Models for supporting forest management in a changing environment

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Abstract

Forests are experiencing an environment that changes much faster than in at least the past several hundred years. In addition, the abiotic factors determining forest dynamics vary depending on its location. Forest modeling thus faces the new challenge of supporting forest management in the context of environmental change. This review focuses on three types of models that are used in forest management: empirical, process-based and hybrid models. Recent approaches may lead to the applicability of empirical models under changing environmental conditions, such as (i) the dynamic state-space approach, or (ii) the development of productivity-environment relationships. Twenty-five process-based models in use in Europe were analyzed in terms of their structure, inputs and outputs having in mind a forest management perspective. Two paths for hybrid modeling were distinguished: (i) coupling of EMs and PBMs by developing signal-transfer environment-productivity functions; (ii) hybrid models with causal structure including both empirical and mechanistic components. Several gaps of knowledge were identified for the three types of models reviewed.

The strengths and weaknesses of the three model types differ and all are likely to remain in use. There is a trade-off between how little data the models need for calibration and simulation purposes, and the variety of input-output relationships that they can quantify. PBMs are the most versatile, with a wide range of environmental conditions and output variables they can account for. However, PBMs require more data making them less applicable whenever data for calibration are scarce. EMs, on the other hand, are easier to run as they require much less prior information, but the aggregated representation of environmental effects makes them less reliable in the context of environmental changes. The different disadvantages of PBMs and EMs suggest that hybrid models may be a good compromise, but a more extensive testing of these models is required in practice.

Introduction

The need for a new forest modeling paradigm

In the 21st century, forests are experiencing an abiotic environment that changes much faster than in at least the past several hundred years. Abiotic factors determining forest dynamics range from temperature limitations in northern boreal and high mountain elevations, to water limitation in the continental and Mediterranean contexts, and include large-scale disturbances such as windthrow, insect infestations and fires. Changes in the climate may therefore have a wide range of effects across Europe (Lindner et al. 2009). Also, while most forest ecosystems have been traditionally nitrogen limited, eutrophication due to atmospheric deposition has led to nitrogen saturation in some of them (Högberg 2007). Forest management across such large areas thus needs to be adaptive to changing conditions. Here we review how forest modeling may assist in adapting management to rapidly changing abiotic conditions. Our focus is on management for forest productivity and carbon sequestration. Forests also provide other ecosystem services, e.g. regulation of the water cycle, protection from gravitative natural hazards, or biodiversity, but these are not frequently covered by output provided by forest models.

Empirical models (EMs) have been used most frequently for studying issues related to sustainable forest management (Pretzsch 2009; Vanclay 1994). Typically, such models are based on statistical analyses of the dependency of target variables, such as timber production, on a number of predictor variables available from forest inventories and site data. These models primarily rely on the classical assumption of the stationarity of site conditions (Skovsgaard and Vanclay 2008; Vanclay and Skovsgaard 1997), and are often inadequate under conditions of a changing environment. However, recent approaches may lead to the applicability of EMs under changing environmental conditions, such as (i) the dynamic state-space approach (Nord-Larsen and Johannsen 2007; Nord-Larsen et al. 2009), or (ii) the development of productivity-environment relationships (Seynave et al. 2005; Tyler et al. 1996), as explained further below.

An alternative approach for modeling forest dynamics is to explicitly consider the processes that are believed to influence long-term forest dynamics (i.e., the abiotic and biotic controls operating on establishment, growth and mortality of trees). In many of these so-called process-based models (PBMs), physiological processes such as photosynthesis, transpiration and respiration are modeled explicitly. As these processes fundamentally depend on environmental conditions, PBMs are likely most relevant for understanding the present and future growth and composition of forests. Thus, PBMs are regarded as promising tools in this context. A classical example of regulation that can be mathematically described in these models concerns water limitations, which affect mesophyll conductance thereby severely impacting the CO_2 concentration in the chloroplast and thus the rate of photosynthesis. However, there is still a considerable controversy regarding which physiological processes are actually limiting long-term forest dynamics (Braun et al. 2010; Bugmann and Bigler 2010; Bugmann and Martin 1995; Körner 1998, 2006; Reynolds et al. 2001). The challenge is to identify the relevant processes, and to describe them in a proper form to be incorporated in forest models for operational management.

A third category of models, the so-called Hybrid Models (HMs), is based on the pragmatic principle that an exhaustive mechanistic description of all processes, though fundamental for understanding forest growth responses, is an untenable approach as it ultimately leads to explaining ecosystem dynamics based on the principles of particle physics (Bugmann et al. 2000). Instead, empirical relationships estimated from inventory data are used in HMs to make up for incomplete knowledge about some mechanisms (e.g., carbon allocation, relationship between growth rate and longevity of an organism) and the resulting partial predictive ability (Mäkelä et al. 2000). Two paths for hybrid modeling can be distinguished: (i) coupling of EMs and PBMs by developing signal-transfer environment-productivity functions (Luxmoore et al. 2002; Matala et al. 2005); (ii) hybrid models with causal structure including both empirical and mechanistic components (Bartelink and Mohren 2004; Landsberg 2003; Mäkelä et al. 2000; Pretzsch 2007; Taylor et al. 2009).

Although physiological processes are directly affected by climate, it is also important to consider indirect effects of the changing environment on disturbance regimes (e.g. fire, storm, pests) and their impacts on forests. Further information on modeling the risk of natural hazards will be provided, in detail, in another review of this special issue (Hanewinkel et al. *in press*).

Models and stakeholders

Most models of long-term forest dynamics are not designed exclusively as research tools within academia, but they should also be suitable for providing decision support in ecosystem management. Thus, the interaction with model users is an important step in model development. Particularly, model users are likely to have a range of objectives depending on whether they belong to the communities of forest management or industry, of the broad public or the academic and scientific communities (Landsberg 2003). In this review, forest modeling is evaluated as a tool for supporting forest management in the context of environmental change. Therefore, it provides a different scope from several other forest model comparisons which have been published before (King 1993; Korzukhin et al. 1996; Landsberg 2003; Mäkelä et al. 2000; Robinson and Ek 2000; Tiktak and van Grinsven 1995; Van Oijen et al. 2008; Van Oijen et al.

2004). This review also brings a more up-to-date view on forest modeling, which is continuously evolving. It was carried out in the framework of the European COST Action FP0603 "Forest Models for Research and Decision Support in Sustainable Forest Management", and emphasis was placed on recent forest modeling advances in Europe. However, this review should be relevant to other parts of the world, despite that there are quite some forested areas (e.g. tropical forests) for which most models presented here are not directly suitable.

Models for forest management can be perceived in two ways: from a user's perspective, which requires operational models to assist forest management, and a modeler's perspective, which needs to understand the strengths and weaknesses of such models in order to identify further needs for model development. Users need to be aware of the range of existing models and their usefulness for simulating forest management under changing environmental conditions. Modelers need to evaluate the conceptual approaches underlying the models, and to understand what new approaches should be adopted to be useful for forest management in a changing environment. The present review therefore intends to provide an overview of present and future modeling options namely: *(I)* to discuss the use of empirical models in a changing environment; *(II)* to identify the main process-based models in use in the European forests and see how they encompass and represent forest management options; *(III)* to discuss the importance and possible implementation of hybrid forest modeling; (*IV)* to identify the key knowledge gaps associated with the different modeling approaches.

1 Using empirical models in a changing environment

Empirical models (EM) for forest management are generally calibrated on forest inventory data or data from long-term forest experiments and are consequently considered as being unable to incorporate the effects of changing environmental conditions on tree and stand growth (Kahle et al. 2008). However, in contrast to the classical 'static' approach of EMs, recent empirical modeling approaches can actually accommodate the dynamics of environmental conditions, including climate change, and are thus capable of reflecting the effects of changing conditions on natural as well as management-driven forest dynamics, at least within the historical range of variability.

1.1 Dynamic state-space approach

More flexible EMs can be achieved using the dynamic state-space approach (García 1994; Nord-Larsen and Johannsen 2007; Nord-Larsen et al. 2009). In this concept, site productivity effects are incorporated implicitly through a combination of common stand-specific parameters at any stage of stand development and the possible interactions between site, tree growth and management actions. By doing so, they account implicitly for (1) temporal variations in site and stand productivity, and (2) the combined effect on stand dynamics and growth as a function of site potential, the genetically determined potential for volume growth, and possible management effects.

The state-space approach assumes that variables describing the current state of a given system at any time include the information needed to predict the future behavior of the system. It is assumed that the n-dimensional state vector at some point in time, $x(t)$, can be predicted by a transition operator F of the state vector, $x(t_0)$, and a vector of input variables, U at some other point in time. Current additional outputs from the model, $y(t)$, are deduced from the current state by a function g (García 1994):

$$y(t) = g\,[x(t)]$$

$$x(t) = F\,[x(t_0), U, t - t_0]$$

The state-space approach thus predicts any future states of the system from the initial state, $x(t_0)$, through iteration. For example, an initial observation of the two-dimensional state vector of height and basal area may be used to predict height and basal area after one period. The new estimates of the two state variables are then re-entered into the model to predict the state after one more period, and so forth. Abrupt changes in, for example, basal area due to thinnings are handled by simulating the shifts in the state vectors (U) and are seen as shifts between different growth paths.

Mortality, growth and stand development may thus be modeled through iterations based on simple site and stand variables combined with numeric information on management actions.

In contrast to classical (i.e., static) EMs and most PBMs, models based on the dynamic state-space approach rely on a minimum of assumptions regarding allometric relations and management effects. For example, no assumptions on mortality due to self-thinning or the relationship between height growth and basal area growth are needed. The use of plot- or stand-specific calibration for operators F and g is fundamental, and it ensures that the model adapts to changing site, stand and management conditions at any time, as they are manifest in simple mensurational variables. Simultaneous estimation procedures are used to account for the joint effects of the variables employed to describe stand dynamics. Updates are possible whenever new data become available, which renders the approach adaptive. .

1.2 Productivity-environment relationships for growth and yield models

Site index – or top height of a stand at a given base age - is a traditional and popular proxy for site fertility in even-aged forestry (Assmann 1970; Skovsgaard and Vanclay 2008). It is a key input to most growth and yield simulators that are applied in forest management (Dhôte 1996; Garcia and Ruiz 2003). Environmental change however challenges the assumption of constant site quality (Bontemps et al. 2009), which underlies the use of the site index concept, and thus the use of these traditional models. Because EMs remain an accurate tool for yield prediction, there has been a renewed interest for uncovering the environmental determinants of site index (Albert and Schmidt 2010; Diaz-Maroto et al. 2006; Seynave et al. 2005), based on regression models of site index against soil and climate environmental indicators.

Such productivity-environment relationships have to be designed at scales much larger than individual stands, to cover a wide range of environmental conditions, ranging from regional (Sanchez-Rodriguez et al. 2002; Szwaluk and Strong 2003) to national (Seynave et al. 2005; Tyler et al. 1996). They are therefore especially relevant for forest management. They further encompass large environmental gradients that often cover a considerable fraction of the species' range, including northern and southern margins, and this is a key advantage for the sound anticipation of species productivity levels in a future climate. At national scales, forest inventories (NFI) were found to be a major support tool for providing comprehensive growth and environmental data (Seynave et al. 2008; Seynave et al. 2005). The specification of climate-productivity relationships should not include implicit climate dependencies. Hence, the use of geography (e.g., latitude/longitude) and topography proxies (e.g., altitude, slope) alone (Chen et al. 2002) or in combination with climate indicators (Albert and Schmidt 2010) should be avoided, despite their usually high predictive power in regression models.

Because empirical growth models are principally well suited for the investigation of a wide range of management alternatives, their coupling with productivity-environment models based on large ecological gradients (Dhôte 1996; Seynave et al. 2008) provides a cost-effective and accurate alternative approach for the prediction of timber production in the context of environmental change.

2. Process-based models in use for simulating natural and management dynamics of European forests

2.1 The structure of PBMs

PBMs were originally designed and used for research purposes, although they have been developed more recently towards use in practical forest management (Monserud 2003). Rather than being based on empirical relationships between productivity and environmental/stand variables at small or large spatial scales, they rely upon the modeling of the underlying processes that are thought to directly determine the rates of productivity and forest development. Great care is taken to incorporate the influence of environmental variables. PBMs have thus been considered particularly convenient for the investigation of forest dynamics under environmental conditions that are not found in current landscapes (Johnsen et al. 2001; Korzukhin et al. 1996; Stage 2003). The PBM approach has initially been concentrated on the growth of trees in even-aged and monospecific stands, facing more recently the challenge of application to multispecies and heterogeneous stands (Mäkelä 2003). PBMs are often regarded as overly complex, requiring too many estimates of parameter values and variables for model initialization to be used as forest management tools (Bartelink and Mohren 2004), despite not being exhaustive in terms of the inclusion of ecological processes and their interactions (Zeide 2003). In addition, the complexity of PBMs often makes it difficult to track a certain model behavior down to the specific causal process representation, which would however be important to assess whether a model is trustworthy and robust. Nevertheless, there are simple PBMs, such as 3-PG, which have already been used operationally in forest management (Almeida et al. 2004). In addition, there are cases where comparisons of forest models have shown that PBMs perform as well as, or even better than, traditional statistical growth and yield models from a forest management perspective (Fontes et al. 2006; Miehle et al. 2009; Pinjuv et al. 2006).

The proper description of plant ecological processes in PBMs and their calibration and validation typically require large quantities of detailed data that are not always available. While there has been an increase in computational capacity, there is still a deficiency in data for model calibration and validation that would encompass a wide range of site, species and management conditions.

Several process-based models have been used in Europe (Table 1). The following trends were identified:

- Although there are already many European countries that have been using PBMs of various types, these models have not yet been utilized in some of them. Hence, the use of PBMs is not yet as widespread as that of EMs;
- PBMs have been parameterized for a range of conifer and broadleaved tree species, typically the most important species in national forest resources;
- PBMs are a relatively new tool in the forestry sector; they have become more widely used since the late 90’s only. This is in stark contrast to EMs, which have a history of more than 200 years (Pretzsch et al. 2008).
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To be useful, PBMs have to deal with a range of processes that take place at very different scales, i.e. from the chloroplast and cell to the stand and landscape level. However, PBMs should not aim to bridge too many levels of biological organization, e.g. they should not attempt to go from chloroplasts to landscapes (Leffelaar 1990).

Appropriate levels are from chloroplasts to foliage; from foliage to canopy processes and stand growth and from stand growth to landscapes. Furthermore, it is important to consider the temporal scale (time step and maximum temporal extent of the simulation) at which the models operate (see Table 2). For instance, a model that is not able to simulate several rotations may be unable to evaluate the long-term impact of a changing environment. Yet, the smaller the simulation time step (e.g., daily, hourly, or even minutes), the more likely it is that there are serious constraints on the simulation extent achievable from a practical point of view (time required for executing the simulation). In addition, the use of smaller time steps in these models – while forest rotations addressed are the same and simulation procedures remain iterative – comes along with increasing prediction uncertainty due to error propagation (Reed 1999). All PBMs reviewed here focus on the stand level, and most of them are able to run on a daily, monthly or at least yearly basis. Most of them can be run during at least a complete rotation or several rotations, and consequently they potentially have a role to play in long-term forest planning.

2.2 Input data for PBMs

Environmental and biological inputs

PBMs vary in their complexity and therefore in their applicability to forest management issues. As a major constraint for models used in operational forest management, they must be capable of running based on easily obtainable input data. A summary of the main inputs necessary to run PBMs is given in Table 3. Temperature and rainfall followed by radiation and vapor pressure deficit (VPD) are the main climate inputs required by the majority of PBMs. Biological data required by most models for the initialization are size distributions of stem diameter (for individual-based models) or biomass in foliage, stems and roots (for more lumped models), as well as the number of trees per ha and stand age, this latter variable only in some models, though. Latitude (to determine sun angle), soil texture and soil depth are the most commonly required site and soil data inputs.

Management operation inputs

As forest managers have to make decisions about operations (thinning, weed control, fertilization, etc.), it is important for them to know which of the available PBMs are able to take into account the effects of such management operations. They also need to know if a model can be used in their forest, which may be mixed-species or mono-specific. These aspects vary considerably across the available PBMs (see Table 5). Most PBMs will consider operations such as thinning or planting, although just a few will consider operations such as weed control and pruning. Fertilization and natural regeneration are taken into account by approximately half of the models. Clearcutting is the harvesting system that is covered by most PBMs. Selection, group selection and conversion system methods are also addressed, but less commonly. Most of the PBMs are suitable for even-aged single species stands, and about half of them are able to deal with uneven-aged and mixed stands.

Disturbances

A strength of PBMs is their ability to simulate responses to changing environments. However, an aspect not yet thoroughly addressed is the ability of PBMs to simulate forests subject to increasingly frequent disturbances (Table 4). Drought is the disturbance that all PBMs are able to deal with. Further, some models are able to deal with fire, grazing and insect pests. However, the majority of PBMs are not currently able to simulate the impact of any other disturbance (e. g. fungal diseases or soil erosion).

2.3 Outputs of PBMs

Wood related outputs

As not all PBMs were developed with operational forest management in mind, it can be expected that their outputs are not always relevant for forest management (see Table 6). In addition, the concepts underlying the model necessarily limit the suitability of outputs for management use. For example, the "tree" scale, which is needed for defining a selection cut system, cannot be simulated by "big leaf" models. However, many of the outputs considered relevant to forest management (Table 6) are addressed by most PBMs. Moreover, most PBMs will predict stand volume, mean dbh, LAI and stand height. Regarding the carbon balance outputs, Table 6 shows that they are addressed by about half the models. This result is mainly due to a group of models that are able to predict all carbon balance outputs such as 3-PGN, 4C, Anafore, etc., whereas another group of models such as ForClim, LandClim or MEPHYSTO are not able to predict any of these outputs because they emphasize the modeling of attributes such as tree diameters and stem size distributions rather than a closed carbon balance.

Non-wood product outputs

Although timber production is usually one of the main aims of forest management, non-wood products (e.g. cork production from cork oak stands) may be locally quite or even most important. The non-wood products as well as the disturbances that are taken into account in current PBMs are summarized in Table 7. Carbon storage is the non-wood product that most PBMs are able to account for. Some PBMs developed for mountain regions also account for gravitative natural hazards. Important non-wood products in southern Europe such as cork and pine nuts are not yet addressed by current PBMs.

3 Hybrid forest modeling

The term ‘hybrid modeling’ refers to approaches that are grounded in both empirical and process-based concepts of forest dynamics (Pretzsch 2007), thus trying to capitalize on the advantages of each approach. Specifically, the underlying idea is to benefit from the predictive ability and parsimony in the calibration data needs of empirical approaches (Zeide 2003) as well as the explicit environment-dependence of process-based formulations (Johnsen et al. 2001). This approach offers potentially the best prospects for developing models to support forest management (Bartelink and Mohren 2004; Battaglia and Sands 1998; Monserud 2003; Pretzsch et al. 2008). To date, hybrid modeling strategies addressing the issue of environmental change have been explored in two ways: (i) coupling of existing EMs and PBMs that were developed for the same forest context. This coupling relies on the development of environment-productivity signal-transfer functions from simulations of the process-based model, that are then incorporated into the empirical model; (ii) the development of hybrid models *sensu stricto*, based on concepts from both empirical and process-based modeling that are embodied within the same piece of computer code. Such models should hence be able to cope with environmental changes while keeping the predictive and parsimonious properties of EMs.

3.1 Signal-transfer modeling

In a hierarchy of models, signal-transfer modeling designates the transfer of input/output relationships (signal functions) established from smaller-scale process models into larger spatial- and temporal-scale models of ecological and economic phenomena (Luxmoore et al. 2002). Signal-transfer modeling approaches have been developed to incorporate the effects of environmental changes in empirical growth and yield models, based on their assessment in more detailed process models (Baldwin et al. 2001; Matala et al. 2006; Matala et al. 2005). As signal-transfer functions are calibrated once for all, the approach avoids the computational complexity of applying process models to large regional forest contexts, and allows forest management alternatives to be addressed in the efficient way of traditional growth and yield models.

In the calibration of signal-transfer functions, an indicator of forest productivity common to each class of model is selected (e.g., tree volume increment, site index). The response surface of the indicator to environmental factors is calibrated from the process-based model outputs based on a high-dimensional simulation design (Luxmoore et al. 2000). Interactions can also be taken into account, for example to extend the effect of climate scenarios to enlarged local site conditions of regional or national case studies (Luxmoore et al. 2000; Matala et al. 2006). The approach thus results in a multidimensional space that can be queried e.g. in a database to yield the appropriate value of the response variable.

This type of approach has been implemented for the main tree species of Finland to estimate future resource use in industrial and energy wood under different management and environment scenarios of temperature and CO_2 (Kärkkäinen et al. 2008; Matala et al. 2006). It was based on FinnFor (a PBM) and Motti (a growth and yield model), and annual stem volume increment was the transfer variable (Matala et al. 2003). An original aspect of the approach was the effective incorporation of environmental scenarios in a simulation system optimizing management scenarios based on economic indicators (Kärkkäinen et al. 2008).

Another example is provided by the coupling of PTAEDA2 (EM) with MAESTRO (PBM) (Baldwin et al. 2001) for *Pinus taeda* across 13 States in the USA, to address changes in five environmental factors (precipitation and temperature, atmospheric CO_2 and ozone concentrations, nitrogen deposition). The objective was to render site index, which is the driver variable of the dynamics in PTAEDA2, adaptive to changing environmental conditions. The simulation system was coupled to a GIS system, thus facilitating the handling of large amounts of environmental data and a cluster analysis of the forest resource in homogenous simulation sets (Luxmoore et al. 2000).

Inherent to the approach, short-term responses of physiological processes to environmental drivers are extrapolated to larger time scales, although some extrapolations such as the long-term stimulation of NPP by CO_2 (Körner et al. 2005; Nowak et al. 2004) may be questionable. Also, because growth and yield models are often calibrated in regional or national contexts, the response of processes to environmental factors may not apply outside these areas (Matala et al. 2006).

3.2 "True" hybrid models

While the functional components of genuine PBMs are all defined at the same level of system organization, "true" hybrid models incorporate both causal (functional) and empirical components at a given level (Mäkelä et al. 2000). They result from the recognition that classical PBMs embody too many uncertainties, due to poorly understood processes such as carbon allocation (Zeide 2003) or parameters for which calibration data are available only rarely or not at all. For example, Valentine & Mäkelä (2005) proposed a process-based model of tree growth where physiological rates and morphological ratios – usually estimated at lower level processes – could be aggregated and calibrated from forest inventory data. Actually, no typical structure may be defined for hybrid models, as there is a continuum from purely empirical to purely process models (Korzukhin et al. 1996). Actually, fully process-based models may not exist, as any model at some point needs to rely on statistical procedures for estimating "process" functions. Hence, tree or stand management models using inventory data-based statistical relationships that incorporate ecophysiological process knowledge are usually also termed "hybrid" (Pretzsch 2007; Zeide 2003).

While the potential of hybrid models for providing reliable estimates of growth responses to new combinations of environmental conditions should not be underestimated (Pretzsch 2007), their use in the exploration of environmental change impacts has remained limited to date. A recent example is provided by the Forest v5.1 growth model (Schwalm and Ek 2004), designed to generate model outputs that are: (i) able to respond to boundary conditions altered by environmental change (including CO_2, O_3 and climate change) and (ii) useful for operational forest management. The model is based on both a comprehensive mechanistic description including photosynthesis, carbon, water and nutrient balance processes as well as empirical weight-dimension allometric relationships, thus allowing it to be initialized from forest inventory data.

The issue of hybrid modeling has also been debated in the specific case of forest gap models (Reynolds et al. 2001), developed for investigating spatial dynamics and succession in forest ecosystems, and thus of interest for assessing at least the relative importance of species in forest resources. Recent developments have shown that they can also be used to simulate managed stands (Didion et al. 2009). The incorporation of process components has traditionally been limited in these models, where the influence of environmental factors mostly relies on empirical relationships (Bugmann 2001). Due to increasing concern regarding long-term forest dynamics in the context of environmental changes, further developments to enhance the robustness and accuracy of these models under climate change scenarios is unavoidable (Reynolds et al. 2001). However it is questionable that process-based formulations can be calibrated for a wide range of species, due to the absence of detailed data for all except the commercially currently most interesting species.

4 Existing gaps of knowledge within current modeling approaches

4.1 Knowledge gaps: EMs

There is no doubt that at least some of the relationships used in EMs will change in a changing environment. However, very little information is available regarding how these changes will materialize, particularly since changes in multiple variables and under partly novel conditions need calibration data that are not easily available. For example, the allometric relationships that provide a very useful framework (if not a theory) for modeling plant growth are based on a limited set of assumptions (Enquist et al. 2009; West et al. 2009). However, parameter estimation of many allometric relationships (such as root-to-shoot ratios of large trees) faces a lack of data under current conditions, and it is not clear how the relationships would change in the range of future abiotic conditions and their interactions. EMs are widely used, although not all of them have been published in the open literature. This partly restricts the overview of possible options considered to ground these models (sets of assumptions), and their scope of application as well as their limitations.

It is noteworthy that for a given phenomenon, such as allocation pattern, a wide range of relationships is used in the different models. It is not clear whether this is due to the fact that empirical relationships inevitably are valid only locally, or whether this just represents historical legacies. In addition, most EMs are restricted to aboveground volume, whereas the assessment of soil C sequestration would be highly relevant (Vallet 2008). Thus, existing EMs need to be upgraded to become more robust in their functions when applied under changing environmental conditions, and they need to be extended to include traditionally overlooked parts of a forest stand such as belowground biomass. Cooperative strategies for acquiring related high-cost data are needed. A promising option for this may lie in the use of airborne laser measurements of belowground biomass (Naesset and Gobakken 2008).

4.2 Knowledge gaps: PBMs

To run PBMs, information is required about a wide range of input variables (Table 3) and parameters. This information is rarely available in a comprehensive manner, which leads to considerable uncertainty in model predictions. This problem is particularly severe when PBMs are used in forest management. PBMs for forests generally operate by simulating the carbon balance of forest stands, and they calculate tree and stand properties (e.g. height, dbh, volume) using allometric functions. This means that the PBMs tend to require values of carbon content or biomass of stems, branches, leaves and roots for initialization – and knowledge about such quantities is rarely available to the forest manager. Modern data assimilation techniques have eased this problem by allowing forest PBMs to be calibrated using Bayesian inversion, where measurements of model output variables like tree height are used to infer what biomass parameter values are plausible (Van Oijen et al. 2005), but this procedure is fairly complicated and does not remove all parameter uncertainty. In addition, systematic analyses of model uncertainty regarding parameter values and initialization data have suggested that highly accurate empirical data would be required in some cases, which often are not available from inventories or ecophysiological investigations (Schmid et al. 2006). Data availability is thus a major challenge to the approach.

Besides information about input variables and parameters, it is also important to analyze the way processes are dealt with in the structure of models. To understand how

PBMs were developed and how they can be used to analyze the way physiological processes are dealt with, several aspects should be considered:

- Although most PBMs include temperature as an input, the way responses to temperature are modelled varies. In carbon balance models, it is standard to emphasize temperature controls on photosynthesis and respiration, often using the Farquhar model for photosynthesis and Q_{10} (or related) relationships for respiration. As mentioned earlier, it is not clear that these are the processes that actually constitute the bottleneck for plant growth, as growth (cell division and elongation) itself is subject to temperature controls (Körner 1998) that are not modeled in any available PBM. In models that emphasize structural aspects of forest stands (e.g., gap models), considerable advances have been made over the past 15 yrs in the representation of abiotic factors (Bugmann 2001; Reynolds et al. 2001), but also there significant uncertainties continue to exist.
- BASFOR, 3PG and some derivatives of that model estimate whole-plant respiration as a constant fraction of GPP. There is good evidence that this is a reasonable assumption (Van Oijen et al. 2010), but it may be argued that the lack of temperature-dependent respiration makes this assumption less appropriate if respiration and photosynthesis do not respond in the same way to temperature increase (Hartley et al. 2006), which may be the case under global change.
- Moisture limitation is crucial particularly in southern Europe, but some PBMs use very simple soil water models that may not be suitable for evaluating the ecological impacts of a changing precipitation regime on plant water availability.

Overall, in spite of their attractiveness the existing PBMs are characterized by important gaps that may severely limit their applicability for managing natural resources under both the current and possible future climates. To recognize the main gaps and the poorly understood processes, on which it is important to focus future research, PBMs need to be made more efficient and effective (Johnsen et al. 2001). Some of these gaps are summarized in Table 8. On a practical side, the use of PBMs in forest management often faces the problem of documentation availability and ease of understanding to managers for their use; this is due to the fact that many PBMs have primarily been conceived as research tools. To date, many PBMs thus tend to be difficult to use by forest managers. Emphasis should therefore be placed on model documentation and updating. The development of decision support simulation systems (de Coligny et al. 2002), is therefore crucial in making models efficiently available to forest managers and model users.

4.3 Knowledge gaps: Hybrid models

By definition, hybrid models combine elements of both EMs and PBMs, and therefore they will inevitably share some of the knowledge deficiencies of the EMs and PBMs. In theory, hybrid models would capitalize on the advantages of either approach without being prone to the respective deficiencies. However, this is rarely the case in practice since few features of any model have only advantages or only disadvantages. In addition, since PBMs are fairly recent, so are hybrid models, and thus more extensive testing of their suitability in practice is needed. There is still a lack of knowledge regarding the best ways to combine EMs with process submodels, and of PBMs with empirical submodels.

Signal-transfer modeling implies using not just one, but two models, including the calibration of signal-transfer functions. This complicates the task, because in addition to the error involved in the existing calibration there will be two other errors coming from an initial input and an intermediate estimate as well as an intermediate input and a final result. The assessment of error propagation from final results based on the initial input suggests a need for further developments in uncertainty analysis (Cariboni et al. 2007).

4.4 General knowledge gaps within current forest modeling

A general issue that deserves attention in future research concerns genetic differences between provenances that may be crucial in projecting growth responses. Forest ecosystem responses to environmental conditions are widely considered species-specific, but intra-specific ecotypic responses may restrict the domain of application of most current models (Kramer et al. 2008; Kramer et al. 2010). In general, we lack virtually any information about differences in parameter values for PBMs across various genotypes. In addition, ecotypic responses may confuse the productivity-environment relationships approach from EMs when these are developed at larger spatial scales (from regional to national). Therefore, there is a need for data to characterize ecotypic variations and, from the point of view of the modeler, unequivocal differences must be identified before attempts can be made to incorporate them in models. In this context, provenance trials should be considered more widely to uncover and model provenance-climate interactions and their effects on the dynamics of forest stands (Matyas 1994). Further information on genetic modeling will be provided in another review of this special issue (Kramer *in press*).

Furthermore, challenges associated with carbon sequestration and bioenergy require a better focus on wood structure, general wood properties and their dependence on the environment. While the integration of these aspects into forest models remains poorly covered (Deckmyn et al. 2008), there are recent insights how wood properties are influenced by environmental changes (Franceschini et al. in press). Briggs (2010) has identified the following gaps of knowledge concerning this issue: «a lack of understanding of how physiological processes, silviculture, and growing environment conditions affect properties of wood at different scales; a lack of models that integrate fiber quality into decision support systems that can be used to improve planning of investment, silviculture, harvest, and marketing activities».

5. Discussion & Conclusions

5.1 The use of empirical models in a changing environment

The dynamic state-space approach, the productivity-environment relationships for growth and yield models approaches, and their use in combination with PBMs in the signal-transfer modeling approach provide promising opportunities for empirical modeling to remain useful in a changing environment. EMs should thus not be disregarded, but there is still a clear challenge for forest researchers to explore in more detail the consequences of a changing environment regarding appropriate assumptions and the structure of this early type of forest models. The issue of site variation in space and its effect on growth and yield relationships has historically been fundamental in model development for forestry. Environmental changes as a cause for temporal site variation now constitute a renewed driver of interest from forest managers and forestry research, regarding the representation of environment in such models. Here, the paradigm of site likely needs to be replaced, and it is actually already evolving towards making explicit the underlying environmental factors (temperature, water and nutrient availability).

5.2 Strengths and weaknesses of process-based forest models

There are already a considerable number of PBMs being applied to European forestry. However, compared with traditional EMs, PBMs have a much shorter history, and therefore it is not surprising that they are not yet as widespread in terms of countries and species covered. PBMs differ amongst each other in many respects, as can be seen from Tables 2 to 7. However, the data collected in these tables reveal several common PBM characteristics:

- All PBMs work at the stand level, and most of them can be run on a daily, monthly or yearly basis and for one or several rotations – making the models potentially suitable tools for long-term forest planning;
- PBMs are mostly designed for single-species and even-aged stands with a clearcut harvesting system, although a few exceptions exist;
- Thinning and planting are the forest operations that most PBMs take into account;

- Temperature and rainfall followed by radiation and vapor pressure deficit (VPD) are the main climate inputs required for PBMs, at varying temporal resolution (from sub-daily to monthly);
- Drought is the disturbance that all PBMs are able to deal with;
- Latitude, soil texture and soil depth are the most required site and soil data inputs;
- Biomass pools of foliage, stem and roots, the number of trees per ha and stand age are biometric input data necessary by many PBMs;
- Most PBMs predict stand volume, mean dbh, LAI and stand height;
- C storage is the non-wood product that most PBMs are able to account for, whereas non-wood products such as cork and pine nuts are not simulated by current PBMs;
- About half the PBMs considered here predict all major components of the carbon balance, whereas the other half provides just a few or none at all.

The above information about PBMs should help to assess the state-of-the-art in current process-based forest modeling. A single "super PBM" to be used in all countries for all species and for all situations could not be identified and is unlikely to ever exist, because modeling is a deliberate simplification of reality, and the simplification will always include and induce site- or at least region-specific aspects. A model cannot at the same time be completely general in its scope and applicability while providing locally highly accurate results (Levins 1966), as it observed in a concrete case study (Didion et al. 2009). Furthermore, there are other challenges to be met, such as:

- data availability;
- to evaluate the accuracy (bias and precision) of PBMs;
- to discuss the importance of creating new model outputs which might be required to assess management-environment interactions, e.g. finding an easy way to understand which thinning regime would allow a lower water consumption under a warmer climate;
- to assess which PBMs could be used in a spatial version with GIS systems, and using information from remote sensing. An example is the model Physiological Principles Predicting Growth from Satellites (3-PGS), a spatial version of the 3-PG model (Coops and Waring 2001; Nightingale et al. 2008). Additionally, see Lemaire et al (2005) and Soudani et al (2006) for an illustration of the use of remote sensing data for assessing leaf area index at higher spatial scales.

Relatively simple models may remain most helpful for forest management in the foreseeable future, whereas the more complex models will keep their key role for improving our scientific understanding of forest ecosystems. There must be a balance between detail and practicality. The real world is immensely variable, and highly detailed models that intend to account for all detail would be as complex as reality itself. Complexity leads to problems with model parameterization and testing. In addition it should be explored whether the best way to test PBMs is at the level of their (stand-scale) outputs, or rather at the level of the simulated processes. Indeed, a model may provide accurate outputs based on misleading but undetectable model formulations where errors may cancel each other under current conditions, and thus produce biased results under changing environmental conditions. For the forest manager, accurate outputs may be sufficient, but a realistic representation of the processes is crucial to increase confidence in model extrapolations whenever they are applied to new conditions.

A way to facilitate the development of PBMs is to identify the current key gaps in knowledge (Table 8). However, even if all knowledge gaps could be considered equally important, due to the inherent high complexity of some it may not be feasibly to tackle all of them in the near future. Priority should be given to research where results in the near future can be achieved.

5.3 The scope for hybrid models

Compared to EMs and PBMs, hybrid models constitute the most recent way to approach forest modeling. Hybrid modeling has been considered the best way to model forest yield and growth to support forest management (Bartelink and Mohren 2004; Battaglia and Sands 1998; Monserud 2003; Pretzsch et al. 2008) and two different paths towards developing hybrid models were considered in this review.

5.4 Synthesis: what model type to use?

This review has focused on three types of models that are used in European forest management: empirical, process-based and hybrid models. The strengths and weaknesses of these model types differ, and therefore it is likely that all three will remain in use. There is a trade-off between how little data the models need to run, and the variety of input-output relationships that they can quantify. PBMs are the most versatile, with a wide range of environmental conditions and output variables they can account for. They can even be used to assess forest ecosystem services other than productivity, but this was not the focus of the present review. PBMs require information on the leaf, tree and stand level which is difficult to obtain , which makes them less applicable whenever data for calibration or initialization are scarce, which unfortunately is often the case. EMs, on the other hand, are easier to run as they require require plot information only, which is relative easily obtained. However, unless specific developments to tackle changing environmental conditions have been accomplished, their simplicity makes them less reliable when environmental conditions change (Spiecker et al. 1996). These different deficiencies of PBMs and EMs suggest that hybrid models may be a good compromise, but the corroboration of this conclusion requires more extensive testing of hybrid models in practice.

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Table 1. Identification of PBMs in use in Europe. Note: the European Country refers to where the model has been applied in Europe and not necessarily where the model has been developed.

Acronym	**Main reference**	**European Country**	**Tree species**
3-PG	(Landsberg and Waring 1997)	Great Britain, Sweden, Finland, Portugal	*Eucalyptus globulus Labill, Picea sitchensis, Picea abies L. Karst.,*
3-PGN	(Xenakis et al. 2008)	UK	*Pinus sylvestris L.*
4C	(Lasch et al. 2005)	Germany	*Fagus sylvatica L., Picea abies L. Karst., Pinus sylvestris L., Quercus robur L., Quercus petraea Liebl., Betula pendula Roth., Populus tremula (L.), P. tremuloides (Michx.), Pinus halepensis Mill., Pseudotsuga menziesii*
ANAFORE	(Deckmyn et al. 2008)	Belgium	*Pinus sylvestris L., Quercus robur, Populus alba, Fagus sylvatica*
BALANCE	(Grote and Pretzsch 2002; Rötzer et al. 2010)	Germany	*Fagus sylvatica L., Quercus robur L., Picea abies L. Karst , Pinus sylvestris L.*
BASFOR	(Van Oijen et al. 2005)	non-Mediterranean countries	Coniferous tree species
BIOME-BGC	(Pietsch et al. 2003; Pietsch et al. 2005; Thornton 1998)	Austria, Slovakia, Czech Republic	* *Picea abies L. Karst., Pinus sylvestris L., Fagus sylvatica L., Quercus robur L./petraea L., Larix decidua, Pinus cembra*
CASTANEA	(Dufrene et al. 2005)	France	*Fagus sylvatica L, Quercus petraea, Pinus sylvestris, Quercus ilex, Picea abies*
EFIMOD	(Chertov et al. 1999; Komarov et al. 2003)	non-Mediterranean countries	Coniferous tree species
EFM	(Thornley 1991; Thornley and Cannell 1992)	non-Mediterranean countries	Coniferous tree species
FINNFOR	(Kellomäki and Vaisanen 1997)	Finland	*Picea abies L. Karst., Pinus sylvestris L., Betula pendula*
Forclim	(Bugmann 1996)	Switzerland	30 tree species
FORGEM	(Kramer et al. 2008)	Netherlands, Germany, Austria,	***Fagus sylvatica L.*** *Quercus spp. L.*

		France, Italy	*Pinus sylvestris L., Pseudotsuga menziesii Mirb. Picea abies L.*
FORSPACE	(Kramer et al. 2006; Kramer et al. 2003)	Netherlands	*Fagus sylvatica L., Quercus robur L., Betula pendula Roth., Pinus sylvestris L.*
FORUG	(Verbeeck et al. 2006)	Belgium	*Fagus sylvatica L., Quercus, Pinus, Picea*
GOTILWA+	(Keenan et al. 2008)	Spain	*Fagus sylvatica L., Quercus ilex, Quercus pubescens, Pinus halepensis, Pinus sylvestris L., Pinus nigra, Pinus pinaster*
GRAECO	(Porte 1999)	France	*Pinus pinaster*
LandClim	(Schumacher et al. 2004)	Switzerland	Several tree species in complex mountain landscapes
MEPHYSTO	(Lischke 2009)	Switzerland	Several (ca 30) tree species in complex mountain landscapes
PICUS	(Lexer and Honninger 2001; Seidl et al. 2005)	Austria	Several tree species in mixed stands
PipeQual	(Mäkelä and Makinen 2003)	Finland	*Pinus sylvestris* L.
Q	(Agren and Bosatta 1998; Rolff and Agren 1999)	non-Mediterranean countries	Coniferous tree species
TreeMig	(Lischke et al. 2006)	Switzerland	Several (ca 30) tree species in mixed stands, temperate/boreal Europe
WoodPaM	(Gillet 2008)	Switzerland	Several tree species in complex mountain landscapes
Yield-SAFE	(Van der Werf et al. 2007)	Netherlands, UK, Switzerland, France, Italy, Spain	*Populus spp., Prunus avium, Juglans hybr, Pinus pinea, Quercus ilex, Eucalyptus globulus, Quercus suber, Pinus pinaster*

Table 2. Spatial scale, time step and simulation duration of PBMs currently used in Europe.

	Spatial scale					**Time step**				**Simulation**		
acronym	individual tree	cohorts of trees	stand	landscape	region to continent	hour or halfhour	day	month	year	part of a rotation	one rotation	several rotations
3-PG			x	x				x	x	x	x	
3-PGN			x	x				x	x	x	x	
4C		x	x				x		x	x	x	x
ANAFORE		x	x			x	x	x	x	x	x	x
BALANCE	x		x				x	x	x	x		
BASFOR			x				x			x	x	x
BIOME-BGC			x	x	x		x	x	x	x	x	x
CASTANEA			x	x		x	x	x	x	x	x	x
EFIMOD	x	x	x					x		x	x	x
EFM			x			x				x	x	x
FINNFOR		x	x	x	x		x	x	x	x	x	x
Forclim	x	x	x					x	x	x	x	x
FORGEM	x		x				x					x
FORSPACE		x	x	x			x	x		x	x	x
FORUG		x	x			x	x	x	x	x		
GOTILWA +	x	x	x			x	x	x	x	x	x	x
GRAECO	x		x			x	x	x		x	x	
LandClim		x	x	x				x	x	x	x	x
MEPHYSTO		x	x	x	x		x	x	x	x	x	x
PICUS	x		x				x	x	x	x	x	x
PipeQual	x	x	x				x		x		x	
Q			x					x		x	x	x
TreeMig		x	x	x	x			x	x	x	x	x
WoodPaM		x	x	x				x	x	x	x	x
Yield-SAFE	x		x				x				x	x

Table 3. Model inputs which are necessary to run PBMs.

	Inputs																			
	Climate								Tree & Stand					Site & Soil						
acronym	radiation	temperature	CO2	precipitation	VPD	frost days	nitrogen deposition	wind speed	Number trees	Stand Foliage biomass	Stand Roots biomass	Stand Stem biomass	Stand Age	Latitude	Fertility rating	Soil texture	Maximum ASW	Soil N	Soil bucket size	soil depth
3-PG	x	x		x	x	x			x	x	x	x	x	x	x	x	x			
3-PGN	x	x		x	x	x	x		x	x	x	x	x	x	x	x	x	x		
4C	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x
ANAFORE	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
BALANCE	x	x	x	x	x		x	x	x	x	x	x		x		x	x	x		x
BASFOR	x	x	x	x	x		x	x	x	x	x	x		x		x	x	x		x
BIOME-BGC	x	x	x	x	x		x		x					x		x				x
Castanea	x	x	x	x	x			x		x	x	x	x			x	x	x	x	x
EFIMOD	x	x		x			x		x	x	x	x	x			x		x		x
EFM	x	x	x	x	x		x	x	x	x	x	x		x		x	x	x		x
FINNFOR	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
Forclim		x		x			x		x	x		x		x		x	x		x	x
FORGEM	x	x	x	x	x		x	x	x	x	x	x	x	x		x		x		x
FORSPACE	x	x	x	x	x		x		x	x	x	x	x	x		x		x		x
FORUG	x	x	x	x	x			x		x	x	x	x	x		x	x			
GOTILWA +	x	x	x	x	x					x	x	x	x	x			x		x	x
GRAECO	x	x	x	x	x				x	x	x	x	x			x	x		x	x
LandClim		x		x					x	x		x		x		x	x		x	x
MEPHYSTO	x	x		x	x	x								x				x	x	
PICUS	x	x		x	x	x	x		x					x	x	x	x	x	x	
PipeQual	x	x		x	x				x				x		x	x			x	x
Q		x					x			x	x	x						x		x
TreeMig		x		x	x	x								x				x	x	
WoodPaM		x		x					x	x		x	x	x				x	x	x
Yield-SAFE	x	x		x					x	x	x	x	x			x				x

Table 4. Disturbances acknowledged by PBMs.

	Disturbance									
acronym	generic, small scale	avalanches	fire	storm	grazing	pests	diseases	soil erosion	flooding	drought
3-PG						x				x
3-PGN						x				x
4C						x				x
ANAFORE										x
BALANCE						x	x			x
BASFOR								x		x
BIOME-BGC			x							x
CASTANEA										x
EFIMOD										x
EFM			x							x
FINNFOR			x	x						x
Forclim					x					x
FORGEM				x					x	x
FORSPACE			x		x					x
FORUG										x
GOTILWA +			x		x					x
GRAECO										x
LandClim			x	x	x	x				x
MEPHYSTO	x									x
PICUS						x				x
PipeQual						x				x
Q										x
TreeMig	x	x								x
WoodPaM					x					x
Yield-SAFE									x	x

Table 5. Silvicultural operations, forest harvesting system and forest types included in PBMs.

	Silvicultural operations						**Harvesting system**				**Forest type**			
acronym	thinning	weed control	planting	fertilization	natural regeneration	prunning	clear cut	selection or shelter cut	group selection	conversion system	even aged	uneven aged	single species	mixed stand
3-PG	x		x	x			x				x		x	
3-PGN	x		x	x			x				x		x	
4C	x	x	x	x	x		x	x		x	x	x	x	x
ANAFORE	x		x	x	x		x		x	x	x	x	x	x
BALANCE	x			x				x			x	x	x	x
BASFOR	x		x	x		x	x				x		x	
BIOME-BGC	x*		x*				x*				x		x*	
CASTANEA											x		x	
EFIMOD	x		x	x		x					x	x	x	x
EFM	x		x	x		x	x				x		x	
FINNFOR	x	x	x	x	x	x	x	x			x	x	x	x
Forclim	x	x	x		x		x	x	x	x	x	x	x	x
FORGEM	x	x	x	x	x		x	x	x	x	x	x	x	x
FORSPACE	x	x	x	x	x		x	x	x		x	x	x	x
FORUG	x										x		x	x
GOTILWA +	x		x		x		x	x	x	x	x	x	x	
GRAECO	x						x				x		x	
LandClim	x	x	x		x		x	x			x	x	x	x
MEPHYSTO					x							x		x
PICUS	x	x	x	x	x	x	x	x	x	x	x	x	x	x
PipeQual	x	x	x		x	x	x				x		x	
Q	x		x	x		x					x		x	
TreeMig					x							x		x
WoodPaM					x		x					x		x
Yield-SAFE	x		x			x					x		x	

Table 6. Model outputs which are produced by PBMs.

	Forest management							Carbon Balance						
acronym	Stand Volume	MAI	Basal Area	Mean DBH	LAI	Stand height	diameters	GPP	NPP	Respiration	Soil carbon stocks	Soil carbon fluxes	NEP	NEE
3-PG	x	x	x	x	x	x		x	x	x				
3-PGN	x	x	x	x	x	x		x	x	x	x	x	x	x
4C	x	x	x	x	x	x	x	x	x	x	x	x	x	x
ANAFORE	x	x	x	x	x	x	x	x	x	x	x	x	x	x
BALANCE	x	x	x	x	x	x	x	x	x	x				
BASFOR	x	x	x	x	x	x	x	x	x	x	x	x	x	x
BIOME-BGC					x			x	x	x	x	x	x	x
Castanea	x	x			x			x	x	x	x	x	x	x
EFIMOD	x	x	x	x		x		x	x	x	x	x	x	x
EFM	x	x	x	x	x	x	x	x	x	x	x	x	x	x
FINNFOR	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Forclim	x		x	x	x	x	x							
FORGEM	x	x	x	x	x	x	x	x	x	x	x	x	x	x
FORSPACE	x	x	x	x	x	x				x	x			
FORUG	x		x	x	x	x	x	x	x	x	x	x	x	x
GOTILWA +	x	x	x	x	x	x	x	x	x	x	x	x	x	x
GRAECO	x	x	x	x	x	x	x	x	x	x			x	x
LandClim	x		x	x	x	x								
MEPHYSTO	x		x	x	x	x	x							
PICUS	x	x	x	x	x	x	x		x		x	x		
PipeQual	x	x	x	x	x	x	x	x	x	x				
Q								x	x	x	x	x	x	x
TreeMig	x		x	x	x	x	x							
WoodPaM	x			x	x	x								
Yield-SAFE	x		x	x	x	x	x			x				

Table 7. Non-wood products acknowledged by PBMs.

	Non-wood product						
acronym	pine nuts	cork	size herbivore populations	C storage	gravitative natural hazards	fodder	livestock
3-PG							
3-PGN				x			
4C				x			
ANAFORE				x			
BALANCE				x			
BASFOR				x			
BIOME-BGC				x			
CASTANEA				x			
EFIMOD				x			
EFM				x			
FINNFOR				x			
Forclim					x		
FORGEM				x			
FORSPACE			x	x			
FORUG				x			
GOTILWA +				x			
GRAECO							
LandClim				x	x		
MEPHYSTO							
PICUS				x	x		
PipeQual				x			
Q				x			
TreeMig							
WoodPaM			x			x	x
Yield-SAFE				x			

Table 8. Knowledge gaps that limit the applicability of PBMs to managing natural resources.

Gaps of knowledge
Downregulation of basic processes such as photosynthesis or respiration is poorly understood and some lab or field experiments give contradictory results: Is there some room to be explored by the models?
Changes in mesophyll conductance beyond certain water thresholds affect assimilation dramatically. Important effects are expected for Southern European forests, especially in a future changed climate. Need to incorporate these effects in models of photosynthesis. Some progress has been made in the last years.
Some aspects of population dynamics are poorly simulated, i.e. the initial steps (seeds, seedlings or saplings), mortality. In forestry, we lack consistent techniques to track tree regeneration and mortality. Need to improve modeling of early seral stages, mainly small trees.
European forest at present can't be understood without a good knowledge of history (including severe disturbances), management and genetics. These components are poorly addressed in our models.
Need to improve simulation of management regimes.
Below-ground biomass accounts for more than 60 per cent of total biomass in some forest types, such as evergreen Mediterranean forests. The belowground component of the forest is rarely addressed in our models (but see Rötzer et al. (2009)) although it represents a large fraction of ecosystem respiration. There is a lack of reliable data on the structure and function of the belowground component.
Interactions between species in mixed forests are complex and depend on the species composition and the proportion of the different species in the stands. This represents a severe limitation for modeling these forests. However, single tree based models like, for example, BALANCE or FORGEM are able to simulate these complex relationships and interactions. More effort needed to understand the mechanisms of interaction.
The rate of adaptation of critical processes (response to water limitation, phenology, growth response), in particular at the limits of species area distribution and how this depends on management actions is a crucial next step for model application. This may be better than treating species as monolithic entities or reparameterizing the model for a species on every new location.
There are lack of information on forest nutrition, many forests in Europe are N-limited, others K- or P-limited. This may be an increasing problem under conditions of elevated CO2, where the nutrients may become more limiting.
The way mycorrhizae and other soil organisms such as decomposers will respond to environmental change including change in soil temperature and the quality of plant litter needs to be better understood

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