2011.0180)
- 16 Grenfell, B. T., Pybus, O. G., Wood, J. L. N., Daly, J. M., Mumford, J. A. & Holmes, E. C. 2004 Unifying the epidemiological and evolutionary dynamics of pathogens. *Science* **303**, 327–332. (doi:10.1126/science.1090727)
- 17 Taylor, C. M. & Hasting, A. 2004 Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *J. Appl. Ecol.* **41**, 1049–1057. (doi:10.1111/j.0021-8901.2004.00979.x)
- 18 Sutherland, W. J., Pullin, A. S., Dolman, P. M. & Knight, T. M. 2004 The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305–308. (doi:10.1016/j.tree.2004.03.018)
- 19 Sutherland, W. J., Fleishman, E., Mascia, M. B., Pretty, J. & Rudd, M. A. 2011 Methods for collaboratively identifying research priorities and emerging issues in science and policy. *Methods Ecol. Evol.* **2**, 238–247. (doi:10.1111/j.2041-210X.2010.00083.x)
- 20 Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F. & Phalan, B. 2008 How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* **23**, 538–545. (doi:10.1016/j.tree.2008.06.012)
- 21 Koh, L. P. & Wilcove, D. S. 2008 Is oil palm agriculture really destroying tropical biodiversity? *Conserv. Lett.* **1**, 60–64. (doi:10.1111/j.1755-263X.2008.00011.x)
- 22 Holmes, J. & Clark, E. 2008 Enhancing the use of science in environmental policy-making and regulation. *Environ. Sci. Policy* **11**, 702–711. (doi:10.1016/j.envsci.2008.08.004)
- 23 Sutherland, W. J. & Woodroof, H. J. 2009 The need for environmental horizon scanning. *Trends Ecol. Evol.* **24**, 523–527. (doi:10.1016/j.tree.2009.04.008)
- 24 Brown, D. 2007 Horizon scanning and the business environment—the implications for risk management. *BT Technol. J.* **25**, 214–218.
- 25 Quiggin, T. 2007 *Seeing the invisible. National security intelligence in an uncertain age*. Singapore: World Scientific.
- 26 O’Malley, S. P. & Jordan, E. 2009 Horizon scanning of new and emerging medical technology in Australia: its relevance to Medical Services Advisory Committee health technology assessments and public funding. *Int. J. Technol. Assess. Health Care* **25**, 374–382. (doi:10.1017/S0266462309990031)
- 27 Sutherland, W. J. *et al.* 2008 Future novel threats and opportunities facing UK biodiversity identified by horizon scanning. *J. Appl. Ecol.* **45**, 821–833. (doi:10.1111/j.1365-2664.2008.01474.x)
- 28 Sutherland, W. J. *et al.* 2010 A horizon scan of global conservation issues for 2010. *Trends Ecol. Evol.* **25**, 1–7. (doi:10.1016/j.tree.2009.10.003)
- 29 Sutherland, W. J. *et al.* 2011 A horizon scan of global conservation issues for 2011. *Trends Ecol. Evol.* **26**, 10–16. (doi:10.1016/j.tree.2010.11.002)
- 30 Sutherland, W. J., Barlow, R., Clements, A., Harper, M., Herkenrath, P., Margerison, C., Monk, K. A., Robinson, J. A. & Thompson, D. B. A. 2011 What are the forthcoming legislative issues of interest to ecologists and conservationists in 2011? *BES Bull.* **1**, 26–31.
- 31 Sutherland, W. J. *et al.* 2009 An assessment of the 100 questions of greatest importance to the conservation of global biological diversity. *Conserv. Biol.* **23**, 557–567. (doi:10.1111/j.1523-1739.2009.01212.x)
- 32 Fleishman, E. *et al.* 2011 Top 40 priorities for science to inform US conservation and management policy. *BioScience* **61**, 290–300. (doi:10.1525/bio.2011.61.4.9)
- 33 Pretty, J. J. *et al.* 2010 The top 100 questions for global agriculture and food. *Int. J. Agric. Sust.* **8**, 219–236. (doi:10.3763/ijas.2010.0534)
- 34 Petrokofsky, G. *et al.* 2010 A participatory process for identifying and prioritizing policy-relevant research questions in natural resource management: a case study from the UK forestry sector. *Forestry* **83**, 357–367. (doi:10.1093/forestry/cpq018)
- 35 Rudd, M. A. *et al.* 2011 Generation of priority research questions to inform conservation policy and management at a national level. *Conserv. Biol.* **25**, 476–484. (doi:10.1111/j.1523-1739.2010.01625.x)
- 36 Morton, S. R. *et al.* 2009 The big ecological questions inhibiting effective environmental management in Australia. *Austral. Ecol.* **34**, 1–9. (doi:10.1111/j.1442-9993.2008.01938.x)
- 37 Pullin, A. S. *et al.* 2009 Conservation focus on Europe: major conservation policy issues that need to be informed by conservation science. *Conserv. Biol.* **23**, 818–824. (doi:10.1111/j.1523-1739.2009.01283.x)
- 38 Armsworth, P. R. *et al.* 2010 The ecological research needs of business. *J. Appl. Ecol.* **47**, 235–243. (doi:10.1111/j.1365-2664.2010.01792.x)
- 39 Cooke, S. J., Danylchuk, A. J., Kaiser, M. J. & Rudd, M. A. 2010 Is there a need for a ‘100 questions exercise’ to enhance fisheries and aquatic conservation, policy, management and research? Lessons from a global 100 questions exercise on conservation of biodiversity. *J. Fish. Biol.* **76**, 2261–2286. (doi:10.1111/j.1095-8649.2010.02666.x)
- 40 Sutherland, W. J. *et al.* 2010 The identification of priority opportunities for UK nature conservation policy. *J. Appl. Ecol.* **47**, 955–965. (doi:10.1111/j.1365-2664.2010.01863.x)
- 41 Lawton, J. H. *et al.* 2010 Making Space for Nature: a review of England’s wildlife sites and ecological networks. Report to Defra. See <http://www.defra.gov.uk/environment/biodiversity/documents/201009space-for-nature.pdf>.
- 42 Jacquet, J., Boyd, I., Carlton, J. T., Fox, H., Johnson, A. E., Mee, L., Roman, J., Spalding, M. & Sutherland, W. J. 2011 Scanning the oceans for solutions. *Solutions* **2**, 46–55.
- 43 Dicks, L. J., Showler, D. A. & Sutherland, W. J. 2010 *Bee conservation: evidence for the effectiveness of interventions*. Exeter, UK: Pelagic Publishing.
- 44 Robinson, R. A. & Sutherland, W. J. 1999 The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. *Ecography* **22**, 447–454. (doi:10.1111/j.1600-0587.1999.tb00581.x)
- 45 Cooke, I. R. *et al.* 2009 Integrating socio-economics and ecology: a taxonomy of quantitative methods and a review of their use in agro-ecology. *J. Appl. Ecol.* **46**, 269–277. (doi:10.1111/j.1365-2664.2009.01615.x)

- 46 Wam, H. K., Hofstad, O., Navdal, E. & Sankhayan, P. 2005 A bio-economic model for optimal harvest of timber and moose. *Forest Ecol. Manag.* **206**, 207–219. (doi:10.1016/j.foreco.2004.10.062)
- 47 Quaas, M. F., Baumgartner, S., Becker, C., Frank, K. & Muller, B. 2007 Uncertainty and sustainability in the management of rangelands. *Ecol. Econ.* **62**, 251–266. (doi:10.1016/j.ecolecon.2006.03.028)
- 48 Tichit, M., Doyen, L., Lemel, J. Y., Renault, O. & Durant, D. 2007 A coviability model of grazing and bird community management in farmland. *Ecol. Model.* **206**, 277–293. (doi:10.1016/j.ecolmodel.2007.03.043)
- 49 Berger, P. A. & Bolte, J. P. 2004 Evaluating the impact of policy options on agricultural landscapes: an alternative-futures approach. *Ecol. Appl.* **14**, 342–354. (doi:10.1890/02-5069)
- 50 Drechsler, M., Watzold, F., Johst, K., Bergmann, H. & Settele, J. 2007 A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. *Biol. Conserv.* **140**, 174–186. (doi:10.1016/j.biocon.2007.08.013)
- 51 Annetts, J. E. & Audsley, E. 2002 Multiple objective linear programming for environmental farm planning. *J. Oper. Res. Soc.* **53**, 933–943. (doi:10.1057/palgrave.jors.2601404)
- 52 Belton, V. & Stewart, T. J. 2002 *Multiple criteria decision analysis: an integrated approach*. Dordrecht, The Netherlands: Kluwer Academic.
- 53 Siriwardena, G. M., Cooke, I. R. & Sutherland, W. J. In press. Landscape, cropping and field boundary influences on bird abundance. *Ecography*. (doi:10.1111/j.1600-0587.2011.06839.x)
- 54 Evans, M. R., Norris, K. J. & Benton, T. G. 2012 Predictive ecology: systems approaches. *Phil. Trans. R. Soc. B* **367**, 163–169. (doi:10.1098/rstb.2011.0191)
- 55 Mustin, K., Sutherland, W. J. & Gill, J. A. 2008 The complexity of predicting climate-induced ecological impacts. *Clim. Res.* **35**, 165–175. (doi:10.3354/cr00723)
- 56 Freckleton, R. P., Sutherland, W. J., Watkinson, A. R. & Stephens, P. A. 2008 Modelling the effects of management on population dynamics: some lessons from annual weeds. *J. Appl. Ecol.* **45**, 1050–1058. (doi:10.1111/j.1365-2664.2008.01469.x)
- 57 Freckleton, R. P. & Watkinson, A. R. 1998 Predicting the determinants of weed abundance: a model for the population dynamics of *Chenopodium album* in sugar beet. *J. Appl. Ecol.* **35**, 904–920. (doi:10.1111/j.1365-2664.1998.tb00008.x)
- 58 Stephens, P. A. & Sutherland, W. J. 1999 Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405. (doi:10.1016/S0169-5347(99)01684-5)
- 59 Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999 Inverse density-dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410. (doi:10.1016/S0169-5347(99)01683-3)
- 60 Courchamp, F. & Berec, L. 2008 *Allee effects in ecology and conservation*. Oxford, UK: Oxford University Press.
- 61 Rees, M., Grubb, P. J. & Kelly, D. 1996 Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *Am. Nat.* **147**, 1–32. (doi:10.1086/285837)
- 62 Sibly, R. M., Barker, D., Denham, M. C., Hone, J. & Pagel, M. 2005 On the regulation of populations of birds, fish, and insects. *Science* **309**, 607–610. (doi:10.1126/science.1110760)
- 63 Hanson, S., Nicholls, R. J., Balson, P., Brown, I., French, J. R., Spencer, T. & Sutherland, W. J. 2010 Capturing coastal geomorphological change within regional integrated assessment: an outcome-driven fuzzy logic approach. *J. Coast. Res.* **26**, 831–842. (doi:10.2112/JCOASTRES-D-09-00078.1)
- 64 Caswell, H. 2000 *Matrix population models*, 2nd edn. Sunderland, MA: Sinauer.
- 65 Queenborough, S. A., Burnet, K. M., Sutherland, W. J., Watkinson, A. R. & Freckleton, R. P. 2011 From meso- to macroscale population dynamics: a new density-structured approach. *Methods Ecol. Evol.* **2**, 289–302. (doi:10.1111/j.2041-210X.2010.00075.x)
- 66 Freckleton, R. P., Sutherland, W. J., Watkinson, A. R. & Queenborough, S. A. 2011 Density-structured models for plant population dynamics. *Amer. Nat.* **177**, 1–17. (doi:10.1086/657621)
- 67 Caswell, H. 1989 *Matrix population models*. Sunderland, MA: Sinauer
- 68 Usher, M. B. 1987 Modelling successional processes in ecosystems. In *Colonization, succession and stability* (eds A. J. Gray, M. J. Crawley & P. J. Edwards), pp. 31–56. Oxford, UK: Blackwell.
- 69 Balzter, H. 2000 Markov chain models for vegetation dynamics. *Ecol. Model.* **126**, 139–154. (doi:10.1016/S0304-3800(00)00262-3)
- 70 Tanner, J. E., Hughes, T. P. & Connell, J. H. 1996 The role of history in community dynamics: a modelling approach. *Ecology* **77**, 108–117. (doi:10.2307/2265660)
- 71 Wilcove, D. 1993 Turning conservation goals into tangible results: the case of the spotted owl and old-growth forests. In *Large-scale ecology and conservation biology* (eds P. J. Edwards, R. M. May & N. R. Webb), pp. 313–330. Oxford, UK: Blackwell Scientific.