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Procedia Environmental Sciences 13 (2012) 331 – 339

Procedia
Environmental Sciences

The 18th Biennial Conference of International Society for Ecological Modelling

Ecological Modelling in the 21st Century: Examining Potential Research Directions and Challenges

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Abstract

Ecological modelling can be considered as a significant research activity in the majority of scientific disciplines related to natural resources. Models have been developed for nearly all types of both terrestrial and aquatic ecosystems and for several animal populations. As many models are available, it is tempting to believe that there are no more significant challenges to be met in ecological modelling. Despite all the recent achievements, there are still important challenges that require basic research work. For the majority of ecosystems, many processes remain poorly understood, which is a major constraint for the derivation of adequate mathematical representations for conducting realistic simulations. Dealing with complexity remains a controversial topic that triggers new challenges. While some modellers believe that ecological models must be as simple as possible, others argue that complex models are essential for representing the complexity of nonlinear interactions. One of the greatest challenges in the 21st century will be to deal with global change issues. In particular, both temperature and CO_2 increases will have interactive effects that scientists are just beginning to understand. Thus, modellers will have to think differently. Another challenge will consist in developing multidisciplinary models. For instance, major progress can be made by extending the concept of ecosystem to include different vegetation types, animal populations or water resources to model the flows of energy, carbon, water or nutrients through a landscape.

Keywords: Global change; Ecosystem processes; Complexity; Uncertainty; Multidisciplinary models

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1878-0296 © 2011 Published by Elsevier B.V. Selection and/or peer-review under responsibility of School of Environment, Beijing Normal University.
doi:10.1016/j.proenv.2012.01.032

1. Introduction

As a scientific activity, the development of ecological models has now reached a high degree of maturity. The number of models that have been developed for many terrestrial and aquatic ecosystems and several animal populations can certainly be estimated to reach a few thousand. Anybody who would like to learn about ecological modelling has access to several sources of information on the internet, such as ecobas.org, several high-quality books (e.g., Jørgensen et al. [1]) or scientific journals (e.g., Ecological Modelling). Also, ecological models are increasingly used for policy making for the management of natural resources.

The number of model users increases constantly, and this trend can be associated with requirements for the addition of features to support the decision making process. For instance, at a workshop on forest productivity models organized in Quebec, Canada, in the spring of 2008, the participants, who were either scientists or forest managers using models, identified several desirable features that should be included in models, such as optimization routines, expert systems, or spatialization or sensitivity analysis tools [2]. It was also mentioned that the next generation of forest productivity models should address issues on soil and habitat disturbances, biodiversity, forest succession and climate change. At the last conference of the International Society for Ecological Modelling in 2009, several modellers envisioned the development of several key features that should be integrated into ecological models [3].

All the great achievements in ecological modelling may leave scientists or model users with the impression that no further development or research is necessary. In other words, no more significant progress can be made and future research would just consist in "re-inventing the wheel". In reality, there are still many challenges in ecological modelling, and further progress can only be made by pursuing basic research. One of the challenges will be to deal with global change issues. In particular, changing conditions under global change trigger new environmental conditions, and it is not certain that existing models can make realistic predictions given the complexity of the interactions involved. The objective of this paper is to suggest and discuss potential future research directions. Addressing these issues for different ecosystem types is a considerable task. Thus, it is not possible to include a comprehensive assessment for all ecosystem types. Some of the ideas, arguments or concepts discussed focus on plant populations, but they can certainly be extrapolated to other types of ecosystems.

2. Lack of understanding of processes

For most ecosystems, there are still many abiotic and biotic processes that remain poorly understood. For instance, in plant populations, competition for site resources, including light, nutrients and water, is one of the processes that requires additional research to better understand the complexity of the mechanisms involved. Plant ecologists well know that competition reduces the growth of individual plants by limiting potential resource uptake. However, the measurement of the impacts of competitors for resource uptake on individual plants is not straightforward. Also, several questions on the asymmetric nature of competition remain unanswered. Asymmetric competition occurs when the largest plants uptake proportionally more resources than the smallest plants within a population [4, 5]. On the other hand, resource depletion is proportional to plant size when symmetric competition occurs. This question remains under investigation, and the consensus among many plant ecologists is that competition for light is asymmetric, while competition for water and nutrients is symmetric (see, Weiner et al. [5], Blair [6], Rewald and Leuschner [7], Stoll et al. [8]). A direct consequence of the lack of understanding of competition, as far as tree populations are concerned, is that the predictions of models based on the representation of inter-tree competition are still characterized by a high degree of uncertainty [9].

A second example that can be used to illustrate the effect of the lack of understanding of basic processes on modelling is bird fecundity (Etterson et al. [10]). According to Etterson et al. [10], a better understanding of bird fecundity is required to improve the modelling of this complex process. There are still several factors that limit the measurement of bird fecundity, such as difficulties in nest detection, estimates in the proportion of females or emigration. Feyrer et al. [11] identified similar issues for a delta smelt (*Hypomesus transpacificus*) fish population in the San Francisco Esturary. In particular, they pointed out that the predictions of their model could be limited by potential changes in the estuary resulting from changes in environmental conditions, such as climate change, or man-made development of water facilities. Brigolin et al. [12] developed a steady-state model of the Venice lagoon food web. Their dataset was quite comprehensive, but remained limited to improving the understanding of the functioning of the Venice lagoon ecosystem.

An important issue that ecological modellers must address is global change. Modifications in climatic conditions resulting from both temperature and atmospheric CO_2 increases and their impacts on ecosystem functioning are occurring gradually, over decades. For long-lived ecosystems, such as forests, ecological models are essential for the prediction of the potential impacts of global change because it is difficult or impractical to perform manipulative experiments that can emulate the gradual changes over long periods (see Luo and Reynolds [13]). Several studies have been conducted to test the effects of CO_2 increase, such as FACE experiments (e.g., DeLucia et al. [14]). However, these experiments last for a relatively short period of time compared to the long-term changes triggered by climate change. Thus, they provide incomplete answers to complex questions. As they are based on the representation of ecosystem processes, ecological models are very useful for predicting the potential long-term impacts of climate change [15].

For the majority of terrestrial ecosystems, several processes will be affected by global change. For example, several direct and indirect effects may occur in forest ecosystems (Fig. 1). There might be direct effects on ecophysiological processes, including photosynthesis, respiration and transpiration, which, in turn, will influence carbon allocation and tree and stand growth. Changes in carbon allocation may indirectly affect wood quality or stress resistance capacity. The natural pathways of natural succession may also be influenced, affecting biodiversity or species migration. More frequent fires, drought or insect and disease outbreaks are also expected. Thus, global change is likely to affect several ecosystem properties, such as the capacity of forest ecosystems to sequester atmospheric CO_2. Several studies or reviews have begun to provide indications on the potential impacts of climate change (e.g., Chmura et al. [15], Boisvenue and Running [16], Mohan et al. [17]), but many questions still remain.

Ecosystem modellers use several types of theoretical or empirical equations in their models. Even though the majority of them are well accepted, it is not futile to test or refine them if necessary. A good example is the representation of temperature effect on processes. Two models have been heavily used: the Arrhenius and Q_{10} functions.

The Arrhenius function is defined as:

$$k = A\, e^{-E_a/RT} \tag{1}$$

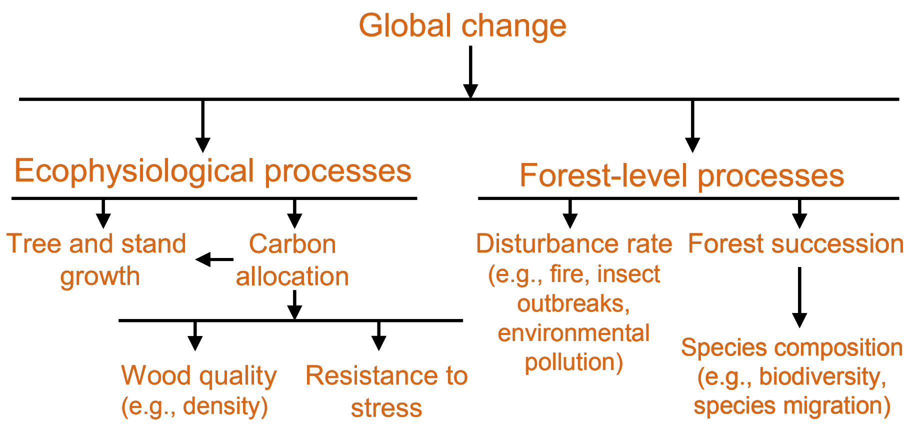

Fig. 1. Illustration of the potential impacts of global change on forest ecosystems.

where k is the rate coefficient of the process, A the pre-exponential factor, E_a the activation energy, R the universal gas constant and T temperature (ºKelvin).

The Q_{10} function is defined as:

$$k = k_{Tref}\, Q_{10}^{(T\text{-}Tref)/10} \tag{2}$$

where k is the rate coefficient at ambient temperature, k_{Tref} the process rate at a reference temperature, Tref the reference temperature, T the ambient temperature and Q_{10} the temperature effect coefficient for a 10ºK temperature increase, which is usually around 2.

Both functions have strengths and weaknesses. The Arrhenius function has a strong theoretical basis [18], but the derivation of the pre-exponential factor or the activation energy can be problematic. On the other hand, the Q_{10} function has a weak theoretical basis, but there is only one parameter to derive. However, the problem with the Q_{10} function is that the value of Q_{10} may vary with temperature, which may result in inaccurate predictions (see Tjoelker et al. [19]). So, the modeller may have the choice between a theoretical function for which parameter derivation may be problematic or an empirical function that may well fit data, but not capture well the effect of a wide range of temperature variation. More investigations are desirable to provide further evidence on the most appropriate model to use.

Recognized theoretical models can also be applied within different frameworks. In plant ecology, the Farquhar and von Caemmerer [20] model of photosynthesis has been used to predict photosynthetic rate for many plant species. However, this fundamental model has surprisingly been tested within relatively few frameworks that consider the effects of variation in leaf temperature or within different crown sections where leaf morphological and physiological characteristics may vary appreciably, such as specific leaf area, effect of proteins on maximum carboxylation rate or potential electron transportation rate (e.g., Larocque [21], Niinemets and Tenhunen [22]). With respect to variation with crown depth, that is, scaling processes from leaf to canopy [23], several algorithms still need to be tested for several species, including the big-leaf approach, where the canopy is considered to have homogeneous characteristics, two-leaf sun/shade models, or multilayer models using foliage distribution with crown depth.

3. Complexity and uncertainty

The debate over model complexity still remains an active subject of discussion. There is no easy answer to that question. If a model is based on highly simplified representations of processes, essential ecosystem mechanisms may be ignored [24]. As a consequence, the capacity to better understand the processes that govern the dynamics of ecosystems may be confined within relatively narrow limits [25]. Also, a simple model may become less flexible for predicting different scenarios of ecosystem dynamics. On the other hand, an extremely complex model may create difficult conditions for understanding the sub-components or calibrating the parameters [24, 26].

Determining of the right level of complexity is closely linked to the objectives of the modelling exercise, but some guidance may be used by considering data requirements, flexibility, sensitivity and error [26]. Relative to simple models, complex models require more data, as they contain more parameters. They are also characterized by a higher degree of flexibility, as the number of assumptions can be minimized. The higher number of parameters in complex models may increase sensitivity because the number of interactive effects of parameter variation increases. Complex models have the potential to better simulate the dynamics of ecosystems than simple models, reducing prediction uncertainty. However, it has been claimed that the development of complex models is a cumbersome exercise that requires dealing with many details. Modellers may get lost in details and experience difficulties in connecting the different sub-components. The support for "models as simple as possible" becomes a strong argument, particularly when it is mentioned that simple models may predict better than complex models (e.g., Halide and Ridd [27], Pace [28]). It is fair to say that complex models may not meet the expectations because of flaws in their structure, inaccurate representation of the mechanisms or lack of appropriate tools or methodologies to analyze complexity. DeAngelis and Mooij [25] mentioned that complex models did not perform as well as originally anticipated when they were first developed (which could explain the concerns reported above), but they also pointed out that advances in concepts and technology have contributed to improving the development of complex models. The large number of datasets that have been developed over the last few decades are becoming increasingly useful to calibrate complex models, and the increasing recognition and application of various types of analytical methodologies help modellers to derive more accurate representations of processes (e.g., Jørgensen et al. [1], Grimm et al. [24]).

There is a lot of discussion about uncertainty in ecological models. However, few ecological models deal with this issue or present uncertainty estimates in their predictions (see, Ascough et al. [29], Cressie et al. [30], Verbeek et al., [31]), possibly because of the complexity of the tasks involved. Also, information on different sources of uncertainty may be lacking. There are several sources of uncertainty in ecological models, including data error, model structure, parameter estimates or natural variability [29, 32]. Ecological modellers should pay more attention to uncertainty issues in their models to ensure that decision makers have a clear idea about model limitations. Without uncertainty estimates, there is a possibility that decision makers use model outputs without full appreciation of potential model limitations. According to Pizer [33], the availability of uncertainty information has a positive effect on the mind of policy makers during the decision-making process. Uncertainty estimates are particularly useful when the simulations of different scenarios are compared. This point can be illustrated by one of the case studies examined by Larocque et al. [2]. Using a soil carbon model, they compared the effects of different scenarios of temperature increase on several soil carbon pools in a balsam fir (*Abies balsamea* (L.) Mill.) forest ecosystem. The computation of uncertainty estimates using the Monte Carlo method allowed them to conclude that the probability of an increase in CO_2 emission through soil respiration following a gradual increase in temperature would occur more rapidly than changes in some of the carbon pools. This result generated questions on the efficiency of carbon sequestration by soils.

4. Multidisciplinary ecological models

The majority of ecological models focus on specific ecosystem or animal population types. For instance, there are many models for river, forest, agricultural or grassland ecosystems, but most of them focus on the modelling of water, carbon or nutrient flows or the dynamics of a specific animal population within ecosystems. There are many models for forest ecosystems, but they mostly focus on the prediction of the productivity of the tree layer, the examination of successional pathways or the dynamics of carbon or nutrient flows. Ecological models based on the representation of the water, nutrient, carbon and energy flows and animal population dynamics within an area (e.g., landscape), that is, models based on the broad application of the concept of ecosystem in which the flows of water, nutrients, carbon and energy occur between soil, vegetation and animal populations are not common. Among interesting examples of multidisciplinary model development in recent years, it is worth taking into consideration the studies of Langmead et al. [34], who examined environmental issues in the northwestern Black Sea by including model components on algal and fish populations, water quality, and socio-ecological variables; of Münier et al. [35], who performed ecological and economic modelling in agricultural land use; or of Zhou et al. [36], who developed an integrated application based on ecological modelling and a geographic information system (GIS) to examine relationships between water and ecological systems in a wetland site of the Honghe National Nature Reserve (China).

There are several factors that may enhance the development of multidisciplinary ecological models. For the last few decades, datasets containing many types of ecological measurements have been created to calibrate models for various ecosystems and processes. Many of these datasets can be easily obtained from internet sites and their descriptions are good sources of information to improve data collection if necessary. The large number of scientific articles on ecological modelling is a reflection of the evolution in knowledge and concepts. As a consequence, there is a large body of literature that allows modellers to better evaluate successful as well as unsuccessful approaches or methodologies and helps them progress conceptually during the modelling development phase. Advances in computer technology have been quite significant in the last few years. It is now possible to store large amounts of data, execute complex algorithms within relatively short periods of time or develop software that integrates different tools, such as GIS, 3D visualization applications or optimization routines, to facilitate the examination and analysis of simulation results. Future progress in multidisciplinary ecological models can best be achieved by teams of modellers with different academic disciplines. This is a trend that has been developing for several years, as the majority of papers on ecological modelling are written by several authors. In particular, the internet facilitates communication among scientists from different locations on the planet.

5. Conclusion

Ecological modelling is a scientific activity that is increasing in importance. The members of the scientific community actively involved in ecological modelling have accomplished many achievements, but there are still many challenges ahead. In particular, it is important that ecological modellers develop strong collaborative networks with scientists in different academic disciplines. As mentioned above, several processes must be better understood, which will probably require conducting additional experimental work to collect the necessary data. Ecological modellers cannot by themselves perform all the tasks required to better understand the processes that will allow them to improve models. Also, they will have to contribute to increasing the level of confidence that model users and policy makers expect from model predictions.

Acknowledgements

I am grateful to the organizers of ISEM 2011 for the kind invitation as a guest speaker. Also, I would like to thank Ms. P. Cheers, Editor at the Laurentian Forestry Centre, and anonymous reviewers for helpful comments.

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