HOW PHYSICS AND BIOLOGY MATTER IN FOREST GAP MODELS

Considerations inspired by the Editorial in the August 1993 issue of 'Climatic Change'

An Editorial Comment

Models are artifacts, products of design. They are designed for a purpose. The purpose of a model determines the physical and biological facts and phenomena to be considered. Constrained by the availability of data, these facts and phenomena determine the temporal and spatial scales at which the model should operate. In turn, these scales determine which processes can and should be considered. Therefore, from a strict design standpoint, physics and biology matter in the design of ecological models. The purpose of this essay is to find out how they matter, both from a theoretical and a practical standpoint, drawing upon our experience with forest gap models (cf. Bonan, 1993).

1. Design Criteria for Ecological Models

Ecological phenomena occur on a wide range of spatial and temporal scales, and an equally wide variety of formulations can be used to represent ecological processes in mathematical models. Out of a desire for better representations of the physics and biology of the problem, better performance, or better predictions, the way in which the interactions between different variables are parameterized and even the choice of state variables may be changed in the course of model development to make it sensitive to certain factors and phenomena, e.g. climate. For example, annual net primary productivity (NPP) may be modelled (1) by simple regressions of measured NPP data against hypothesized driving variables like radiation, temperature, and/or moisture (e.g., Kauppi and Posch, 1988); (2) by taking into account the annual balance of gross photosynthesis and respiration (e.g., Bugmann, 1994); (3) by using detailed ecophysiological models distinguishing photosynthesis, respiration, and allocation on a temporal resolution of minutes to hours (e.g., Running and Gower, 1991).

Which model formulation is most appropriate for a given problem? Most ecologists will agree that it is not feasible to explain the behaviour of ecosystems by scaling up the knowledge gained from particle physics (O'Neill *et al.*, 1986). However, the choice of a certain level of resolution for explaining an ecological phenomenon is not arbitrary; it is strictly constrained by the purpose of the model, i.e., the model must not exceed its range of validity.

Thus, the question arises how to judge model validity. Shugart (1984, p. 70) provides a detailed discussion of this issue, stating that in a validation procedure the

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model is "*tested on its agreement with a set of observations that are independent of those observations used to structure the model and to estimate its parameters.*" We believe that the comparison of model results with independent observations is a necessary, but an insufficient test of model validity, because any function can be fitted to a data set given a merit function; in other words: a model may be right for the wrong reasons. A second criterion may be equally important: Model validity also depends on how well fundamental natural processes are captured by the model, i.e., how well physical and biological phenomena are parameterized. For example, consider a model that incorporates three processes, A, B, and C; from empirical evidence or theoretical reasoning we know that process A determines most of the behaviour of the real system. If the model yields the 'right' behaviour even if process A is ignored, or if process A contributes little to the simulated dynamics, we have to conclude either that the model does not provide a valid description of the real system, or that our current understanding of the causes of system behaviour is inappropriate.

In the following, we will elaborate criteria that we consider to be relevant in the context of the development of ecological models for application under climate change. First, the principle of Parsimony (often called 'Ockham's razor') will be evaluated. Then we discuss the advantages and drawbacks of increased model complexity, and the problem of computational expense.

2. Parsimony

"*It may pay not to try to describe in the analysis the complexities that are really present in the situation*" (Tukey, 1961, p. 202). The principle of Parsimony implies that when two parameterizations yield very similar or identical results, it may be worthwhile to choose the simpler one. Clearly, the principle of Parsimony does not carry the weight of law (Tudge, 1994), but it is a useful guideline to follow when developing an ecological model. Specifically, our explanations should become more complicated only when the forces we know about at a specific level of resolution have failed to provide a consistent picture of reality. This will be illustrated using the case of forest gap models:

During the last 25 years, forest gap models have been adapted successfully for a wide range of forests around the world. It is fascinating to see how realistically they behave at many scattered sites under current climate (e.g., Shugart, 1984). However, recent analyses suggest that many of these conventional models contain parameterizations of climatic influences that are too simple to be valid for studying the impact of climatic change on forests. Many of these models implicitly assume that climate is constant, as pointed out e.g. by Martin (1990, 1992), Bugmann and Fischlin (1994), and Fischlin *et al.* (1994): For example, they contain parameters prescribing the length of the growing season or the maximum aboveground biomass, which in fact depend on climate. Moreover, in the Thornthwaite and

Mather (1957) bucket model of soil moisture it is a standard practice to reset soil moisture to field capacity at the beginning of every simulation year (e.g., Pastor and Post, 1985), thus assuming that precipitation is abundant enough during winter to recharge soil moisture completely. It is questionable to assume that a certain climatically dependent behavior will be unaffected by altered climatic conditions. Arguably, some of the results obtained on this basis may not be reliable.

On the other hand, Bonan and van Cleve (1992), Bonan and Sirois (1992), and Martin (1990, 1992) found that differences among models in biophysical and physiological complexity can lead to different sensitivities to climate, especially concerning the formulation of drought stress. As an example, in EXE (Martin, 1990, 1992), drought stress occurs when the atmospheric demand for water vapor exceeds the water supply by root uptake from the soil, whereas in LINKAGES (Pastor and Post, 1985), it occurs when the water content of the soil falls below a certain absolute threshold. This difference in parameterization can lead to markedly different responses to climate change scenarios, forest growth being impeded, in some instances, by different limiting factors. Bonan and van Cleve (1992) and Bonan (1993) suggested that the detailed models are more accurate, and therefore the detailed models are needed. However, the fact that a model is sensitive to the parameterization of a given ecological factor is a necessary, but not a sufficient condition to show that a certain level of detail is required to model that factor. For example, Fischlin *et al.* (1994) found that the traditional approach of expressing the influence of drought on tree growth (the 'dry days' approach, Pastor and Post, 1985) contains a threshold effect that leads to the simulation of unrealistic forest dieback phenomena. When they replaced this drought index with the equally simple evapotranspiration deficit (Cramer and Prentice, 1988; Prentice *et al.*, 1993), they obtained more reliable forest dynamics under current climate, but at the same time also strongly differing sensitivities to climatic change, paralleling the findings by Martin (1990, 1992).

Thus there arises the question whether some of the oversimplified parameterizations used in conventional models can be replaced by more accurate, but still simple equations. The replacement of the 'dry days' approach mentioned above may serve as a first example. Moreover, Fischlin *et al.* (1994) showed that the conventional estimation of the annual sum of degree-days from monthly mean temperatures used in most forest gap models (Botkin *et al.*, 1972) is prone to a site-specific bias, which also influences the simulated species composition under climatic change. One might conclude that a more detailed approach such as the one by Allen (1976), which requires daily minimum and maximum temperatures, is required to model the sum of degree-days accurately. One way to meet the requirements set by this conclusion is to increase the realism and the temporal resolution of the model and, for instance, to make growing degree-days a function of canopy and soil temperature and photo-period rather than air temperature and climatological atlas data on the start and the end of the growing season (Martin, 1990, 1992). An alternative (e.g., Bugmann, 1994) is to develop a method for estimating the annual sum of degree-days that is still based on mean monthly temperatures only, but approximates Allen's (1976) results much better than the method by Botkin *et al.* (1972). The example set by this latter solution shows that, at least in some instances, it is possible to derive simple yet realistic parameterizations of climatic influences without detailed biophysical or physiological submodels.

Dealing with climatic change issues, we also should not forget that forest gap models contain a number of ecological assumptions that are truly independent of climate. Recent analyses suggest that forest gap models are sensitive not only to the parameterization of climatic influences, but also to the number of ecological factors included in the models. For example, Bugmann and Fischlin (1994) and Bugmann (1994) compared the FORECE model (Kienast, 1987) and a descendant of it that included only a subset of the ecological factors of FORECE. Under current climatic conditions, they found only slight differences among the models at many sites along an altitudinal gradient in the European Alps. When the models were applied under the same scenario of climatic change, however, their projections differed substantially. Similar results were obtained by Martin (1990, 1992), who compared the LINKAGES (Pastor and Post, 1985) and the EXE (Martin, 1990, 1992) models. The reason for this behavior appears to be that forest gap models are tuned to the current climate at a set of locations, but they may yield unreliable results when applied along climate gradients. Thus, the formulations of both abiotic and biotic factors in forest gap models should be scrutinized carefully in order to obtain models that portray ecological dynamics along climate gradients more reliably.

3. Complexity

It is intuitive that model complexity is related to insight or information output in a positive manner. At some point, however, the complexity of a model becomes untenable; put another way, the predictive ability of a model initially increases with model complexity, but then probably begins to decline as the model becomes too complicated. Several aspects of this complexity/insight relationship are important:

First, complex models contain more functional dependencies that are formulated in a more complicated manner, and consequently, these models require to estimate more parameters. Every model can become so complex that there is insufficient data to estimate the required parameters. Parameter estimation then becomes speculative, and the uncertainty in the model output increases, i.e. its predictive ability decreases. This is especially true when dealing with the long-term dynamics of near-natural ecosystems, e.g. forests, where parameters have to be estimated for a large number of species.

Second, enhanced resolution does not necessarily increase the validity of a model. The resolution of a model may be increased in space, in time, or in detail; the response on the larger scale then is obtained by integration. Like this, small errors on the small scale may become amplified, and the resulting response may be less accurate than a simpler formulation on a lower level of resolution. In other words: Enhanced resolution in a model may add noise instead of signal.

Finally, adding sensitivity by increasing the complexity of a model is worthless if not detrimental, if it does not have physical and biological meaning and reflects natural sensitivity better.

The modeller's task is to find a tenable way between too simplified and too complex process formulations. Optimally valid models are obtained only when the appropriate resolution in between the two extremes is identified and the model is formulated accordingly.

4. Computational Expense

The properties of non-linear, realistic ecological models, such as their stability, parameter sensitivity, and sensitivity to input data segments, most often cannot be derived analytically. Instead, such investigations have to be performed by extensive simulation studies. Unfortunately, model complexity comes at great cost computationally (e.g., Bonan, 1993), which precludes detailed experimental model analyses and often restricts the significance of the results (cf. Bugmann and Fischlin, 1992, 1994). For example, the simulation study by Bonan and van Cleve (1992) covered 25 years only, although the model actually treats forest succession, which operates on the time scale of decades to centuries (Shugart, 1984).

Indeed, only models which are efficient to run make possible detailed analyses of their behaviour, e.g. along climate gradients, or to study their parameter sensitivity. Such analyses are required especially with complex models, whose behaviour and sensitivity can be very complex and generally are not known a priori. Detailed model analyses should also be conducted before applying the models for extrapolation, e.g. before studying the impact of climatic change on the tree species composition of near-natural forests.

Hence, we are facing a considerable dilemma: Complex models may be more realistic and valid than simple ones. Complex models should be analysed very carefully in terms of their behaviour and sensitivity. However, model complexity is inversely related to the feasibility of model analyses. We believe that it may be more useful to learn a lot from extensive simulation studies with a simpler, possibly less realistic model, than to perform a few studies with a complex, possibly more realistic model whose properties remain unknown. Again, physics and biology do provide guidelines as to the level of detail to be included in ecological models.

5. Conclusions

The processes to be incorporated in ecological models can be formulated on a wide variety of resolution levels; we fully agree with the conclusion drawn by Bonan

(1993) that "*a future challenge for ecologists is not to merely show that climate change affects ecosystems, but rather to consider what level of physiological and biophysical detail is needed to accurately model climate change impacts*." We have discussed important features of model validity and have elaborated three criteria that can be used to evaluate the level of detail to be included in ecological models: Parsimony, complexity, and computational expense.

Recent analyses show that many conventional forest gap models contain parameterizations of climatic influences that are too simple. Keeping the principle of Parsimony in mind, the failure of these formulations does not necessarily call for greater resolution in the models. Instead, we advocate a stepwise improvement of the formulation of biotic and abiotic factors in current forest gap models, which would give us the freedom to stop adding more detail when we start to add noise instead of signal. Submodels that incorporate many biophysical and physiological details may be required if they can be shown to capture some aspect of reality that cannot be portrayed adequately with more aggregated schemes. The different sensitivities to climate found in the studies by Bonan, Martin, and Friend *et al.* (1993) indicate clearly which factors have to be scrutinized carefully in order to derive more reliable formulations. The influence of temperature and soil moisture on tree growth may serve as examples.

The above three criteria would keep forest gap models as lean and as amenable to analysis as possible. Detailed model analyses and quantitative model comparisons would be desirable to shed more light on the nature and behaviour of this unique class of models, a class of models that holds much promise for studying the response to global change of managed as well as unmanaged forest ecosystems.

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