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BIO 9010

SCALING VEGETATION ACROSS SPACE AND TIME
-
Simplifying complexity to model complex systems

EXAMEN DE SYNTHÈSE
PRÉSENTÉ
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As far as the laws of mathematics refer to reality, they are not certain; as far as they are certain, they do not refer to reality.

Any intelligent fool can make things bigger and more complex... It takes a touch of genius --- and a lot of courage to move in the opposite direction.

Everything should be made as simple as possible, but not simpler.

The world we have made, as a result of the level of thinking we have done thus far, creates problems we cannot solve at the same level of thinking at which we created them.

Albert Einstein
(1879 – 1955)

1. INTRODUCTION

1.1 The problem of scale – what's the issue?

The term scale – in a broad sense – has several meanings including a measuring device (to weigh objects), an indicator having a graduated series of marks (such as a ruler), a flake of dead epidermis (such as a fish scale) or something more abstract such as the ratio of the size of an object and its representation (e.g., scale of a map) and the relative magnitude of something (WordReference 2006). As with scientific research, scale may refer to the assessment of entities, patterns or processes. Here, one might use a nominal scale (e.g., presence or absence of species), ordinal (e.g., rankings based on some variable), continuous or discrete (e.g., counts of entities or measurements of their attributes) or some other scale (e.g., ratios).

The problem of scale in ecological (and other) research arises from the fact that space (and time) has both an absolute and a relative nature. In the absolute definition, space has a Euclidean, linear character where trigonometric rules apply. Here, space is considered a rigid structure containing objects in defined and steady spatial relationships. In the relative definition, space is dependent on the spatial entities and processes under consideration and varies depending on the viewpoint of the observer. For example, two potential habitats may lie close to each other in terms of absolute space but may be considered distant if a barrier to transfers and interactions is present (Marceau 1999).

The importance of the concept of scale has been recognized a long time ago by geographers, social scientists (e.g., Gehlke and Biehl 1934, Yule and Kendall 1950) and ecologists (e.g., Collins 1884, Murphy 1914) showing the dependence between a variable and the scale at which it is measured. Since most variables can only be measured on small scales and over short periods of time whereas natural phenomena often act on broader scales (i.e. large areas and over decades or even longer), most questions cannot be addressed simply by *"scaling locally measured variables directly to larger areas and longer times"* (Schneider 2001, p. 545).

Hence, ecologists are confronted with the challenge of finding a way to deal with pattern and scale as the *"central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology"* (Levin 1992, p. 1943). The new 'buzzword' in ecological research (Wiens 1989) is the subject of an ever increasing proportion in ecological literature (Schneider 2001).

In scientific research scale translates beyond the obvious properties of the measuring procedure into the extent and grain of an investigation. The extent refers to the study area whereas the grain is the size of the plot or the sampling units. Obviously, the scale of investigation has a major impact on the outcome of a study through its relationship with the scale at which processes and patterns operate. For example, the dynamics of litter decomposition will depend, at the local scale, on the properties of the litter and the decomposer community whereas at a larger (e.g., regional) scale climatic conditions will determine decomposition rates (Meentemeyer 1984). Also, the close link between climate and vegetational composition on a regional scale is loosened, on the local scale, by other factors such as competition and resource availability (Woodward and Williams 1986). Hence, the effect of scale in scientific research depends on the spatial extent of the process or pattern under investigation versus the grain and extent of the study.

This also implies that a researcher cannot simply extrapolate her findings beyond the extent of the investigation nor detect processes and patterns that act below the grain of the study (Wiens 1989). In order to make predictions across more than one scale, a researcher needs to go through four steps: (1) identify the appropriate scale for the phenomenon of interest, (2) understand the changes through scales of the influence that different variables have on the phenomenon, (3) develop methods to translate information from one scale to the next, and (4) sample and experiment across scales as to test predictions made in (3) (Turner et al. 1989).

Obviously, each step has its pitfalls. In (1), the choice of the appropriate scale needs to be based on either the objective of the study or the characteristics of the study object (e.g., a bird species). If anthropocentric scales are used (i.e. scales that are convenient or intuitive to human observers), the scale can seem ‘right’ to the researcher but might not be appropriate for the species considered. For example, if one studies the nesting behaviour of the Northern Spotted Owl (*Strix occidentalis caurina*) a ‘suitable’ (to the researcher) survey area of 100 hectares would not be suitable for the species since one single Spotted Owl pair requires an area of 1000 to 2000 hectares of continuous forest. Hence, the choice of scale should rather be based on whether the research aims to promote key species conservation or species richness (therefore using either patch size or landscape scales, respectively) or on the size of the breeding or feeding habitat of the species considered (e.g, Noss 1987, Addicot et al. 1987).

Translating from one scale to the other (scaling) can be done in a “bottom-up” or “top-down” manner. The former is based on the assumption that a broader phenomenon, for which empirical information is lacking, can be explained through the interactions of its components. In the “top-down” approach one considers the coarser scale as the limiting factor on fine-scale processes. For example, global patterns of evapotranspiration can be predicted from solar radiation (“top-down”) whereas stomatal conductance may be used to predict evapotranspiration on the leaf or whole plant level (Jarvis and McNaughton 1986). Hence, scaling naturally spans across three levels and leads to a hierarchical structure (O’Neill et al. 1986): scale zero (0) at which the phenomenon operates; the scale below (-1) which encompasses the patterns and processes leading to the phenomenon and the level above (+1) for which the phenomenon constitutes one of its components.

However, levels of hierarchy might not always be identified as easily as stated above and often a phenomenon, its patterns and processes may change continuously with scale, severely limiting extrapolations across scales. Regions of the scale spectrum where changes in patterns and processes are not continuous are called domains of scale. Within domains, the linear behaviour allows extrapolation across scales and the identification of domains is helpful to establish aggregation schemes (e.g. canopy layer) (Wiens 1989).

Verifying predictions across scales based on experiments or observations may sound obvious but requires that the choice of scale for the phenomenon of interest has been appropriate to begin with. Designing experiments or surveys on very small or very large scales may also be costly and/or difficult to undertake. However, these experimentations might be essential to obtain an understanding of the changes through scales in the influence that different variables have on the phenomenon (Kratz et al. 2003). For example, leaf productivity is driven by light absorption from incident solar radiation. However, at the scale of the canopy, self-shading (light extinction through the canopy) comes into play and modifies leaf-level productivity estimations. These changes can be difficult to predict theoretically due to non linear relationships between processes and variables and due to the heterogeneity in properties (e.g., sun vs. shade leaves) that determine the rates of the processes within and across scales (Jarvis 1995).

The transpiration rate of a forest canopy equals, theoretically, the sum of the transpiration rates of all its leaves. Since not all leaves of a canopy can be measured individually, canopy transpiration rates are usually estimated through upscaling from measurements of single leaves and estimations of the amount of leaves in the canopy. A simple linear extrapolation (summation) from one scale (leaves) to the next (canopy) would require that all leaves in the canopy have identical transpiration rates and that the driving variables such as relative air humidity are identical for all leaves in the canopy. This, however, is known to be erroneous. Hence, scaling (up or down) needs to account for these problems.

Scaling usually requires the use of models. These can be simple mathematical equations representing a correlative relationship between the observed phenomena and some measured parameter of the system or more complex systems of equations that simulate mechanistically the underlying processes of the phenomenon (Rastetter et al. 2003). For any correlative relationship scaling calls for the specification of the bounds for which the scaling properties are known to be stable (i.e. within a canopy layer). A typical formulation of a scaling model is the power law:

$$Q = km^{\beta}$$

where the quantity Q is obtained through measurements of m with constants k and β. Another form of the power law highlights why power laws offer themselves naturally for scaling purposes:

$$\frac{Q(m)}{Q(m_0)} = \left(\frac{m}{m_0}\right)^{\beta}$$

here the relationship between the quantity Q and the measurements at a finer scale and a larger scale is defined through the their scopes, the ratios of the grain (minimum resolution, m) and extent (maximum extent, m_0). Hence, this form allows specifying the scale domain over which the power laws holds (Urban 2005).

Even though power laws seem to be able to scale many processes occurring in nature, they are of phenomenological quality and are not theoretically derived but rather statistically fitted (Schneider 2001). This implies that these laws are not generally applicable but need to be fitted for each new system over again.

Another way of considering non linearity in functional relationships and across scales is to account explicitly for the heterogeneity (patchiness) observed in many natural systems. Scaling is then not limited to the domain of scale for which the law has been developed but can be performed across scales of different domains. Methods for doing so are the averaging and the aggregation scheme (Jarvis 1995). Averaging process rates necessitates the system (e.g., a canopy) to be subdivided into its major components (e.g., layers) and each of these components sufficiently sampled to minimize intra-component variance (McNaughton 1994). Parameters of process rates are than averaged across components as to simulate the average behaviour of the phenomenon. Although sampling intensity may be considerably reduced when the component are stratified with respect to the major sources of variation (i.e., age, position), the sampling effort will still be very large (Jarvis 1995).

Aggregating is somewhat similar to averaging as one has to stratify the components of the system according to differences in the driving variables of the processes (e.g., canopy conductance). The process rates are than calculated for each of these ‘patches’ or ‘tiles’ and summed over the larger system (e.g., landscape) (Jarvis 1995).

Another way of scaling across scales is the use of individual-based simulation models. Here the mechanistic understanding of the underlying processes allows modelling from finer to coarser scales through the implicit formulation of system heterogeneity (Rastetter et al. 2003). Using fine scale knowledge to predict coarse scale phenomena is extremely desirable in modeling applications (Rastetter et al. 1992). Although ever increasing computer power and speed make ‘brute force’ simulations, i.e. fine scale computations run at larger scales, progressively more operational and yield *“a wealth of model output, it would not necessarily provide any greater insight into the system”* (Urban 2005, p.1997; Law and Dieckmann 2000b). Yet, changing (environmental) conditions require large-scale models to be flexible, a quality that is only achieved when underlying, i.e. small-scale, processes are mechanistically linked. Hence, we need detail to accurately describe large-scale phenomena but too much detail will yield intractability and over-complexity.

To achieve simplicity at larger scales while maintaining detail from fine scale processes, different aggregation and approximation methods have been developed for and employed in modeling. Aggregation involves the lumping of large numbers of fine scale components in some form of aggregate component. The 'big leaf' (e.g., Sinclair 1976) is one such aggregation where all leaves in the canopy are treated as a single big leaf. Also, the lumping of biodiversity in discrete groups of functional similarity is a form of aggregation that allows simplification of fine scale processes. Although generally the behavior of the aggregate might only inadequately be simulated from that of the constituting individuals (O'Neill 1979) the associated error accumulation through the estimation of a large number of parameters in non aggregated models will outweigh this inaccuracy (O'Neill 1973).

Approximations derived from other disciplines such as statistical physics, aim at simplifying fine scale complexity at larger scales but are, unfortunately, themselves of great mathematical complexity. Here, I will discuss two approximation methods that are often used to simplify spatial model simulations at larger scales: (1) mean field and (2) moment equations based approximations (Picard and Franc 2004).

Developed in statistical mechanics, the mean field approximation assumes that individuals encounter one another in proportion to their average abundance over space and that the behavior of one particular individual is influenced only by the average behavior of all others. However, this is an unrealistic assumption as highlighted by the following example. According to the mean field theory the spatial behavior of a sand pile can be described based on an average description of each grain of sand in the pile. But, falling at the right moment, one single grain of sand might sweep along the whole pile thus exerting a very particular influence on the spatial behavior of the pile. Yet, mean field theory does not allow such a possibility and will thus fail to adequately describe numerous phenomena in particular situations (Ward 2002).

In ecology, the mean field approximation can be compared to the transformation of distance dependent competition indices to distance independent indices where locally distinct interactions are averaged and assumed to be equal for all plants in the system (i.e. stand, Picard and Franc 2004). In the Moorcroft article, the mean field approximation gives (see solid line in Figure 4a) the overall behavior of all gaps when horizontal (i.e. between gap) light heterogeneity is ignored. When each gap is assumed to receive, for individuals of a given height, the same amount of light, the mean field approximation underestimates aboveground biomass accumulation compared to the 10 runs of the stochastic gap model and the field data. The same shortcomings have been documented in predicting forest structure (Pacala et Deutschman 1995).

Moment equations consider gap dynamics as a stochastic point pattern process over time and space (Picard and Franc 2004). The state of the system is then thought of as one of an infinite number of possible realizations of the stochastic processes generating the system state. Moment equations thus replace the spatial pattern observed with statistics (i.e. probability distributions) that describe this pattern characteristics and then use these statistics to express the dynamics observed (Law and Dieckmann 2000a). The use of moment equations, also referred to as distribution based modeling, remarkably reduces computing time and is thus a means to expand the use of gap models to large scale vegetation dynamics from fine scale interactions (Lischke et al. 1998).

Moments of a distribution can be easily understood with a one dimensional distribution such as a set of values. Moments are the sums of integer powers of these values. The first, or central, moment is the estimation of the value around which clustering occurs (e.g., mean, median, mode). The second moment describes the spread around the central moment (variance), the third gives information about the symmetry of this spread (skewness), the fourth specifies the form of this symmetry (kurtosis) and so forth (Press et al. 1992). Hence, each additional moment will add some information to the preceding and the set of values can be completely described by the ensemble of infinite moments. However, usually a limited number of moments will give a sufficiently accurate description in most applications.

Spatial distributions (of points, individuals etc.) append the complexity of this concept by adding one dimension. The first spatial moment then becomes the mean density of the population, such as the mean field state variable (Murrell et al. 2004). Since the first moment does not contain any information on the spatial distribution of the individuals across space, the addition of the second moment will include details about the density of pairs of individuals with a given distance (Law and Dieckmann 2000a & 2000b, Murrel et al. 2004). The second moment is thus closely related to other second order spatial statistics widely used in ecology (e.g., Wiegand and Moloney 2004).

However, the first two moments are only the beginning in the hierarchy of spatial moments, as is the case with one dimensional moments. Since the complexity of the calculations increases remarkably with each hierarchical level, moment closure procedures are applied assuming that higher order densities quickly equilibrate over time and that lower order densities (i.e. pair densities) describe sufficiently well the spatial structure of the system (Bolker and Pacala 1997). Whilst the mean field approximation is attained by setting the second order term equal to the square of the mean density, the second order approximation seeks to replace the higher order moments in terms of the first and second order moments. Although second order closure seems a minimum to satisfactorily describe spatial interactions in a point pattern process (Murrell et al. 2004), the closure at a higher order might be necessary if important properties of spatial structure lie in higher order moments (Law and Dieckmann 2000a). Hence, there is no rule of thumb in moment closure procedures (Gandhi et al. 2000).

As has been shown in this brief revue, a considerable amount of insight into the problem of scaling has been developed in different disciplines over the last 25 years (Schneider 2001).Yet, scaling still remains an active field of research and a major challenge in (ecological) science.

2. CRITIQUE OF MOORCROFT ET AL. (2001)

2.1 Article overview

Moorcroft et al. (2001) give a description of their individual-based, terrestrial biosphere model, the ecosystem demography model. The ED serves the purpose to model large-scale (i.e. regional to global) vegetational characteristics from fine-scale (i.e. physiological) processes (Fig. 1). As heterogeneity is an inherent quality of terrestrial ecosystem, the modeling procedure uses a stochastic, process-based forest gap model to predict carbon dynamics in individual plants at the scale of a forest gap (approx. 15 × 15 m). Through this stochasticity (e.g., tree mortality) and by accounting for plant functional diversity, the ED simulates endogenous fine-scale ecosystem heterogeneity whereas soil properties and climate account for exogenous ecosystem heterogeneity.

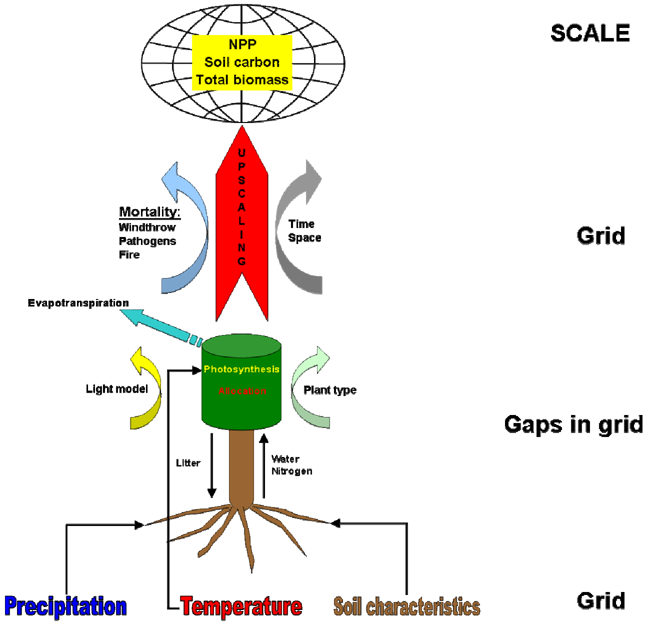

Figure 1. Schematic representation of the ED. Climate data at the grid level govern physiological processes of vegetation in gaps which are then upscaled to the grid level and over specified temporal horizons through an age (mortality) stratified procedure. Resulting biomass, soil carbon, and total biomass estimations cover the extent of the input data.

The gap model simulations are then scaled up to 1° × 1° global grid cells, corresponding to the resolution of the input data. Although brute-force simulations could be used to achieve the upscaling from gap to grid, these have the disadvantage of high computing cost and mathematical as well as analytical intractability. Moorcroft et al. (2001) overcome these limitations by using a size- and age-structured (SAS) approximation for the first moment of the stochastic fine-scale modeled processes. This methodology allows preserving the stochastic nature of the fine-scale simulations, thus maintaining the simulated ecosystem heterogeneity throughout the scaling procedure, while simultaneously creating simplicity and tractability.

Moorcroft et al. (2001) use a system of partial differential equations (PDE) derived from moment expansion closure as an approximation method and validate the approximations against repetitive runs (10 runs of 25 gaps) of the stochastic gap model. Model upscaling is undertaken for tropical and subtropical South America (15ºN to 15ºS) to equilibrium state (200 – 500 yrs). Resulting model biomass simulations are compared to large-scale data for this region and, finally, the model is validated in more detail on data from six sites spanning a gradient of climatic conditions and vegetational characteristics.

2.2 General remarks

The ecosystem demography model (ED) uses only climate and soil properties to predict above- and belowground ecosystem structure, fluxes of carbon and water within the ecosystem and between the ecosystem and the atmosphere. It is therefore strongly dependent on the data quality of these two sources. Although several aspects of the input data show severe shortcomings (e.g. climate data coverage for only two years, no intra-grid variability of the data), the authors are aware of these shortcomings (e.g., p.560) and suggest means for remediation (e.g. interactive input from a climate model).

Hence, my critique will not cover these aspects. Also, a critical assessment of the conceptual as well as mathematical underpinnings of the moment expansion procedure is beyond the scope of this synthesis. The concept and the techniques involved are quite complex and any attempt to critically evaluate this methodology would require a thorough knowledge in advanced statistical mathematics which is impossible to acquire in only six weeks.

I will restrict my critique on conceptual shortcomings of the general model procedure as I, in my modest understanding of this dense matter, recognize them. However, one should keep in mind that the overall complexity in ecosystem modeling does not allow me to produce a profound review. This again would require a higher level of insight than I could achieve in the given time frame.

The ED article can be coarsely subdivided into three sections: the stochastic gap model, the scaling procedure, and upscaling results. Hence, my synthesis will follow this structure preceded by a more general section treating the scaling problem. Considering the scope of the modeling approach (large-scale predictions) it is only consistent that my critique is centered on the context of climate change, a large-scale problem with major implications on human development and welfare.

2.3 Detailed critique

2.3.1 The forest gap model

2.3.1.1 What is a forest gap model good for?

The world's forests comprise more than 80% of the global aboveground carbon (Waring and Running 1998). This highlights the importance of forests in the processes of global carbon dynamics and explains why forest models are a major tool in estimating the impact of climate change on the earth's vegetation (Norby et al. 2001a).

It is widely accepted that static, deterministic models linking present day climate to vegetational properties are inadequate tools for predicting ecosystem responses to future climate conditions and increasing CO_2 levels (Emanuel et al. 1985, Woodward and Smith 1994). This had led, especially since the early 1970's, when digital computer technology became readily available, to a major thrust in the development of gap models (e.g., Botkin et al. 1972, Shugart et West 1977, Huston et al. 1988, Urban 1990, Pacala et al. 1996).

These models, in which the ecosystem (e.g., a forest) is represented as a composite of many small and independent (i.e. no interaction between gaps) patches of land of different ages and successional stages, incorporate several interconnected submodels (i.e. resource availability, establishment, growth, and mortality) (Bugmann 2001). By linking these submodels, a gap model describes the behavior of a system through the interaction of its components which are considered to represent the underlying mechanisms that give rise to the observed behavior of interest (Reynolds et al. 1993). Therefore, gap models are often referred to as mechanistic models.

Process-based (gap) models use physiological and other processes as baseline units for model simulations. Since gap models are usually centered on individuals (the sub-units of a plant community), ecophysiological processes integrate in these individuals and represent therefore a natural fine-scale level for ecosystem modeling. Thus, "*ecophysiology is, in a sense, preadapted for large-scale* [modeling] *problems*" (Field and Ehleringer 1993, p.1-2).

Naturally random events such as mortality, recruitment, and disturbance are often incorporated in gap models as stochastic processes (Hawkes 2000). By defining probability density functions that closely match or estimate natural occurrences of the stochastic events, stochasticity in models allows reproducing observed randomness of ecosystem processes (Gratzer et al. 2004).

Other processes such as litter turnover, soil moisture dynamics, and nutrient cycling are also treated in gap models (Shugart and Smith 1996, Bugmann 2001) and so gap models combine key processes of interactions between plants and their environment. Since gap models function at the same level at which management data are collected, they can be easily parameterized from field data (Pacala et al. 1996) and validated on survey data in a straightforward manner. The temporal grain (i.e. the time step of simulations) in gap models ranges from days to years and their temporal extent (i.e. simulation horizon) spans decades to centuries (Reynolds et al. 2001).

Moorcroft et al. (2001) use a forest gap model similar to the HYBRID model (Friend et al. 1997). HYBRID simulates the cycling of carbon, water, and nitrogen within terrestrial ecosystems interacting with the atmosphere (Fig. 2). It has been intended to predict ecosystem behavior (exchange of carbon and water with the atmosphere), ecosystem structure (vegetation type, carbon accumulation), and dynamic processes (biomass turnover, succession) from climate alone (Friend et al. 1997).

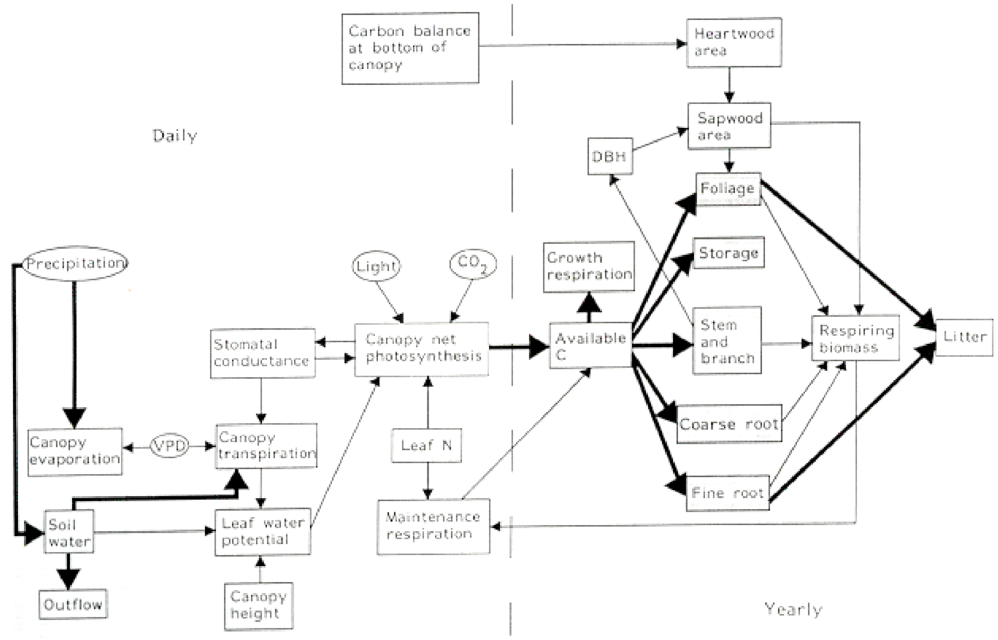

Figure 2. Principal physiological and hydrological features of the process-based, terrestrial biosphere model of ecosystem dynamics (HYBRID v3.0) (figure reprinted from Ryan et al. 1996)

Computation of physiological processes (i.e. photosynthesis, nitrogen uptake) operates on a daily basis whereas simulation output (e.g., carbon allocation, litter turnover) usually has an iterative annual rotation. Species diversity is represented through different general plant types (GPT; e.g., grasses, broadleaf trees, needle-leaf trees) with different physiological characteristics. Plants in each gap compete for light, water, and nitrogen. The model is size-structured meaning that taller plants use proportionally more resources and deprive those from their competitors. However, resource availability is horizontally (within the gap) homogenous, corresponding to the non spatial nature of plant distributions within gaps.

The model simulates physiological processes, translates them into carbon gain, and allocates carbon to divers sinks such as live tissue maintenance, respirational demands, reproduction, and growth. Growth influences competitive interactions and, together with stochastic processes such as mortality and fire, will yield ecosystem structural and compositional heterogeneity (Friend et al. 1997). Underlying physiological processes like photosynthesis are based on commonly accepted ecophysiological models (e.g., Farquhar and Sharkey 1982).

The stochastic gap model in Moorcroft et al. (2001) predicts, as HYBRID does, ecosystem structure using only climate and soil properties as input. However, time steps for physiological processes are hours instead of days. This higher resolution is obtained by interpolating the three-hourly climatology of the ISLSCP I global climatological data set (Sellers et al. 1995). Moreover, climate data are provided for an average day of each month on a 1º×1º spatial grid only. The resulting hourly resolution of the climate data is then is of theoretical nature since climate input parameters have not been measured (or modeled) at this resolution. Hence, the interpolation seems an unnecessary effort to extent artificially the temporal grain but without effective gains.

2.3.1.2 Are gap models adequate for upscaling?

Gap models, particularly process-based gap models, have been used for more than 30 years to model forest dynamics on varying spatial and temporal scales and, more recently, under numerous climate change scenarios (e.g., Botkin et al. 1972, Kohyama and Shigesada 1995, Bugmann 1996, Pacala et al. 1996, Shugart and Smith 1996, Cao and Woodward 1998). Although other approaches like ecological response functions and biogeographic correlations are often employed to estimate the effects of climate change on forest, these methods show a severe conceptual limitation. By only considering climate as determinant of species distributions, they neglect other important factors like competition and pathogen activity which might then be confounded in the modeled vegetation response. Predictions are hence based on the realized niche of a species rather than the fundamental niche which dramatizes vegetation response in a changing environment (Pacala and Hurtt 1993, Loehle and LeBlanc 1996).

Mechanistic models also use climate data as input for plant physiological processes but extend the resulting carbon gain in competitive interactions (Bugmann 2001). This alleviates niche confounding to some extent. However, by omitting the physiological tolerance of plants to climate extremes, by failing to consider physiological plasticity as well as population genetic dynamics, forest gap models in their current formulation still lead to overestimation of forest sensitivity to climate change (Loehle and LeBlanc 1996). These topics will be discussed in section 2.3.2.

A powerful alternative for gap models are spatially-explicit, individual-based models such as ZELIG (Urban 1990, Urban et al. 1991) or SORTIE (Pacala et al. 1993&1996). Here, the forest is treated as an ensemble of individual trees rather than small patches of vegetation. The major advantage of this resolution is that resource availability is vertically AND horizontally heterogeneous within gaps. Thus, competitive interactions between individuals are three dimensional and can therefore be more realistically simulated than in gap models. Also, seed dispersal, seed predation, herbivory, and soil resource heterogeneity can be integrated more accurately in these models (Gratzer et al. 2004). However, the complexity of competitive interactions and the lack of a universally appropriate mechanistic representation of competitive interactions among different species in a natural (i.e. species-rich) setting require that spatially-explicit, individual-based models are parameterized through field data as to closely match the conditions of the environment to be modeled. This strong dependence on data entails the need to parameterize the model for each new system de novo (Hawkes 2000) and is thus counterproductive to the mechanistic understanding of ecological theory especially when extrapolation for management purposes is desired (Levin 1992&1999). Data from multiple sites, spanning a gradient in the prevalent environmental conditions, can reduce the data dependence to some extent but this space-for-time approach might not reflect realistically vegetation response over time (Norby et al. 2001a). Also, spatially-explicit individual-based models are computationally demanding and therefore limited to stand scales (Gratzer et al. 2004). Hence, spatially-explicit gap models are the only feasible modeling technique currently available for large-scale applications (Bugmann 2001, Pascual 2005). These facts justify the model choice of Moorcroft et al. (2001).

2.3.1.3 Submodels and routines

The ED is a combination of a forest gap model and a complex upscaling procedure. This allows extrapolating fine-scale processes across spatial and temporal scales and thus gives the ED the quality of a global vegetation model. Consequently, the predictions originate from the individual gap model components which I will describe below. With this information in mind, a more comprehensive analysis of the validity of the underlying assumptions and mechanisms will be undertaken in a subsequent section (2.3.2 Model assumptions).

i. Growth

The ED models growth in a mechanistic process-based manner, i.e. growth is NOT an aggregate function of a measured variable such as light intensity like, for example, in SORTIE (see Pacala et al. 1993&1996). This also implies that the ED has no explicit growth model but rather a growth routine that links several key processes of plant growth. Inspired by HYBRID, the ED gap model simulates growth by linking carbon acquisition (photosynthesis), carbon loss (respiration and litter), and allocation (partitioning of carbon toward divers sinks). Photosynthesis is constrained by resource availability (light, water, nitrogen) through stomatal limitations and through competition for resources, thus entirely mechanistic. However, carbon (and nitrogen) allocation as well as carbon loss are based on assumptions derived from field measurements and are therefore of rather empirical nature. This has a negative impact on model flexibility especially in the context of changing climatic conditions as will be discussed below.

As to account for differences in species characteristics while trying to limit model complexity, Moorcroft et al. (2001) use a simplification based on plant functional groups. The ED uses four groups: C_4 grasses, early-, mid-, and late successional tree types (all C_3 photosynthesis). These groups assume different allocational schemes which lead to differences in competitive capacity, growth and mortality rates among groups and are thus a means to simulate successional dynamics and compositional as well as structural diversity.

ii. Recruitment

Recruitment in the ED is a very coarse approximation of natural regeneration dynamics. Here, seed production is modeled through (assumptive) allocation schemes, whereas dispersal and establishment are random processes. Seedlings are randomly dispersed among gaps of a same grid cell; they all have the same size at 'birth' and the same survivorship. Hence, spatial variability in seedling distributions stems from these random processes only and not from seed source distribution and species (i.e. functional group)-specific dispersal capacities.

iii. Mortality

Mortality is a stochastic process in the ED and is assumed to originate from two sources. Firstly, there is a negative relationship of mortality probabilities with functional type (grasses to late successional trees) and, secondly, a more mechanistic mortality component based on carbon balance. Early successional plants have a higher probability of mortality to account for their lower lifespans and plants with a negative carbon balance (through climate limitations or competition) have higher mortality probabilities because of higher vulnerability to other stresses (Bugmann 2001).

iv. Light

Light is modeled as above-canopy PAR (photosynthetically active radiation) that decays exponentially as it travels vertically through the canopy. A plant's light availability is determined as the PAR attaining the mid-point of its crown.

v. Soil hydrology

Soil hydrology, although primarily dependent on the grid-scale input from the climate data, is modeled by a one-layer hydrology model that accounts for the differences in evapotranspiration between gaps. This then leads to differences in soil hydrology between gaps even if the input is identical for all gaps of the same grid cell. Further, soil water dynamics are modeled with respect to runoff and percolation where hydraulic conductivity is computed from soil moisture content, soil depth, and soil texture.

vi. Decomposition and nutrient cycling

Belowground processes such as soil water dynamics, nutrient cycling and litter decomposition are important factors of plant growth. The ED relies on a simplified version of the soil sub-model of CENTURY (Parton et al. 1993) which models belowground dynamics based on a pool of five dead organic matter compartments. Decomposition rates vary according to the N:C ratio of each type of organic matter and are overall dependent on soil temperature, moisture, and texture interacting with soil nitrogen mineralization dynamics and carbon fluxes (Friend et al. 1997).

vii. Disturbance (Fire)

The only type of disturbance explicitly considered in the ED is fire. Based on the fire model of Neilson's (1995) mapped atmosphere-plant-soil system (MAPSS), the ED improves the resolution of the original model by determining fire frequencies for each gap (instead of the grid) as a function of fuel quantity and climate data.

2.3.2 Model assumptions

A major shortcoming of the article is the lack of detail in the description of the stochastic gap model. Although basic mechanisms are briefly mentioned such as leaf physiology, the authors do not give sufficiently detailed information about the underlying assumptions and this even in the online supplement. For example, net carbon uptake and transpiration is defined as the product of the per-leaf-area carbon and water fluxes and the total leaf area minus growth and tissue respiration (p.562). Without any further information (including the online supplement), one must assume that the model extrapolates individual-leaf carbon and water fluxes linearly to the whole plant which is a prohibitive assumption (Wang et al. 2001). However, the parent model (HYBRID) uses a stratified approach where photosynthetic capacity varies in the canopy depending on relative canopy layer position (Friend et al. 1997). Since Moorcroft et al. (2001) don't specifically mention to what extent their model is 'similar' to HYBRID it is difficult to judge their model without further details.

Some concern centers on the adequacy of the underlying mechanistic relationships governing carbon uptake and allocation, water fluxes, and resource interactions under changing environmental conditions. The ED has since been used to predict the future of the U.S carbon sink spanning the period from 1700 to 2100 (Pacala et al. 2001, Hurtt et al. 2002). Consequently, its application as a tool for predicting vegetation response under changing environmental conditions entails profound model requirements. Although Moorcroft et al. (2001) cover only tropical and subtropical South America (15º N to 15º S), the potential of their modeling approach is not restricted to this particular geographic range. Furthermore, the upscaling procedure employed makes it rather appropriate for large-scale modeling up to the global scale and over large temporal horizons. Therefore, the model should be armed for this purpose. Even though some of the following issues (e.g., phenology) might not apply to the specific – subtropical and tropical – context of Moorcroft et al. (2001), these points should be kept in mind when one considers its potential and already extended use (to the U.S. and spanning four centuries) to other ecological settings.

The following paragraphs will critically highlight aspects of the ED that constrain, in the context of global climate change, its ability to adaptively predict vegetation responses. Some of the driving forces (e.g., temperature rise) have effects on several plant processes and functions in the gap model so I use the latter as a structure (section a – e) of my critique. However, the ED has shortcomings also in the coverage of recruitment, dispersal, and disturbance that act on the grid cell level. These will be discussed in sections f and g.

a. Photosynthesis and growth processes

There is substantial evidence that a CO_2-increase mediated global warming and changes in atmospheric water dynamics have a significant influence on plant growth (Myneni et al. 1997, Nemani et al. 2003) and should be considered in modeling strategies (Cramer et al. 1999, Cramer et al. 2001). Also, it has been shown that physiological responses to CO_2 increases vary between species (Tjoelker et al. 1998&1999) and even between genotypes of the same species (Wang et al. 2000). The ED, relying on a mechanistic process-based approach, does account for climatic change (e.g., temperature rise, CO_2 increase) by explicitly incorporating climate variables in the underlying leaf-level physiological equations although upscaling to the plant level might still be a problematic issue (Jarvis 1995).

It has been shown that plants adjust their photosynthetic responses to increased CO_2 concentrations by down-regulating net carbon uptake (Sage et al. 1989) through reduced leaf nitrogen, specific leaf area (Curtis 1996) or the reduction in the amount or activity of rubisco (Bowes 1991). However, there is still ambiguity about the general applicability of those mechanisms (Curtis and Wang 1998) and further research, maybe through model exploration, might be useful to clarify how plants react to increased CO_2 concentrations over longer horizons. Hence, the ED ought to include an intrinsic flexibility of the photosynthetic processes to altered climatic conditions. In its current configuration, the ED lacks such flexibility and accounts only for direct influences of climate change (e.g., CO_2 and temperature increase) on physiological processes without adjustment for acclimation.

Besides its effects on physiological processes of individual plants, temperature also alters ecosystem composition. Carbon dioxide assimilation rates as a function of temperature have an inversed U-shaped form, indicating the existence of a lower and upper limit as well as an optimum temperature (Taiz and Zeiger 1998). However, the use of this relationship in predicting responses in photosynthetic activity at the population level and under long-term temperature changes might be unjustified. It ignores the fact that photosynthesis and respiration rates acclimate to prevailing temperatures through genetic differentiation of geographic populations (Gunderson et al. 2000).

Potential temperature adjustment schemes are elegantly illustrated in Norby et al. (2001a). Without acclimation (Fig. 3A), the response just moves along its idealized path either towards or away from the theoretic optimum depending on the geographic location of the population. This is the situation under the current ED settings. When the optimum temperature does not change but the species' response is greater at every given temperature, response increases in the northern populations would compensate for loss of performance as one moves closer to the southern edge of the species' distributional range (Fig. 3B). With acclimation, the response stays constant by adjusting the temperature range in the same direction as the shift occurs (Fig. 3C). Adaptation represents the case where the response curve is considered the average response of different populations and where some of these are better adapted to the new conditions although with a lower response (Fig 3D). The latter two cases (Fig. 3C, 3D) dampen the effect of a temperature increase on population-level plant physiology.

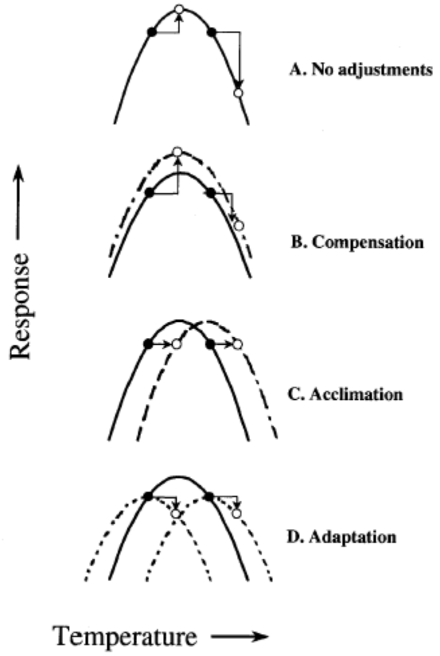

Figure 3. Potential mechanisms of responses adjustment to temperature rise. Solid lines are idealized temperature ranges where northern populations are to the left of the optimum and southern populations to the right. Dashed lines illustrate the mechanism of adjustment. See text for details. Reprinted from Norby et al. (2001a)

Adjustment mechanisms of photosynthetic and respiration rates as shown above can also be applied to other physiological responses and are likely to integrate into different competitive interactions among ecotypes of a same species and among species (Bazzaz 1990, Post and Forchhammer 2001). This would, on the long run, translate into a genetic shift of the species toward the more adapted genotype through intra- and interspecific competition. Resulting community change will influence ecosystem functioning and productivity for which model simulations and upscaling procedures should account for but which is not the case under the current ED configuration.

b. Phenology

Temperature (i.e. global warming) also impacts on growth through the lengthening of the growing season (Keeling et al. 1996) which results in higher net primary productivity (NPP; Myneni et al. 1997). Changes in plant phenology in response to climate change have been recorded for four European deciduous tree species (Menzel et al. 2001). This implies that plant phenology and potential responses should also be explicitly included in the model. HYBRID (v3.0) uses a combination of heat-sum/chilling-day estimates to determine the length of the plant growing season. However, this approach might not account for acclimative responses and a more mechanistic approach, based on carbon economy, might be necessary when modeling across geographical regions and over extended periods in a changing environment (Friend et al. 1997, Arora and Boer 2005).

c. Allocation

Allocation is another critical point of the ED. Most of our understanding of allocation within plants is phenomenological, not mechanistic since the underlying physiological mechanisms that drive allocation are still largely unknown (Wilson 1988, Ingestad et Ågren 1991). The ED allocation scheme is based on inverted, empirically-derived allometric relationships of aboveground biomass partitioning of plants in relation to their height, diameter, and wood density. This entails that *"plants in our model thus allocate to stay on data-defined allometries"* (p.564). In this case the model has a restricted predictive potential to the point that *"if you provide a measurement, then the model will provide a prediction of that measurement"* (Norman 1993, p.49). However, this deterministic approach is hardly adequate in predicting vegetation responses under changing climatic conditions (Emanuel et al. 1985, Woodward and Smith 1994).

For example, leaf-area index (LAI)-stem volume allometry seems to change in CO_2 enriched stands once canopy closure is attained (DeLucia et al. 1999, Norby et al. 2001b). This indicates a LAI adjustment of canopies under CO_2 increases to control nitrogen demands and thus relaxes constraints on stem growth through N limited photosynthetic rate under increased CO_2 concentrations (Curtis 1996). However, this adjustment of allometry is not included in the ED and fixed LAI-stem volume allometry causes therefore a reduction in biomass increases through N limitations (Norby et al. 2001a).

Carbon allocation to fine roots is considered equal to foliar biomass allocation in the ED. Sapwood cross-sectional area is calculated from a pipe model that relates sapwood allocation proportionally to foliar biomass (Shinozaki et al. 1964). Since foliar biomass is derived simply from the partitioning of active biomass into leaf, roots, and sapwood, this fixed relationship has a major implication under changing environmental conditions. Under the current model configuration, a decrease in soil resources (through altered precipitation patterns or competitive interactions) negatively impacts aboveground productivity (less photosynthesis) and decreases therefore also belowground carbon allocation (Wullschleger et al. 2001). There is, though, a solid body of literature indicating that plants modify their allocation scheme in favor of root growth under conditions of limited soil resource availability (e.g., Canham et al. 1996, Wang et al. 1998, but see Berntson et al. 1997). Hence, the implementation of allocation schemes that directly account for soil resource availability in a mechanistic manner should be investigated as to better predict NPP and thus global biomass responses in a changing world (Friedlingstein et al. 1999).

d. Belowground processes

With respect to decomposition and nitrogen cycling, the ED leaves out some important aspects of belowground dynamics such as atmospheric nitrogen inputs, biological fixation, denitrification etc. (p.566). This reduces its capacity to predict the effects on ecosystems of the long-term human-induced alteration of the nitrogen cycle (Vitousek et al. 1997).

Also, the growth routine of HYBRID (v3.0) assumes symmetric competition for belowground resources such as water or nitrogen. Consequently, the resources are shared among competitors according to their demand which is greater for taller individuals. Whilst this formulation is suitable among competitors of the same functional group (where demand is defined through group-specific plant tissue nitrogen concentrations) it may wrongly represent interactions of competitors of different groups. Here, greater competitiveness due to size could be dampened through superior capacity to compete for a specific resource such as nitrogen. This might be even more so when climatic changes modify the competitive interplay between different species (or functional groups) through a differential acclimative response (Fig. 3). Hence, functional groups should also be characterized by their competitiveness which is presently not the case in the ED.

As mentioned above, temperature changes can alter community composition directly through acclimative or adaptive adjustment to prevailing conditions. However, there is also the potential for a secondary feedback through litter quality changes. Since temperature influences nitrogen mineralization, shifts in species composition through higher temperatures (assuming abundant precipitation) towards rich-litter species (e.g., substitution of conifers by deciduous trees) can amplify these changes. Richer litter creates conditions more suitable for these species and will give them a competitive advantage (Post and Pastor 1996). However, the inverse will occur when a temperature rise is accompanied by a reduction in precipitation (e.g., in more southern regions). This dynamic can not be modeled adequately under the present settings of the ED. But, a refinement of the competitive interactions in the soil resource model could improve its ability to correctly approximate these dynamics.

e. Plant functional diversity

Plant diversity is simplified by the use of plant functional groups. These are defined based on (i) leaf life span [LS] (ii), specific leaf area [LA], (iii) leaf nitrogen content [LN], (iv) wood density [WD], and (v) maximum height [MH]. Whilst parts of this classification (LS, LA, LN) is based on empirical data of net photosynthesis (Reich et al. 1997), there is some ambiguity concerning the scientific basis of WD and MH. Although the concept of plant functional group characterization is further developed in Wright et al. (2004, 2005), extending leaf trait relationships to leaf phosphorus and potassium concentrations, photosynthetic N-use efficiency, dark respiration rates, and N:P ratios, the link to WD and MH is not specified. Moorcroft et al. (2001) do not identify the source of wood density and maximum height relationships and this is, albeit the intuitive agreement between successional stage and wood density/maximum height, a lack of scientific rigor and needs to be highlighted.

Also, functional diversity might be underrepresented by the four functional groups. Since functional plant types lie on a continuous gradient rather than being divided into distinct functional type classes (Wright et al. 2004), the broadening of functional diversity might allow a better representation of diversity *per se* and thus a greater flexibility to environmental conditions and changes.

f. Recruitment

Recruitment in the ED is modeled through a combination of allocation (carbon input into seed production), dispersal and establishment. The allocation pattern is static and inflexible: *"the fraction* [of carbon] *going to reproduction is a constant for all species and is set to a value consistent with seed trap data"* (p.564). Not knowing how this data has been collected, one wonders whether this takes into account species-specific interannual variation in seed production that takes place in regular intervals and is known as a species' masting behavior. Masting in trees occurs in basically all types of forests, ranging from boreal (Smith et al. 1990) through temperate (Allen and Platt 1990, Sork et al. 1993) to tropical forests (Janzen 1974, Ashton et al. 1988). It has been shown that climate change can alter a species' masting behavior and cause changes in seed predator populations with potential devastating effects on reproductive success (McKone et al. 1998). This in turn has important impacts on community composition and structure (Clark and Ji 1995) and should be considered in the modeling process which is not the case in the ED.

Dispersal is considered a random process between gaps of the same grid cell. The authors acknowledge that they have implemented *“the simplest of dispersal and recruitment models”* (p.564) thus recognizing potential limitations. However, it should be highlighted that this is a symptomatic phenomenon in gap models. Initially neglected due to a lack of detailed knowledge of regenerative processes and due to computational limitations, the treatment of regeneration in gap models has not significantly changed over the last 15 or so years (Price et al. 2001). More recently, dispersal has received more attention by developing conceptual models that allow acquiring a realistic and, even more important, mechanistic understanding of this key process of spatial structure and composition in plant communities (Nathan and Muller-Landau 2000, Nathan et al. 2001).

Yet, even a more realistic treatment of dispersal will not allow a complete mechanistic representation of the whole regeneration process. Other components such as vegetative reproduction, seed storage, germination, and establishment need to be specified (Fig. 4).

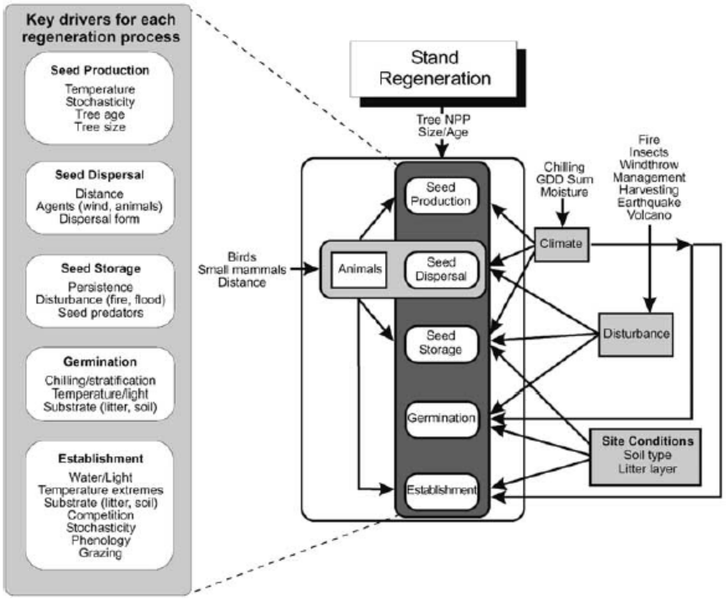

Figure 4. Suggestive representation of component processes in a mechanistic regeneration model. Vegetative reproduction is not specified but could also be integrated. See text for details. Reprinted from Price et al. (2001)

As shown in Fig. 4, climate (and thus climate change) potentially influences all of the components in the regeneration process. Hence, an aggregated representation of regeneration where saplings are scattered across the modeling landscape at random as to simulate natural variation in regeneration success between species, might not adequately capture the dynamics that develop when these processes are affected by changing climatic conditions (Price et al. 2001). Once again, the predictive capacity of the ED might suffer from a lack of mechanistic relationships especially when modeling across large temporal and spatial scales, its main objective.

g. Disturbance

The ED considers explicitly only fire as disturbance. However, herbivores and pathogens are important determinants of species composition, ecosystem function, and socioeconomic values of forests. Surprisingly enough, this major component of forest productivity is basically ignored in forest gap models, at least in the form of mechanistic relationships. To my knowledge, only Lexer and Hönninger (1998) have accounted for bark beetle-induced mortality in conifer stands by coupling a gap model with a two-stage stand risk model.

Due to the short life cycle and the sensitivity of physiological processes to temperature which translates into an enormous reproductive potential, insect herbivore population dynamics can be dramatically altered even from small climatic changes (Ayres and Lombardero 2000). Vertebrate herbivory might be altered through the impact of elevated CO_2 on forage quality of leaves (lower nitrogen content) and changes in concentrations of defense substances such as alkaloids and tannins. This can lead to a 40% increase in per-herbivory consumption and can cause, under certain conditions such as drought, a 2 – 4 fold increase in herbivory rates (Coley 1998).

In the context of climate change, pathogens and herbivores disturbances regimes could be modified through direct effects on their survival and development (overwintering success, accelerated life cycle), physiological changes in the defense system of trees, and through changes in patterns of predation, mutualism, competitors or disease. Although changes in plant-pathogen interactions cannot be easily predicted due to their specificity, it is recognized that climate change will modify these interactions (Volney 1996, Coakly et al. 1999) thus also impacting on plant allocational patterns (Loehle 1988). Forest pest activity should therefore be modeled in a mechanistic manner and could be linked, like the fire submodel, to climate and vegetation variables although this will require the assessment of empirical relationships as a first step (Coakely et al. 1999).

The fire submodel also shows significant shortcomings. Since fire propagation is computed by redistributing total (grid cell) ignited fuel among a proportional number of gaps in the grid cell, the fire model misses to simulate the spatial distribution of fires, an important factor of vegetation structure and pattern (Peterson et al. 2005). Also, fire intensity is not accounted for which leads to the simplification that a fire, when it occurs, burns the entire vegetation of an ignited gap. This assumption is too severe and might dampen its general applicability (Neilson 1995). Since fire severity also governs the post-fire successional pathway (Graham et al. 2004) a need to include this parameter in the modeling process could improve model prediction, especially under changing (warmer and thus locally drier) climate.

2.3.2 Upscaling procedure: moment approximation

Moorcroft et al. (2001) use a first-order approximation arguing that higher-order (i.e. second-order) approximations *"are not generally useful due to instabilities arising from the omission of higher order terms and the large number of covariance equations necessary for approximating a functionally diverse community"* (p.568). Their approach is therefore basically a mean-field approximation neglecting spatial heterogeneity in resource availability. Since this has been proven to be grossly inadequate for predicting the mean behavior of the individual-based forest simulator SORTIE (Pacala and Deutschman 1995), they refine their approximation by conditioning on patch heterogeneity thus accounting for spatial (horizontal) resource heterogeneity indirectly (Hurtt et al. 1998). This yields an approximation based on two equations, one defines the demography of patches (horizontal heterogeneity) and the other the dynamics of plants in these patches (vertical heterogeneity) (Kohyama 1993, Kohyama and Shigesada 1995).

Whether or not the 'mechanics' of this approach are appropriate (i.e. partial differential equations derived form moment expansion [and closure]) is beyond the scope of this paper. Undeniably, the methods are among the most advanced in theoretical and computational ecology (Pascual 2005). The numerical treatment of partial differential equations is a vast subject by itself. They are at the heart of most computer analyses or simulations of dynamical, continuous systems, such as fluids or interactive particle systems. These equations establish, unlike algebraic equations, relations among the rates of change or fluxes of variables rather than relations among the variables themselves. Given initial values and boundary conditions, these equations propagate themselves forward in time and are thus a means to describe time evolution processes (Fig. 5, Press et al. 1992).

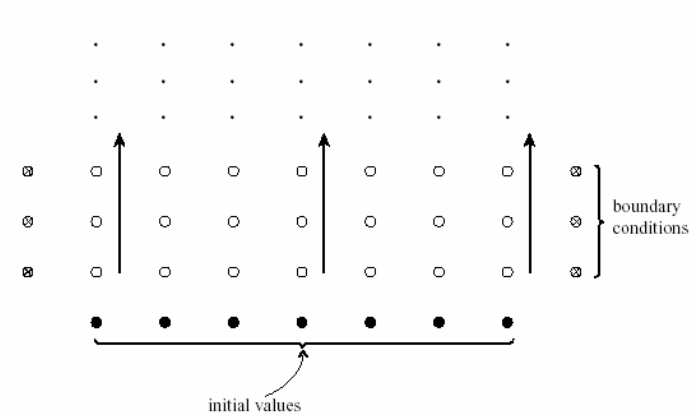

Figure 5. Schematic representation of a partial differential equation algorithm. Given initial values (●) and transitory boundary conditions (⊗), the algorithm propagates itself through time (indicated by arrows) and establishes the relationship between changes in quantities of variables (○) (Adapted from Press et al. 1992)

Hence, a serious critique would require a solid expertise in the field. However, one can question the appropriateness of the general method in the context of climate change, thus under changing input values. Do the assumptions of the approximation hold when the underlying conditions change?

As mentioned above, moment equations are based on a statistical description of the spatial pattern of interest. This requires that the probability distributions have to be parameterized, based on empirical estimates or derived from the mechanistic relationships of the underlying physiological (e.g., photosynthesis) of physical (e.g., light availability) processes. Whilst the appropriateness of the underlying mechanistic relationships depends on their flexibility to changes in climatic conditions (as discussed earlier), parameterization through empirical estimates will almost always give only a snapshot of existing conditions and is thus questionable in terms of flexibility.

For example, one component in the age structure term of the approximation stems from mortality-inducing disturbance (windthrow, pathogen attacks), with a specified height threshold (i.e. where trees become more vulnerable to windthrow or pathogen attack) and at a defined probability. The probability function is derived from observed mortality rates and thus a non-mechanistic component (see online supplement: appendix F). Although height growth might account for impacts of climate change on mortality probabilities through altered growth or allocation (if physiological acclimation to climate change is explicitly modeled), the specified probability at which mortality occurs remains empirically predefined. This is an erroneous assumption since both pathogen activity (Ayres and Lombardero 2000, see section 2.3.2) and wind storms (Watson et al. 2001, Fuhrer et al., in press) will be affected from observed and anticipated climatic changes. Hence, there should be a more flexible link between pathogen activity, wind velocity patterns, and mortality probabilities. For instance, in areas with anticipated increases in wind speed or occurrences of wind gusts, mortality probabilities at a given tree height should be higher than in areas where storm patterns remain unchanged. Also, in regions where particular forest pests are, under current climatic conditions, of marginal occurrence, mortality probabilities should change in a way that is consistent with the alterations of population dynamics of these pests under changing climate (e.g., warming).

To highlight the lack of flexibility of their approach, the density-dependent mortality component, determined by an individual's carbon balance, is *"governed by a single parameter, whose value is set to give reasonable understory size structure within forested grid cells"* (p.565). Besides the fact that appendix F specifies TWO parameters (m_1 and m_2), parameter 'tweaking' to obtain "*reasonable"* results is obviously a doubtful measure in an otherwise mechanistic modeling approach. In agreement with Classen and Langley (2005) that a model should not just get the right answer, but it should get the right answer for the right reason, this parameter 'adjustment' is a conspicuous violation of the causal link between carbon balance and mortality probability. Analogously, this also applies to the fire model, which two parameters have been *"set to give reasonable landscape patterns of fire"* (Appendix I). That these parameter settings will give reasonable understory and fire patterns under changed climatic conditions is rather doubtful.

2.3.3 Model validation: the results

I will only shortly discuss the results of the model simulations and this for two reasons. First, the authors acknowledge the shortcomings of the 'regional' data sets used to validate the model predictions (e.g., *"…anomalous soil characteristics in the ISLSCP data set"*, p.573; and ”*…regional estimates themselves are subject to a high degree of error and uncertainty"*, p.579). This gives the regional validation a *"cursory"* (p.572) quality that eases the need to discuss their findings in great detail. Even the authors themselves do not spend too much effort on a detailed discussion which is highlighted by the fact that Figure 10 receives only superficial attention. Secondly, the authors did, in my opinion, a good job in critically evaluating their own results at the local scale. Hence, I will only insist where their comments seem incomplete.

Concerning the regional results, the general agreement of the biomass, carbon stocks, and NPP predictions (Moorcroft et al. 2001, Figures 8-10d) is an indication that the model does reasonably well predict large-scale ecosystem functioning from fine-scale processes and thus validates the methodology. Though, the disagreement in belowground biomass estimations due to high moisture regimes (i.e. the dependence of decomposition on soil moisture) highlights the need to account for climate change in the ED. As climate change will cause an alteration of precipitation patterns, the sensibility of the soil submodel to moisture regimes might introduce further simulation error of difficult analytical tractability.

There are some astonishing aspects of the simulation results. For example, the fact that C_4 grasses are extinct at equilibrium for the San Carlos simulation is supportive for the adequacy of the, albeit simplistic, recruitment submodel for the purpose of this study. In this situation, less frequent disturbances create a mosaic of vegetation patches across the grid cell where, due to gap age, C_4 grasses cannot persist although random recruitment across the grid would allow seedling propagation among all gaps. Hence, the competitive interactions in the patch mosaic correctly prevent persistence of this functional type. Also, the development of the fire regime within the Calabozo ecosystem impressively mimics adaptive dynamics in vegetation-atmosphere interactions.

Overall, the model simulations are supportive of the adequacy of the modeling process, including the stochastic gap model and the upscaling procedure through the size- and age structured moment approximation. However, as the authors mention, *"future studies may find it necessary to move beyond our formulation and include sub-grid scale heterogeneity in land-use,…"* (p.581). This brings us to the following section.

3. PROPOSING THE ED AS A TOOL

3.1 Forest management strategies as carbon mitigation measures

The missing integration of land-use in the upscaling procedure seems to introduce prediction errors through the biomass overestimation in areas under agricultural management (p.573). However, this statement also raises a question about the utility of the ED altogether. Human land-use and other activities (e.g., burn-and-slash, fossil fuel consumption) are the causal link to climate change. If the ED would adequately predict the biomass stocking and NPP of the globe's ecosystems – assuming that modifications to account for acclimative responses of vegetation to changing environmental conditions have been applied – could the model then also be used as a tool to mitigate human impacts on climate change? Even though the authors see the ED as a means to gain *"analytical insights about the connection between local ecosystem processes and large-scale ecosystem functioning"* (p.581), therefore attributing a rather theoretical role, one could argue that the essential role of science is to provide the best existing knowledge as to decrease human-induced impacts on the earth's ecosystems (e.g., loss of biodiversity) but also to increase and strengthen human welfare. Hence, I propose the use of the ED as a tool for developing climate change mitigation strategies.

Carbon sequestration strategies, as a means to mitigate the negative impact of greenhouse gas (GHG) emissions from combustion of fossil fuels and changes in land-use, will most likely be encouraged in the near future through incentives measures such as emission taxes (Apps et al. 2001). The Kyoto protocol already allows emission trading where countries can sell their unused emission units (i.e. "*excess capacity"*) to countries that are over their targets. The limits on GHG emissions set by the Kyoto Protocol are thus a way of assigning a monetary value to the earth's shared atmosphere (UNFCCC 1997a). Considering the importance of terrestrial ecosystems, especially forests, as global carbon reservoirs (Table 1), these measures will generate the development of numerous carbon offset strategies in forest management (e.g. Brown et al. 2000).

Table 1. Estimates of global carbon stocks (GtC = 10^9 tons of carbon) in vegetation and soils to 1 m depth (Reprinted from Apps et al. 2001)

Biome	Area (million km^2)	Carbon stock (GtC) Vegetation	Soils	Total
Tropical forests	17.6	212	216	428
Temperate forests	10.4	59	100	159
Boreal forests	13.7	88	471	559
Tropical savannas	22.5	66	264	330
Temperate grasslands	12.5	9	295	304
Deserts and semi deserts	45.5	8	191	199
Tundra	9.5	6	121	127
Wetlands	3.5	15	225	240
Croplands	16	3	128	131
Total	151.2	466	2011	2477

For example, fire and insect control, forest conservation, establishment of fast-growing stands, planting trees in urban areas, and re-planting grasses or trees on cultivated lands are among potentially effective mitigation strategies (Boscolo et al.1997). Also, wood plays several important roles in carbon mitigation. It is itself a carbon reservoir; can replace construction materials that require more fossil fuel input, and can be burned instead of fossil fuels as a renewable source of energy. However, mitigation strategies are often of suboptimal nature. Although some strategies can be considered "no regret" or "win-win" solutions, most of them will be compromises. Additionally, the effectiveness of mitigation strategies will most probably change over time as a response to altered climatic conditions (Apps et al. 2001). However, these changes are difficult to foresee and an adaptive approach that takes into account the impact of climate change on the carbon sequestering and stocking capacity in ecosystems might be needed (e.g. Tian et al. 1999, Xiao et al. 1997). Hence, there should be a way of developing ecosystem (and forest) management strategies not only under present climatic conditions but also under the anticipated climate change.

3.2 A size-, age-, and land-use structured terrestrial ecosystem demography model

The ED could play an important role in doing so by using human land-use as another source of horizontal heterogeneity. Then the effectiveness of forest ecosystem management strategies to mitigate GHG emissions (e.g. Chen et al. 2000) could be predicted over longer horizons and under several climate scenarios. As to predict economic impacts of these strategies, the ED could be linked to a model of forest economics yielding information about the changes in human welfare (e.g., Irland et al. 2001, Perez-Garcia et al. 2002). The results of such simulations could then be traced back to land-use distributions and applied to develop forest management strategies.

The ED would then become a size-, age-, and land-use structured approximation of the adaptive (to climate change) stochastic gap model. Size structure would be determined through the already existing vertical resource heterogeneity, but age- and land-use structure would be derived through several controlled components. The development of scenarios of potential management strategies may be based on existing studies (e.g., Chen et al. 2000) and developed to contrast present land-use patterns which can be assessed through satellite data (Vogelmann et al. 1998).

Prevailing land-use patterns would be the base-line scenario for the management impact study. Hurrt et al. (2002) drew on land-use information from 1700 to 1990 to estimate the impact of land-use on the terrestrial carbon sink in the coterminous United States. While this approaches the proposed use of the ED to some extent, their study did not make use of the ED's potential to develop management scenarios maximizing carbon sequestration. Only fire suppression had been utilized in a binary manner, that is, their projection of the U.S. carbon sink had been simulated with or without fire suppression (Hurtt et al. 2002). Furthermore, land-use scenarios were based on historical data and the model was constrained, like the allocational patterns of the underlying gap model in the ED, to stay in between these historical bounds. This, however, is an unrealistic assumption when one considers the political pressure on land-use planning that arises from the ratification of the United Nations Convention on climate change and the Kyoto Protocol (UNFCCC 1997b).

That's why the proposed implementation of land-use in the ED accounts for user-defined changes in land-use to optimize carbon sequestration in terrestrial ecosystems on a global scale. Hurtt et al. (2002) categorize land-use coarsely in five classes: natural forest, crop, pasture, secondary forest, and plantation. However, I find it necessary, considering the importance of land conversion from diverse sources to settlements (i.e. habitation, transportation, and industry, Meyer and Turner 1992), to introduce another class, urbanization. These classes are the initial conditions (see Fig. 5) that need to be assessed using remote sensing or a combination of different data sets (e.g., Ramankutty and Foley 1998, Klein Goldewijk and Ramankutty 2004). Each of these conditions uses an individualized system of partial differential equations to track their respective size-, age-, and land-use structure evolution. Boundary conditions, tracking recruitment and disturbance events, will then modify the initial conditions by means of natural events such as establishment and disturbance (fire, pest) as in the ordinary ED, but furthermore through five management activities:

1. Fire and pest control

Obviously, fire is a direct carbon leak as it releases sequestered carbon through the combustion of above- and, depending on its severity, belowground vegetation (Robichaud et al. 2000). Under the present settings of the ED, an occurring fire completely destroys the aboveground vegetation only. Belowground biomass is not directly affected although a part of the released aboveground carbon (as well as nitrogen) is loaded into the soil submodel (Moorcroft et al. 2001).

As in Hurtt et al. (2002), fire control can be achieved through constraints of the area of fire-prone gaps. When, as proposed earlier, pest activity is included in the modeling process (for example through a pathogen model similar to the fire model), constraints on the area affected by tree-killing pests could then act as a management tool for pest control.

2. Forest conservation

Tropical and boreal forests are major carbon sinks with the highest carbon storage capacities among biome types (Table 1). Hence, a decrease in the total area of forests represents a net decrease in the carbon sequestering capacity of the Earth’s vegetation.

Deforestation for agricultural purposes or urbanization can be viewed as conversion of forested areas to either non-forested productive (i.e. crop lands, pastures) or unproductive (i.e. urbanized areas) land-use types. Forest conservation can therefore be achieved through constraints on existing land-use conversion patterns in a way that the transition of forest types to agriculture and urbanization is restricted or prohibited.

3. Harvest rotation length

Although the Kyoto protocol regards forest harvests as a carbon leakage (i.e. return of sequestered carbon in the carbon cycle), others have demonstrated that harvests can contribute positively to carbon storage when product storage and fossil fuel substitution is accounted for. Furthermore, reductions in harvest rotation length have positive effects on overall carbon stocking since, for a given time frame, earlier and more products are exported from the forest (Perez-Garcia et al. 2005, see also Lippke et al. 2003). However, the replacement of old-growth forests with short-rotation plantations might have adverse effects (Schulze et al. 2000).

Rotation length can be modified in the ED through the forcing of gap age in the PDEs of secondary forests and plantations. The exported carbon will then be attributed product partitioning coefficients, turnover rates, and fossil fuel substitution efficiency coefficients (e.g. Kurz et al. 1992). To prevent the conversion of old-growth forest to young managed forests and plantations, the transition of natural forests to other types can be prohibited which would also have positive effects on biodiversity (Franklin and Spies 1991).

4. Establishment of fast-growing stands

The Kyoto protocol specifies afforestation and reforestation as mitigation measures. Afforestation leads to a net increase in the forested area whereas reforestation will accelerate the re-establishment of a harvest stand. Reforestation might have negative impact on biodiversity (e.g., Moore and Allen 1999, Guerra et al. 2000) whereas afforestation generally has a positive effect on both carbon sequestration and biodiversity (e.g., Christian et al. 1998, Wood et al. 2000).

The establishment of fast growing stands can be implemented through the conversion of forested (reforestation) or non forested gaps (afforestation) to plantation gaps where a functional type similar to the early-successional species in Moorcroft et al. (2001) would be ‘regenerated’.

5. Nitrogen fertilization

Since nitrogen is the most limiting soil resource to plant growth in most forest ecosystems (Vitousek and Howarth 1991), nitrogen amendments should enhance tree growth and thus biomass accumulation in ecosystems where precipitation is abundant. Also, soil nitrogen dynamics altered through human activity (Vitousek et al. 1997) could be accounted for even though atmospheric nitrogen deposition seems to have little effect on carbon sequestration in forests (Nadelhoffer et al. 1999).

Nitrogen fertilization (or deposition) can be implemented through modifications of the available nitrogen pool for restrained areas (plantation, secondary forest) of selected plant types. These will then develop under relaxed nitrogen limitations (to photosynthesis and below-ground processes) and will thus show stimulated plant growth and carbon sequestration (Johnson 1992, Oren et al. 2001).

3.3 Additional considerations

A second ISLSCP initiative has been finalized in 2005 (Hall et al. 2005). This new global climatological data set has a higher resolution (0.5° and 0.25° grid cells) and covers now 10 years of climate data. Hence, the simulations could run at these scales which would be more accurate for developing management strategies than the very coarse 1° x 1° grid used in Moorcroft et al. (2001), covering approximately 12,000 km^2 (!) at the equator.

Running the ED under the above mentioned management actions will require establishing threshold conditions. For example, fire suppression should only be applied where carbon offset credits outweigh fire suppression costs. Hence, the ED will need to be fed with economic data such as treatment costs and carbon offset equivalence values (Dixon et al. 1993, Adams et al. 1999). Also, accessibility and proximity to transformation utilities and potential markets should be considered because intensive management activities such as nitrogen fertilization might easily be implemented in the ED but should also be economically operational. Otherwise, the ED will incorrectly consider the fertilization of remote boreal or tropical forests a carbon mitigation action as effective as the fertilizing of a fast-growing plantation in proximity of a paper mill.

Although the ED already tracks CO_2 leaks in form of respirational demands, combustion (fire) as well as decomposition of litter and dead plants, the export of wood through harvest should also be considered in estimating the sequestration potential of the global vegetation (Fig. 6). Here product lifespans and the potential of forest products to substitute fossil fuel directly (e.g. biomass energy) or indirectly through reduced fossil fuel needs in the fabrication of alternative construction materials (e.g. steel) would need to be considered. Chen et al. (2000) used this type of information in estimating the carbon offset potential of forest management strategies in a Canadian case study.

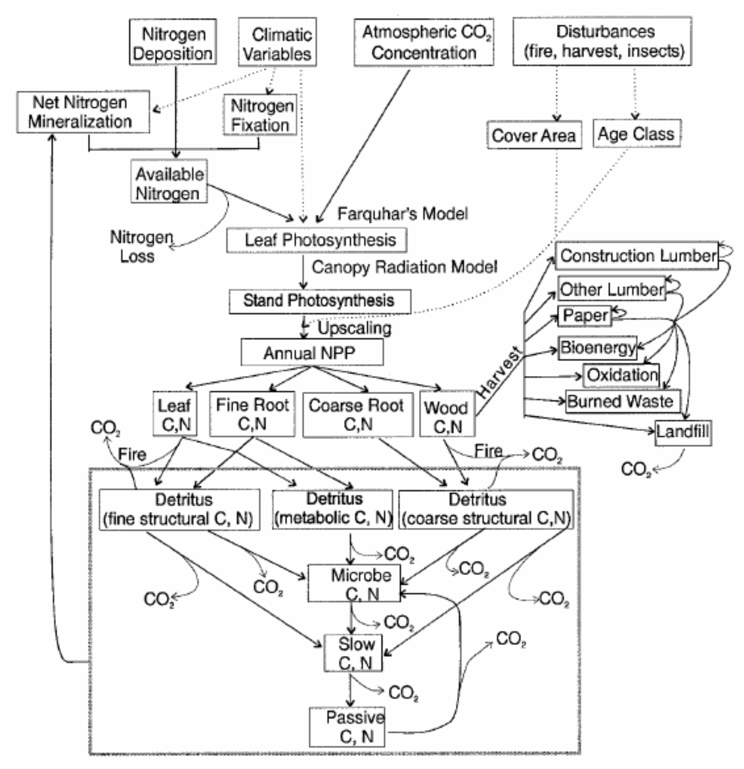

Figure 6. Example of an extended ecosystem model where harvest is a carbon export to diverse destinations (products). Each of these products will have a distinct turnover rate and fossil fuel substitution coefficient. Reprinted from Chen et al. (2000).

There will be a large number of such considerations. For example, there is evidence that low-impact soil treatments (e.g. no tilling) on agricultural lands minimize CO_2 leakage of soil carbon (Sauvé et al. 2000). The same seems to apply to forest harvests where low-impact disturbances of stand canopies and soils enhance soil carbon preservation (see Lal 2005 for review). Hence, further implementations of these aspects could be useful in promoting management practices that help mitigating the impacts of increased atmospheric carbon dioxide concentrations on the global climate.

Also, ethical issues will have to be discussed. For example, how can biodiversity concerns and carbon offset strategies be reconciled? Is the loss of biodiversity more threatening than the effects of global warming or are they intimately interconnected? And how can one measure this threat or compare the value of a species against the value of 1 Mg of sequestered carbon? Can we assign economic values to ecosystems and their services (Constanza et al. 1997) and use these to weigh the benefits of different management actions against each other?

Once again, the scope of this paper is not to take into account all these issues. Interdisciplinary research, combining economic, ecological, and societal expertise will be necessary to accomplish this task. Rather, the goal is to show that the ED can be an efficient tool in demonstrating how todays actions (mitigation measures) will take effect over a large temporal horizon in a changing world and how this knowledge can be used to alleviate the causal underpinnings of the human-induced changes to the global ecosystem.

Running the ED to develop mitigation strategies will produce scenarios of management options that maximize carbon sequestration by assigning varying areas (number of gaps) of terrestrial ecosystems to treatments (i.e. fertilization, fire suppression, harvest) and land-use classes. Optimization implies that goal values for future conditions are specified and this will be a political task. Therefore, the ED in this application should not be confounded with forest management software for which social, economic and ecological values are preset as optimization constraints. Considering its spatial extent, the ED can only be viewed as a tool to provide information for large-scale (regional to international) policy making.

However, the resulting scenarios will need to be implemented in the real world. How to distribute these areas on the map and where to apply the treatments is another matter. The effects of alternative management strategies on landscape-scale forest patterns will need to be modeled separately (e.g., Wallin et al. 1994, Mehta et al. 2004). Here, everything starts all over again, just at another scale: from the complex to the simple… and back.

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