Cell PRESS

Ecological models supporting environmental decision making: a strategy for the future

Amelie Schmolke[1], Pernille Thorbek[2], Donald L. DeAngelis[3] and Volker Grimm[1]

[1] UFZ, Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany
[2] Syngenta, Environmental Safety, Jealott's Hill International Research Centre, Bracknell, Berkshire RG42 6EY, UK
[3] USGS/Biological Resources Division and Department of Biology, University of Miami, PO Box 249118, Coral Gables, FL 33124, USA

Ecological models are important for environmental decision support because they allow the consequences of alternative policies and management scenarios to be explored. However, current modeling practice is unsatisfactory. A literature review shows that the elements of good modeling practice have long been identified but are widely ignored. The reasons for this might include lack of involvement of decision makers, lack of incentives for modelers to follow good practice, and the use of inconsistent terminologies. As a strategy for the future, we propose a standard format for documenting models and their analyses: transparent and comprehensive ecological modeling (TRACE) documentation. This standard format will disclose all parts of the modeling process to scrutiny and make modeling itself more efficient and coherent.

Decision making requires models

Currently, virtually all ecological systems are directly or indirectly affected by human activities. This impact is increasingly being regulated by public authorities and policies [1,2]. However, the complexity of ecological systems makes it hard to predict effects of regulations and management measures. Owing to the interaction of numerous factors, and the extent of temporal and spatial scales of concern, empirical approaches are often too limited to inform policy and decision making.

Ecological models have the potential to solve this problem. They are simplified representations of key mechanisms and factors that explain the behavior of ecological systems in a certain context. They can include processes on different scales and hierarchical levels, including individuals, populations, communities and ecosystems. Existing knowledge and experimental data can be extrapolated to larger temporal and spatial scales [3,4]. Thus, ecological models represent an indispensable tool for supporting environmental decision making by exploring the consequences of alternative policies or management scenarios in various fields, for instance, habitat and endangered species management, forest and fisheries management, and chemical risk assessment [5–8].

Corresponding author: Schmolke, A. (amelie.schmolke@ufz.de).

Although ecological models have been used to support some environmental decision making for a long time, we think that they will need to be used much more widely in the future. This trend is confirmed by the increasing interest shown by authorities and industry in ecological models and their applications [9–11]. In addition, it is now widely recognized that we need to understand how ecosystems function and how human activities interact with them in order to guide environmental protection more effectively [12–14]. Ecological models can facilitate such understanding. However, the development of ecological models for decision support is a challenging process.

Ecological models for decision support

Ecological models are developed for different purposes: exploration of ideas and theories, demonstration of concepts, understanding of general principles and patterns, predictions of ecosystem behaviors, and many more [15,16]. This has led to a great variety of model types and modeling styles. When submitted for publication in the scientific literature, models are assessed mainly with regard to their scientific originality. However, especially if ecological models are to be used for supporting decisions affecting the real world, further assessment of model quality and suitability is critical, because decisions regarding environmental issues are so vital. Rykiel [17] lists two crucial elements of model evaluation: first, determining 'if the model is acceptable for its intended use, i.e., whether the model mimics the real world well enough for its stated purpose'; and second, 'how much confidence to place in inferences about the real system that are based on model results'.

To be able to make these judgments about model utility, transparent modeling approaches and comprehensive model tests and analyses are required. However, current modeling practice is neither transparent nor comprehensive in its testing and analysis of models. Concerns include *ad hoc* model design [18,19], unknown sensitivities and uncertainties of model predictions, unclear sources of parameterization [20], inappropriate domains of application [7,21,22], lack of understanding of the model's behavior, and lack of thorough model analysis [17,20,22]. Consequently, the risk is still high that ecological models will support wrong and often irreversible decisions, as they have in certain cases in the past [23–26]. Therefore, to ensure the quality of ecological models, a 'good modeling practice' is needed, which would be a standard protocol for model formulation, documentation, testing, analysis and application.

Need for good modeling practice

The recognition of the need for establishing good modeling practice is not new. It has been acknowledged for many years and across many different disciplines in which ecological models are used for supporting decision making [27–29]. Although there have been very useful and detailed attempts to propose such guidance [30–33], the state of the art of ecological modeling for decision support is still unsatisfactory. One possible explanation we initially proposed is that there is a lack of consensus on the important elements of good modeling practice.

To test the validity of this explanation, we reviewed reviews and methodological publications, published since 1995, that explicitly discuss ecological models in the context of environmental decision making. We reviewed publications from various fields, including biological conservation, natural resource management, agriculture, pest management and chemical risk assessment and indentified important elements from across the whole modeling process (Table 1; for details, see Online Supplementary Material). In 41 publications from various fields of application, we found 13 convergent issues; i.e. elements of the modeling process that were considered critical to the role of ecological models for supporting environmental decision making (Table 1). The issues raised were not dependent on discipline or on the year of publication. Some issues were raised by several authors, but were referred to using different terminologies. For instance, the terms model evaluation, validation and verification have been subject to argument in the literature, and are not used coherently [17,34,35].

The main conclusion from this review is that, in fact, there is a general consensus on which elements need to be addressed for good modeling practice. These elements have been described clearly in numerous publications. In a perfect world, all modelers would agree on and thoroughly address all issues listed in Table 1, and all decision makers would perfectly understand and appreciate this work. In the real world, however, this is not the case [36]. How is this so?

Challenges for the establishment of good modeling practice

We think that good modeling practice has not been established so far for three main reasons: lack of sufficient involvement of decision makers and stakeholders in the modeling process, lack of incentives for modelers to follow good practice, and lack of coherent terminology regarding the elements and issues of the modeling process.

As emphasized in nine out of the 41 publications in our review, decision makers and other stakeholders should play an essential role in the process of ecological modeling for decision support. Ecological modeling is an iterative

Table 1. Elements of good modeling practice identified from the literature

Element	Description	Refs[a]
Inclusion of stakeholders	Ongoing communication between stakeholders and modelers during model building, which is a critical factor for the success or failure of modeling projects.	[19,27,31,32,38–40,49,50]
Formulation of objectives	Definition of objectives at the outset of a modeling project, which includes the assessment of the actual management issue, key variables and processes, data availability, kind of outputs required, and how they will inform decisions.	[17,19,28–32,38,39,49,51–54]
Conceptual model	Formalization of the assumptions about the system and preliminary understanding of its internal organization and operation.	[19,21,31,32,39,49,54]
Choice of model approach	Identification of the most appropriate modeling approach in the context of the goal of the modeling project.	[18–21,31,49,51,52,55–58]
Choice of model complexity	Determination of the optimal complexity level for the problem at hand.	[19,27,31,51,53,55,56,58–62]
Use of multiple models	Application of multiple models to the same problem, which can decrease the uncertainty about the appropriate model approach and main assumptions.	[17,31,41,55,58,63]
Parameterization and calibration	Determination of model parameters from empirical data or by means of calibration of the model outputs on the basis of data.	[17–21,30–32,41,49,55,57,58,60,64,65]
Verification	Assurance that the modeling formalism is correct; i.e., that the model has been implemented correctly.	[17,19–21,28,31,66,67]
Sensitivity analysis	Systematic testing of the sensitivity of model results to changes in parameter values.	[17,20,28–32,39,41,53,55,68,69]
Quantification of uncertainties	Determination of the confidence limits of the model outputs, which is essential for the judgment of the usefulness of the model and its outputs in the contexts of decisions.	[19,21,22,30–32,41,53,54,58,65,68–72]
Validation	Comparison of model outputs with independent empirical data sets; i.e., data that have not been used for parameterization or calibration of the model.	[17,19–22,28–31,54,55,58,65,67,68,70]
Peer review	Quality assessment of a model and its analyses by independent experts.	[17,28,31,39]
Documentation and transparency	Accurate communication of models, and transparency of the modeling process, which can be achieved through a clear and complete documentation of the model and its evaluation.	[6,7,20,27–31,39,50,65,68,72]

[a]The reviewed publications covered various domains (number of publications): species or habitat management and conservation (11); fisheries and marine ecosystem management (4); forest and land use management (5); natural resource management (including water management; 9); agricultural systems (2); pest management (2); chemical risk assessment (5); general modeling (3) (for details, see Online Supplementary Material).

process, because models often turn out to be incomplete or inconsistent, and this requires going back and revising the formulation of the model, the underlying conceptual model, or even the original problem formulation [37]. During this process or cycle, decision makers need to set and review model objectives, model outputs and acceptance criteria repeatedly [19,38–40] (i.e. the modeling process can be seen as joint learning process between modelers and decision makers). Without involvement of decision makers, it would be impossible to formulate good modeling practice [7,41], but since no standardized approaches exist, decision makers would face the task of assessing all kinds of different modeling studies on a case-by-case basis, for which they usually have neither training nor time.

Ecological modelers commonly pursue goals (i.e. their own research agenda and academic publications) that might not correspond to the scope of the policy or management problem at hand [40]. Scientists might also lack understanding of the issues that need to be addressed before model results can be used to support environmental decision making. In addition, modelers would face a considerably higher workload than that for a purely scientific modeling exercise, if all essential elements of the modeling process, as identified in the literature (Table 1), have to be addressed thoroughly. Thus, incentives to follow good modeling practice would have to include benefits for the scientists; for instance, by increasing the acceptance of model approaches in decision contexts, and by making the modeling process itself more efficient and fit for publication.

Inconsistent and controversial terminology [17,34,35] also hampers the establishment of good modeling practice. The fact that a consensus about the elements of the modeling process exists is obscured by the contradictory use of terms like verification, validation, evaluation, uncertainty, etc.

How can these challenges be overcome? In principle, good modeling practice could be made a requirement for ecological models in decision making processes, but there is a question about who would have the power to do this, and whether such power would be desirable. Even a large agency like the Environmental Protection Agency (EPA) of the USA hesitates to impose guidance but emphasizes the use of a "non-mandatory language" [31]. Such guidance cannot be made up out of thin air, but has to be based on a consensus in the field. In order to reach such a consensus, a vast body of experience would be necessary, as is the case in empirical disciplines (e.g. test methods in chemical risk assessment).

Thus, a better solution would be to initiate a bottom-up process that leads decision makers and modelers towards incrementally implementing good modeling practice through a more or less self-organizing process. We propose that a standardized documentation of ecological modeling projects would be the necessary starting point for such a process.

Documentation as starting point for good modeling practice

Standardizing the model documentation does not standardize the model approaches themselves but assures that all modeling aspects are readily available for scrutiny. Such documentation should be understandable by nonmodelers, and thus, work as a tool for decision makers to assess model suitability. A standardized documentation is effective, because it raises readers' expectations about what information should be expected and where it can be found. Accordingly, the use of a standardized protocol would ensure transparency and comprehensiveness of model documentation, and would allow readers to easily assess necessary information, something which is not always possible currently.

The fulfillment of readers' expectations is crucial for the acceptance of new information. In a seminal article about scientific writing, Gopen and Swan [42] note that 'readers make many of their most important interpretive decisions about the substance of prose based on clues they receive from its structure.' This is most obvious with the structure of scientific publications: readers expect an article to follow the sequence: title, abstract, introduction, materials and methods, etc. (Figure 1). Not having this established structure would cause considerable confusion. We would not

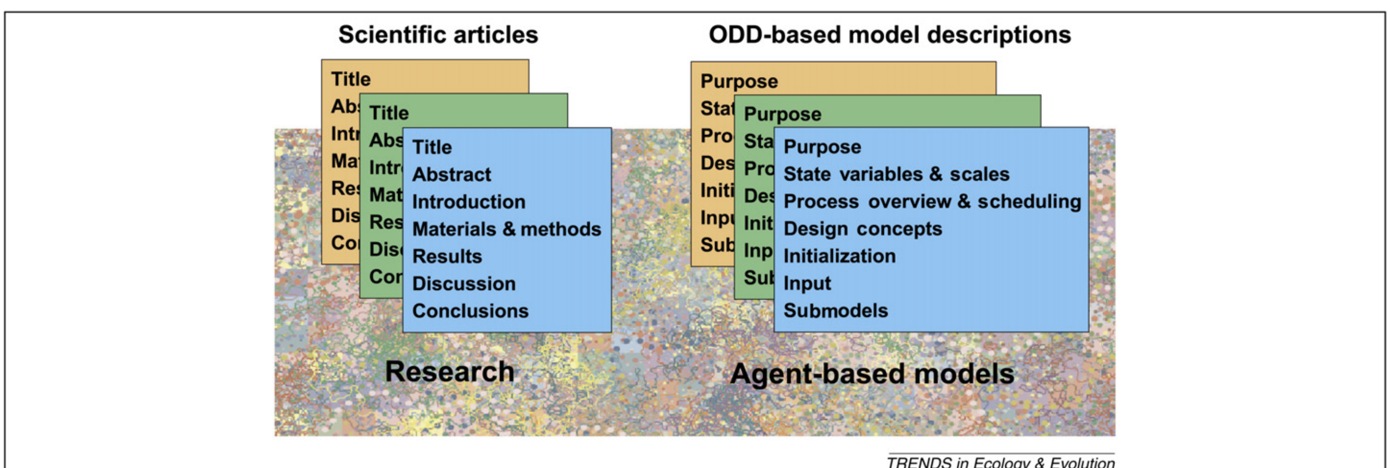

Figure 1. Standard documentation formats. Standard formats for documentation allow transparent and comprehensive communication even if the things to be communicated are extremely diverse and sometimes complex. Scientific articles always have more or less the same structure, despite the virtually unlimited diversity of scientific issues, methods, and concepts. Likewise, descriptions of individual- or agent-based models that are based on the ODD (Overview, Design concepts, Details) protocol [43] always have the same structure, independent of the idiosyncrasies of a model.

know where to expect what, so we would have to read every article word by word, and ask ourselves for every sentence whether it is interpretation or fact, and so forth. Gopen and Swan [42] conclude: 'Information is interpreted more easily and more uniformly if it is placed where most readers expect to find it.'

Thus, a standard can be established by first raising, and then fulfilling readers', or users', expectations. This has been tried recently for documenting individual- and agent-based models (IBMs and ABMs; [43]). The ODD protocol (Figure 1) provides overview, design concepts and details about the model. This protocol was explicitly designed not only to produce a transparent and comprehensive model description, but also to raise and establish readers' expectations, an approach which currently seems to be gaining ground in the community of individual- and agent-based modelers: about 20% of all publications in this field in the years 2008 and 2009 cite the ODD protocol and about 13% actually use it. Modelers start using ODD as a hierarchical checklist for formulating models. Likewise, readers, not all of whom are modelers themselves, learn that model descriptions based on ODD are complete, easy to read and understand, and follow a structure that is completely independent of the idiosyncrasies of any particular model.

We propose that a similar bottom-up strategy should be employed for establishing a standard, good modeling practice for ecological modeling used in decision support; using the strategy of raising and establishing readers' expectations regarding the documentation of the entire modeling process or cycle. In the following, we introduce a framework for transparent and comprehensive ecological modeling documentation, or TRACE documentation for short.

Transparent and comprehensive ecological modeling (TRACE) documentation

We propose TRACE as a standard format for documenting model development, testing and analysis, and application (Box 1). This format consists of the essential elements of the modeling process that we identified in our review (Table 1). The elements are arranged in the sequence corresponding to the sequence of tasks in the iterative modeling cycle (Figure 2). The TRACE documentation is more comprehensive than the ODD protocol. For IBMs and ABMs, an ODD protocol would be part of a TRACE documentation, mainly under the subheader *Model description* (see Box 1).

The TRACE documentation is not restricted to the description of the model itself, but encompasses the whole modeling process; i.e. model development, testing, analysis and application. This is necessary, because models for decision making can only be assessed in the context of their applications. Model suitability is determined not only by the modeling approach, but also, and perhaps to an even greater extent, by the assumptions and data sources that are used for model design, parameterization and calibration, and validation. The outcomes of the different testing and analysis procedures are decisive for the usefulness of a model for a specific purpose, and uncertainties need to be determined thoroughly, if real world decisions are to be based on a model.

Box 1. TRACE (transparent and comprehensive ecological modeling) documentation structure

I. Model development

Problem formulation: *Context* in which the model will be used, and the type of audience addressed; *specification of the question(s)* that should be answered with the model; statement of the *domain of applicability* of the model, including the extent of acceptable extrapolations; assessment of the *availability of knowledge and data*; specification of necessary *model outputs*.

Design and formulation: Description of the *conceptual model*; description and justification of the *modeling approach* used and of the *complexity*; *entities and processes represented* in the model; most important, the applied *assumptions* about the system.

Model description: Detailed *description of the actual model* and how it has been *implemented* (programs, software platforms, scripts).

Parameterization: *List of all parameter values* used in the model, the *data sources*, and how the parameter values were obtained or calculated; *uncertainties* associated with each parameter.

Calibration: Documentation of the *data sets used* for calibration; *which parameters* were calibrated; what *optimization method* was used.

II. Model testing and analysis

Verification: Assessment of whether the model is working according to its specifications; documentation of what tests have been conducted.

Sensitivity analysis: Exploration of the model behavior for *varying parameters*; documentation of which *parameter combinations* have been tested; *justification* of used parameter ranges and combinations.

Validation: Comparison of model or submodel outputs with *empirical data that were not used for parameterization or calibration*; documentation of *data sources*; what *parts (submodels) have been validated*; what *validation methods* were applied.

III. Model application

Results: Outputs that are used to *inform decisions*; description of *simulation experiments (scenarios)* conducted; *statistics applied* to analyze model outputs.

Uncertainty analysis: *Uncertainties in model outputs* used for recommendations; description of *variance, noise, and bias in empirical data*; determination of *stochasticity* in the model; description of *model uncertainty* which can be assessed through application of different models or submodels; best- and worst-case scenarios.

Recommendation: Description of how *initial question(s) could be answered*; summary of *conclusions* drawn from model; clarification of *extrapolations* used (in time and space).

Depending on the initial questions, and the modeling approaches used, certain elements of the modeling process might not have been conducted by modelers during the development of a model. Nevertheless, they have to be addressed in the TRACE document (i.e. the modelers have to justify *why* those elements were not necessary).

On the one hand, the TRACE documentation framework serves as a checklist for modelers and stakeholders. Decision makers can check if all issues have been addressed in the modeling project. Modelers are provided with a 'floor plan' of the modeling project. In addition, the TRACE documentation framework enables modelers to raise issues that need to be resolved in cooperation with stakeholders: deciding, for instance, what to do about data gaps, what kind of output is necessary, how much uncertainty is acceptable, when the model can be accepted as successfully validated, what extrapolations in time and space are required, etc.

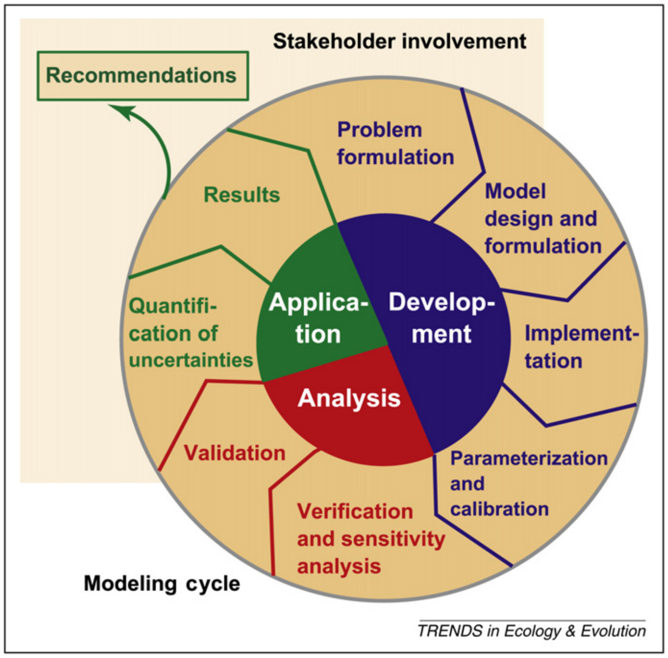

Figure 2. **Modeling cycle for ecological models in decision support.** The elements of the cycle correspond to the elements of the TRACE documentation format, which are grouped in Model Development (blue), Model Testing and Analysis (red), and Model Application (green). Ecological models are developed by several iterations of the modeling process or parts of it. The documentation of the whole modeling process is essential, and should accompany the modeling project on a day-to-day basis using a modeling notebook. The modelers' task is to implement, test and analyze a model, but decision makers and stakeholders need to be involved in problem formulation, assessment of uncertainties and results, and formulation of recommendations.

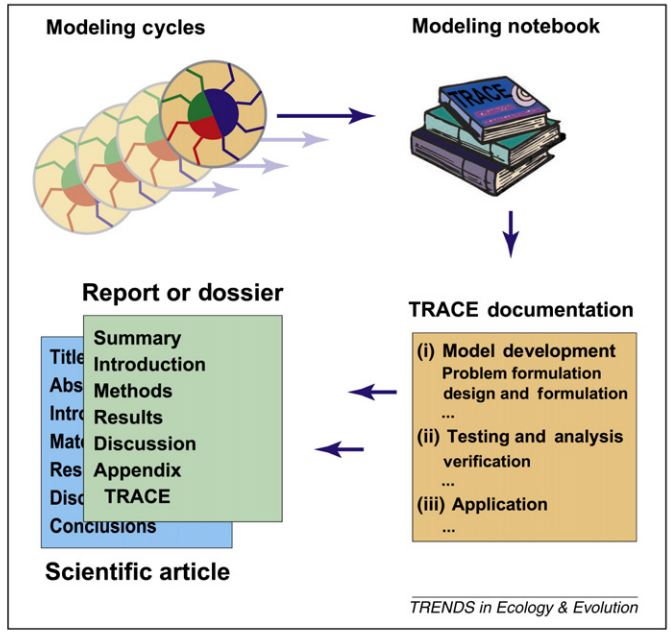

Figure 3. **From modeling notebook to TRACE documentation to report and publication.** The iterative process of modeling, or modeling cycle, is documented on a day-to-day basis in the modeling notebook. The notebook uses the TRACE documentation format. From the notebook, a TRACE documentation of the final model version is compiled, which then is included in the report or dossier for decision makers. The TRACE documentation also can be used for scientific articles. The full documentation would go into an electronic appendix or a website, but a concise version of the key parts of the documentation can go into the main texts in the articles.

On the other hand, the TRACE documentation is also aimed at being the basis of model review by any party involved in the decision process. TRACE documentation will help stakeholders to assess the suitability of a model for the specific problem; that is, the stakeholders are given a tool for the evaluation of ecological modeling approaches, which they can use even if they are not experts in ecological modeling themselves.

In order to achieve these goals, TRACE documentations need to follow the framework as introduced here. Terminology and order of elements of the TRACE documentation framework have to be followed closely. Documentations that only ‘largely’ follow TRACE are not compatible with the basic idea of TRACE as a standard: if the label ‘TRACE’ is used for a modeling documentation, readers should know exactly what to expect, and in what order, independent of the problem addressed, model type used and background of the model developer.

TRACE documentations thus aim to provide a common format and terminology, which would make it easier to involve stakeholders in the modeling process and for all parties to learn from existing models and their applications. However, it is also important to consider the ways in which the TRACE standard format for documentation provides direct benefits to the modeler.

Modeling notebook

The format of TRACE documentations follows the sequence of tasks in the modeling cycle (Figure 2). Accordingly, this format can also be used for modeling notebooks; i.e. for the day–to-day planning and documentation of a modeling project (Figure 3). Such notebooks are common practice in empirical work where they are referred to as laboratory notebooks [44,45]. A laboratory notebook is an important and indispensable document of working hypothesis, experimental setup, laboratory conditions and data. In modeling projects, similar issues arise: simplifying assumptions, specific implementations of functions, data sources used, parameter settings, tests that were conducted with the model and its submodels, and, most important, identification of which version of the model they refer to. Although these issues strongly resemble laboratory practice, the need for a modeling notebook as common practice has not been recognized so far, although lab notebooks were recommended in the context of computational biology [46]. Such a notebook is essential if inconsistencies and questions arise during the modeling process or model review. As is the case for laboratory notebooks [44,45], modeling notebooks can be maintained electronically [46–48].

The modeling notebook should use the same elements as the TRACE documentation framework, and serve as a basis for the compilation of the final TRACE documentation (Figure 3). Whereas the final TRACE documentation should refer to a single version of the model, the modeling project usually has gone through several rounds of testing and changes in previous model versions. Simulation models usually consist of multiple modules, which can and should be tested independently. With a notebook it is possible to keep track of whether tests were conducted with the final version of the module, and what tests and parameter ranges have been applied.

From TRACE documentation to good modeling practice

TRACE documentation and the modeling notebook will ensure that models are not applied as black boxes, but can be assessed by decision makers and other stakeholders for their suitability to answer the question at hand. If accepted as a standard by decision makers and modelers alike, compilation and review of TRACE documentations will be greatly facilitated through experience and readers' expectations.

Despite these considerable benefits, TRACE documentation by itself is not sufficient for good modeling practice, which should also provide guidelines on *how* modeling projects should be carried out. This includes guidelines on what modeling approaches should be used in defined contexts, how models should be implemented (or what existing software should be used), how model evaluations should be conducted and what statistical methods should be applied to model analysis and validation procedures, how model results should be translated into recommendations about (for example) management decisions, and much more.

Detailed and binding guidelines on methods used in modeling projects for decision support need to be based on long-term experience. Models need to be applied in real world contexts, and the decisions that were (at least partly) based on model results should be evaluated. Only when a large body of such data is available, will it be possible to come to a consensus about good modeling practice. Such expertise is not yet available because ecological models have not been applied systematically and their performances have, so far, not been evaluated on a broad scale. By documenting models using the TRACE framework, the acceptance of models for decision support will be facilitated, and accordingly, more model applications will be available as test beds for good modeling practice.

Whether or not good modeling practice is in place, a transparent and comprehensive documentation of ecological modeling projects, including the modeling notebook, is essential. Thus, the TRACE framework is an important contribution to the field by itself. Good modeling practice guidelines might have to be specific to particular fields (e.g. environmental toxicology), whereas the TRACE framework applies to ecological modeling approaches in general, as can be concluded from our literature review.

Conclusions

Although ecological models are gaining importance in decision support, no general guidelines exist for their development, testing and analysis, and application. In a review of literature, we find that guidance has been discussed and solutions introduced for many parts of the modeling process. However, articles are usually restricted to one or a few elements of the modeling process, and advice is scattered across disciplines, even though similar issues arise.

As a strategy for the future, we introduce a standard framework for transparent and comprehensive ecological modeling (TRACE) documentation. The elements of the framework are derived from the issues raised in the literature across several disciplines, and the framework comprises the whole modeling process. The TRACE documentation framework assures that every important element of the modeling process is thoroughly addressed in a well structured document. If accompanied by TRACE documentation, modeling projects will be easy to assess by any party. The TRACE documentation framework brings together the expertise from various fields of application of ecological models, and it can be applied generally to the documentation of any ecological modeling project. In addition, the routine day-to-day documentation, which is an indispensable part of empirical research, should be adopted by modelers. Such a modeling notebook should make use of the elements of the TRACE framework. Accordingly, the TRACE framework provides a valuable tool for modelers and decision makers (or any other reviewers of modeling projects) alike. The suitability of models for particular questions can be determined, which can lead to a more common application of models in decision contexts.

Outlook

The TRACE documentation framework can only become established as a standard if it is applied and refined by numerous projects. The CREAM project [9] funded by the EU (http://cream-itn.eu) encompasses more than a dozen ecological modeling projects with the objective of application in chemical risk assessment. All modeling projects are conducted in close collaboration with decision makers, and will apply the TRACE framework for documentation. Accordingly, CREAM currently functions as a test bed, and at present is producing a collection of examples for TRACE.

Acknowledgements

We would like to thank the members of the CREAM project (http://cream-itn.eu) for helpful suggestions and discussions during the CREAM kickoff meeting. Thanks to three anonymous reviewers for comments on a previous version of the manuscript. This work was supported by funding for AS by Syngenta. DLD was supported by the Biological Resources Division of the U. S. Geological Survey.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2010.05.001.

References

1 U.S.Fish and Wildlife Service (1973) Endangered Species Act of 1973.
2 European Commission (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora ('Habitats Directive').
3 Bugmann, H. *et al.* (2000) Scaling issues in forest succession modeling. *Climatic Change* 44, 265–289
4 Duarte, P. *et al.* (2003) Mathematical modelling to assess the carrying capacity for multi-species culture within coastal waters. *Ecol. Model.* 168, 109–143
5 Forbes, V.E. *et al.* (2009) Ecological models in support of regulatory risk assessments of pesticides: developing a strategy for the future. *Integr. Environ. Assess. Manage.* 5, 167–172
6 Pretzsch, H. (2007) Analysing and modelling forest stand dynamics for practical application - an European review and perspective. *Eurasian J. Forest Res.* 10, 1–17

7 Rose, K.A. and Cowan, J.H., Jr (2003) Data, models, and decisions in U.S. marine fisheries management: lessons for ecologists. *Annu. Rev. Ecol. Syst.* 34, 127–151
8 DeAngelis, D.L. *et al.* (1998) Landscape modeling for Everglades ecosystem restoration. *Ecosystems* 1, 64–75
9 Grimm, V. *et al.* (2009) CREAM: a European project on mechanistic effect models for ecological risk assessment of chemicals. *Environ. Sci. Pollut. Res.* 16, 614–617
10 Preuss, T.G. *et al.* (2009) Mechanistic effect models for ecological risk assessment of chemicals (MEMoRisk) - a new SETAC Europe Advisory Group. *Environ. Sci. Pollut. Res.* 16, 250–252
11 U.S. Environmental Protection Agency (2009) Summary Report. Risk Assessment Forum Technical Workshop on Population-Level Ecological Risk Assessment, EPA/100/R-09/006.
12 Liu, J.G. *et al.* (2007) Complexity of coupled human and natural systems. *Science* 317, 1513–1516
13 Liu, J.G. *et al.* (2007) Coupled human and natural systems. *Ambio* 36, 639–649
14 Ostrom, E. and Nagendra, H. (2006) Insights on linking forests, trees, and people from the air, on the ground, and in the laboratory. *PNAS* 103, 19224–19232
15 Hall, C.A.S. and Day, J.W., Jr (1977) *Ecological Modeling in Theory and Practice*, John Wiley & Sons
16 Jakeman, A.J. *et al.* (1993) *Modelling Change in Environmental Systems*, John Wiley & Sons
17 Rykiel, E.J. (1996) Testing ecological models: the meaning of validation. *Ecol. Model.* 90, 229–244
18 Ferrier, S. and Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *J. Appl. Ecol.* 43, 393–404
19 Jakeman, A.J. *et al.* (2006) Ten iterative steps in development and evaluation of environmental models. *Environ. Model. Softw.* 21, 602–614
20 Schmolke, A. *et al.* (2010) Ecological models and pesticide risk assessment: current modeling practice. *Environ. Toxicol. Chem.* 29, 1006–1012
21 Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186
22 Electric Power Research Institute (EPRI) (2000) Instream flow assessment methods: guidance for evaluating instream flow needs in hydropower licensing, EPRI Report 1000554.
23 Comiskey, E.J. *et al.* (2004) Evaluating impacts to Florida panther habitat: how porous is the umbrella? *Southeastern Nat.* 3, 51–74
24 Gross, L. (2005) Why not the best? How science failed the Florida panther. *PLoS Biol.* 3, e333
25 Pilkey, O.H. and Pilkey-Jarvis, L. (2007) *Useless Arithmetic*, Columbia University Press
26 Patterson, B.R. and Murray, D.L. (2008) Flawed population viability analysis can result in misleading population assessment: A case study for wolves in Algonquin park. *Canada. Biol. Conserv.* 141, 669–680
27 Parker, P. *et al.* (2002) Progress in integrated assessment and modelling. *Environ. Model. Softw.* 17, 209–217
28 Prisley, S.P. and Mortimer, M.J. (2004) A synthesis of literature on evaluation of models for policy applications, with implications for forest carbon accounting. *Forest Ecol. Manag.* 198, 89–103
29 Janssen, S. and van Ittersum, M.K. (2007) Assessing farm innovations and responses to policies: a review of bio-economic farm models. *Agric. Syst.* 94, 622–636
30 Bart, J. (1995) Acceptance criteria for using individual-based models to make management decisions. *Ecol. Appl.* 5, 411–420
31 Pascual, P. *et al.* (2003) Draft guidance on the development, evaluation, and application of regulatory environmental models, Council for Regulatory Environmental Modeling.
32 Pastorok, R.A. *et al.*, eds (2002) *Ecological Modeling in Risk Assessment: Chemical Effects on Populations, Ecosystems, and Landscapes*, Lewis Publishers
33 Crout, N. *et al.* (2008) Good modelling practice. In *Environmental Modelling, Software and Decision Support: State of the Art and New Perspectives* (Jakeman, A.J. *et al.*, eds), pp. 15–31, Elsevier
34 Oreskes, N. *et al.* (1994) Verification, validation, and confirmation of numerical models in the Earth Sciences. *Science* 263, 641–646
35 Bellocchi, G. *et al.* (2010) Validation of biophysical models: issues and methodologies. *A review. Agron. Sustain. Dev.* 30, 109–130
36 Rose, K.A. *et al.* (2001) Compensatory density dependence in fish populations: importance, controversy, understanding, and prognosis. *Fish Fisheries* 2, 293–327
37 Grimm, V. and Railsback, S.F. (2005) *Individual-Based Modeling and Ecology*, Princeton University Press
38 Landsberg, J. (2003) Modelling forest ecosystems: state of the art, challenges, and future directions. *Can. J. Forest Res.* 33, 385–397
39 Nicolson, C.R. *et al.* (2002) Ten heuristics for interdisciplinary modeling projects. *Ecosystems* 5, 376–384
40 Oxley, T. *et al.* (2004) Integrated modelling and decision-support tools: a Mediterranean example. *Environ. Model. Softw.* 19, 999–1010
41 Harwood, J. and Stokes, K. (2003) Coping with uncertainty in ecological advice: lessons from fisheries. *Trends Ecol. Evol.* 18, 617–622
42 Gopen, G.D. and Swan, J.A. (1990) The science of scientific writing. *Am. Sci.* 78, 550–558
43 Grimm, V. *et al.* (2006) A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198, 115–126
44 Beveridge, W.I.B. (1950) *The Art of Scientific Investigation*, The Blackburn Press
45 Kanare, H.M. (1985) *Writing the Laboratory Notebook*, American Chemical Society
46 Noble, W.S. (2009) A quick guide to organizing computational biology projects. *PLoS Comput. Biol.* 5, e1000424
47 Rabin, R. and Pastorius, E. (2005) Electronic laboratory notebook systems. *Genet. Eng. News* 25 (http://www.genengnews.com/gen-articles/electronic-laboratory-notebook-systems/1075/).
48 Denny-Gouldson, P. (2007) Meeting the specialized requirements of the biologist through a biology-focused electronic laboratory notebook. *Am. Lab.* 39, 26–28
49 Jackson, L.J. *et al.* (2000) An introduction to the practice of ecological modeling. *BioScience* 50, 694–706
50 Perry, G.L.W. and Enright, N.J. (2006) Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progr. Phys. Geogr.* 30, 47–72
51 Bartell, S.M. *et al.* (2003) Realism and relevance of ecological models used in chemical risk assessment. *Hum. Ecol. Risk Assess.* 9, 907–938
52 Boorman, D. *et al.* (2007) A model selection protocol to support the use of models for water management. *Hydrol. Earth Syst. Sci.* 11, 634–646
53 Jakeman, A.J. and Letcher, R.A. (2003) Integrated assessment and modelling: features, principles and examples for catchment management. *Environ. Model. Softw.* 18, 491–501
54 Radomski, P.J. and Goeman, T.J. (1996) Decision making and modeling in freshwater sport-fisheries management. *Fisheries* 21, 14–21
55 Beissinger, S.R. and Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *J. Wildlife Manage.* 62, 821–841
56 Jongejans, E. *et al.* (2008) Dispersal, demography and spatial population models for conservation and control management. *Perspect. Plant Ecol. Evol. Syst.* 9, 153–170
57 Petersen, J.H. and DeAngelis, D.L. (2008) An overview of methods for developing bioenergetic and life history models for rare and endangered species. *Trans. Am. Fish. Soc.* 137, 244–253
58 Wiegand, T. *et al.* (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos* 100, 209–222
59 Fulton, E.A. *et al.* (2003) Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.* 253, 1–16
60 Mooij, W.M. and DeAngelis, D.L. (2003) Uncertainty in spatially explicit animal dispersal models. *Ecol. Appl.* 13, 794–805
61 Nelson, W.A. *et al.* (2008) Balancing ecological complexity in predictive models: a reassessment of risk models in the mountain pine beetle system. *J. Appl. Ecol.* 45, 248–257
62 Wennergren, U. *et al.* (1995) The promise and limitations of spatial models in conservation biology. *Oikos* 74, 349–356
63 Cary, G.J. *et al.* (2006) Comparison of the sensitivity of landscape-fire-succession models to variation in terrain, fuel pattern, climate and weather. *Landscape Ecol.* 21, 121–137
64 Brook, B.W. (2000) Pessimistic and optimistic bias in population viability analysis. *Conserv. Biol.* 14, 564–566

65 Glaser, D. and Bridges, T.S. (2007) Separating the wheat from the chaff: the effective use of mathematical models as decision tools. *Integr. Environ. Assess. Manage.* 3, 442–449

66 Ferson, S. (1996) Automated quality assurance checks on model structure in ecological risk assessments. *Hum. Ecol. Risk Assess.* 2, 558–569

67 Oriade, C.A. and Dillon, C.R. (1997) Developments in biophysical and bioeconomic simulation of agricultural systems: a review. *Agric. Econ.* 17, 45–58

68 Holst, N. *et al.* (2007) Field weed population dynamics: a review of model approaches and applications. *Weed Res.* 47, 1–14

69 Jager, H.I. *et al.* (2005) Spatial uncertainty analysis of population models. *Ecol. Model.* 185, 13–27

70 Brook, B.W. *et al.* (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* 404, 385–387

71 Fuller, M.M. *et al.* (2008) Testing the robustness of management decisions to uncertainty: Everglades restoration scenarios. *Ecol. Appl.* 18, 711–723

72 Scheller, R.M. and Mladenoff, D.J. (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecol.* 22, 491–505