

# THE USE OF FOREST MODELS FOR BIODIVERSITY ASSESSMENTS AT THE STAND LEVEL

**M. J. LEXER<sup>1</sup>, W. LEXER<sup>1</sup>, H. HASENAUER<sup>2</sup>**

<sup>1</sup> Institute of Silviculture, University of Agricultural Sciences, Vienna  
Peter-Jordanstrasse 70, A-1190 Vienna  
lexer@edv1.boku.ac.at

<sup>2</sup> Institute of Forest Growth Research, University of Agricultural Sciences, Vienna  
Peter-Jordanstrasse 82, A-1190 Vienna

## SUMMARY

There is an increasing demand to include biodiversity assessments as an additional management input within silvicultural decision making. A number of forest models are in use to support forest management planning. However, none of these models was explicitly designed to consider the biodiversity of forest ecosystems and how this may change under different silvicultural treatments. In this paper prominent attributes and measures of biodiversity and the data requirements for their calculation are identified based on a review of the literature. Existing forest models are classified with respect to the general modeling approach (i.e. empirical vs. process-based models), structural attributes and phenomena considered. After comparing the required data for biodiversity assessments and the available output of forest model types, we discuss to what extent existing models can satisfy the information needs for biodiversity assessments at the stand level. The main conclusion is that an extension of existing growth models is needed to incorporate biodiversity issues in forest management planning. Probably the most promising approach lies in the development of the family of distance dependent individual tree growth models because they explicitly address horizontal and vertical structural diversity of forest stands. A major limitation is the lack of information on genetic diversity.

**KEY WORDS:** Biodiversity  
Environmental indicators  
Forest models  
Forest ecosystems  
Assessment

## INTRODUCTION

Since the construction of the first yield tables (Réaumur, 1721; cited in Pretzsch, 1992) many forest growth models have been developed to support forest management planning and predict forest stand development. While in the past models were mainly developed to estimate stand growth (i.e. volume, stem numbers), an increasing demand for nontimber values such as recreation or wildlife has led to the adoption of forest models

which simultaneously address these sometimes conflicting interests (Kohm and Franklin, 1997, Kangas and Kuusipalo, 1993, Pukkala and Kangas, 1993, Vacik and Lexer, 1999). Within a short period the information needs concerning the current and future development of our forests have grown drastically (Pretzsch, 1997, Sterba, 1997). Substantial changes in forest manager's expectations from forest models are evident and lead to the question whether current modeling approaches and existing forest models can meet these needs.

Recent developments in forest policy have emphasized the conservation of biological diversity as an essential element in forest management (e.g. Ministerial Conference on the Protection of Forests in Europe, Anon., 1993). The relevance of biodiversity for sustainable development of forest ecosystems is based on theoretical considerations that a high diversity in terms of systems elements, structural complexity and functional relationships increases the variety. Variety is defined as the number of potential states of a system and characterizes the spectrum of a system's reactions to changing environmental conditions. According to Ashby (1974) a certain level of diversity is required to ensure the viability of the system. Within ecology, a specific level of biodiversity can be considered as a prerequisite for ecosystem resilience and adaptivity (Hattermer and Gregorius, 1996). To evaluate the expected impact of forest management on forest ecosystem biodiversity, forest resource managers need reliable tools to project future forest states under a variety of silvicultural regimes.

The objective of our work is to discuss and evaluate the applicability of existing modeling techniques to biodiversity issues. As a prerequisite we briefly outline the conceptual content of the term biodiversity with respect to forest ecosystems. We then present a list of prominent measurable attributes which might serve as indicators for biodiversity. Finally we discuss different approaches in forest modeling and, based on a classification of forest models, assess whether they can be used to project the proposed indicators of biodiversity at the stand level.

## BIODIVERSITY

### Definitions

A widely accepted general definition of «biodiversity» is given by the Helsinki Resolution H2 (Anon., 1993):

«Biological diversity means the variability among living organisms from all sources including *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.»

A similar definition which also features «the trilogy of standard components of biodiversity» (Kaennel, 1998), addressing genes, species and ecosystems is included in the Convention on Biological Diversity (Anon., 1992). It is worth noting that both definitions only refer to «the variability among living organisms (...) and ecological complexes». Zeide (1998) points out that this expression may be misleading if interpreted statistically because the variance, the standard deviation or the range of traits does not change if the number of items, e.g. species, is reduced.

### Concepts of Biodiversity

It is common to separate the biotic diversity of organisms, populations, species and communities from diversity in structure. Structural diversity consists of both biotic and abiotic elements and can be characterized as landscape-ecological or eco-morphological diversity. It has long been recognized in ecology that there exists a strong correlation between structural diversity and species diversity. An increase in spatial-structural heterogeneity and habitat complexity is equivalent to a provision of niches and resources which usually leads to an enrichment of species (Odum, 1983; Begon *et al.*, 1990).

Conceptual approaches which distinguish different spatial levels with regard to species diversity and structural diversity (e.g. Bastian, 1994), have a major disadvantage: they fail to integrate or even mention ecological processes and thereby ignore the functional dimension of biodiversity (Noss, 1990). Functions and processes include all kind of interactions and interdependencies between single elements of a system, a subsystem, different hierarchical levels of a system and between a system and its environment. Examples of such processes include biomass production, energy flows, nutrient cycles, gene flow, information flows, intra- and interspecific interrelationships and both natural and anthropogenic disturbances. In this context it makes sense to speak of a functional diversity. According to Franklin (1988), Noss (1990) and Noss and Cooperrider (1994) three main components of biodiversity can be identified: (i) composition, (ii) structure and (iii) function.

Noss (1990) extends this concept of biodiversity components to a nested hierarchy of four closely related levels of biological organization: (1) the genetic level, (2) the population/species level, (3) the community/ecosystem level and finally (4) the regional landscape level. A higher level incorporates the attributes and constrains the behavior of each lower level (Gaston and Spicer, 1998).

Ecological function as a main attribute of biodiversity involves all kinds of processes. Processes are inevitably associated with some changes over time and often result, if composition and structure are affected, in changes at the space level. Because the dynamic aspect of diversity is a basic property of nature, biodiversity cannot be considered as a static feature. The fundamental capability of ecosystems to evolve, change and re-organize themselves, is a prerequisite for the sustainability of viable systems (Ashby, 1974; Beer, 1973) and implies the spatio-temporal variability of biodiversity.

In this paper we focus on biodiversity aspects at the stand level because this corresponds well with the population and community/ecosystem level of biological organization including the genetic level. Because a forest stand can cover up to 10 hectares, it can be a quite heterogeneous area so that landscape aspects are also involved.

### Key attributes and indicators of biodiversity at the stand level

Indicators are a prerequisite for considering biodiversity in forest management planning because they allow the impact of stand treatments on biodiversity to be assessed and evaluated (Rennings, 1994; SRU, 1994). Furthermore, indicators can be used to estimate and quantify desired future conditions (DFC) by defining target levels of biodiversity. The process of identifying suitable attributes and the deduction and aggregation of corresponding indicators is a critical step. The selected indicators must be representative for

the entity that is the object of the assessment, they must give relevant information and should be adequate to the issue of interest. Their function is to reduce the complexity of the real world and improve interpretation by simplifying and aggregating the available information (Rennings, 1994). Sets of indicators for biodiversity must integrate compositional, structural and functional attributes. In our case these attributes should be extractable from forest simulation models.

In the following sections selected attributes and indices of biodiversity are presented according to two criteria: (i) recommendations from the literature; (ii) floristic elements utilized in the calculation of a given index. The importance of the latter derives from the need to compare data requirements for calculating biodiversity indicators with output provided by forest vegetation models.

### *Composition*

The most common method of defining diversity at the ecosystem level is the species. The simplest species-related diversity measure is species richness. It is defined as the number of species per specified number of individuals or biomass. Species density is the number of species per unit area. This type of measure lacks information about abundance. The comparative analysis of species abundance distributions based on species abundance models with associated diversity indices can provide valuable information on the diversity of a community (Magurran, 1988). These rank/abundance distributions can be characterized by indices such as Fisher's alpha, the log normal index and the Q-statistic index. Data required to calculate these indices are the number of species and the number of individuals per species.

Another important biodiversity indicator is species diversity. It consists of two fundamental components: a) the number of species in the community (species richness), and b) the relative (proportional) abundance or degree of dominance of individuals among different species. The latter is usually referred to as evenness or equitability and measures the extent to which species are equally represented in a community. Several species diversity indices incorporate both properties, species richness and evenness. Both an increase in richness and evenness leads to higher numerical values of such diversity indices. They differ mainly in the way they emphasize one of the two components.

A prominent species diversity index is the Shannon (-Wiener) index. This index requires the total number of individuals in the sample and the number of individuals of each species for calculating proportional abundances as input variables. The Shannon (-Wiener) index is relatively independent of sample size and has a tendency towards stressing rare species (Odum, 1999). The Brillouin index is recommended when the full composition of the plant community is known. The calculation procedure of this index is time-consuming but has the considerable advantage to discriminate between different communities, while the Shannon index will always give the same value providing the number of species and their proportional abundances remain constant (Magurran, 1988). Another well-known dominance indicator is Simpson's index. This index is heavily weighted towards the most abundant species in the sample but less sensitive to species richness. Other similar indices of species diversity include the McIntosh index, the Berger-Parker index and the sequential comparison index (Magurran, 1988). Table 1 lists selected attributes and indices of ecosystem composition.

TABLE 1

**ATTRIBUTES OF ECOSYSTEM COMPOSITION, RELATED INDICATORS, NUMERICAL INDICES AND DATA REQUIRED FOR THEIR CALCULATION***Atributos de la composición de los ecosistemas, indicadores relacionados, índices numéricos y datos necesarios para su cálculo*

| attribute     | indicator                             | selected numerical indices  | data requirements                        |
|---------------|---------------------------------------|-----------------------------|--|
| species       | species richness                      | —                           | number of species                        |
|               | species density                       | —                           | number of species per area unit          |
|               | species abundance                     | Fisher's alpha              | number of species, number of individuals |
|               | species diversity                     | log normal index            | relative abundance of species            |
|               |                                       | Q statistic index.          |  |
|               |                                       | Shannon index               |  |
|               |                                       | Simpson's index             |  |
|               |                                       | Brillouin index             |  |
|               |                                       | McIntosh index              |  |
|               |                                       | Berger-Parker index         |  |
|               | presence/absence                      | sequential comparison index | species category of each individual      |
|               |                                       | —                           | species list                             |
| genes/alleles | genetic diversity (allelic diversity) | index of Nei (1973)         | alleles, comparable set of gene loci     |
|               |                                       | index of Gregorius (1987)   | alleles, comparable set of gene loci     |

Species diversity indices provide less information about the identity of a species, the environmental conditions and the functional role of a species within ecosystems. Contrary to that, the absence or presence of species, e.g. of certain indicator species or species that occupy an ecological key-function, can give valuable information concerning the status of biodiversity within an ecosystem. This applies also to the absence/presence, number and proportional abundances of endemic, native, introduced, alien, exotic, endangered and threatened species (Zeide, 1998). At the genetic level, genetic diversity may be characterized by allele diversity, presence/absence of alleles, enzyme variability or the frequency of a gene in the genetic pool of a population (compare Noss, 1990).

*Stand structure*

Indices of structural diversity quantify the arrangement of structural elements of a system in space. A set of measures for horizontal and vertical distribution of structural elements is listed in Table 2 reflecting the variety of indices for structural diversity. Regarding indices for horizontal and vertical forest structure see Kint *et al.* (this volume). Furthermore, the demographic structure, i. e. the diversity of age-states within tree populations and plant communities determine structural diversity. Uneven-aged mixed species stands usually possess a more diverse vertical structure (especially layering), than even-aged pure stands. The phenomenon that old and young plant individuals of the same species often have markedly different growth forms also contributes to structural diversity.

Architectural complexity, defined as the number of structural categories into which the vegetation at each site could be divided, reflects types of micro-habitats occupied by invertebrates. Examples are: bark on dead and living wood and the structure of its surface, upper and lower leaf surface, flower buds, open and dead flowers, ripening fruits, dead-wood, mosses and lichens on vegetation etc. (Magurran, 1988). Similar to architectural complexity is the investigation of niche width. Niche width is a measure of the breadth or diversity of resources used by either a species or an individual. Usually the Shannon or Simpson's index is used for calculating niche width. In doing so the number of species in the equation is replaced by the number of resource categories observed, like types of food eaten or varieties of habitats utilized. An example is the measurement of trophic diversity, defined as the width of the feeding niche. In contrast to species diversity measures, habitat diversity and niche width indices can be difficult to interpret because the definition of habitat types and categories of resources may differ between studies, making comparisons very difficult or even impossible.

Deadwood is an important component of structural diversity particularly in old-growth primeval and natural forests (Söderström, 1981, Lähde *et al.*, 1999). It is a resource and habitat for algae, fungi, lichens, mosses, an immense number of invertebrates and even some vertebrate organisms that are cavity-specialists. The presence of deadwood is *per se* an indicator for major ecological processes such as decomposition and nutrient cycling. Standing dead trees and fallen logs have to be distinguished ecologically because these two types of deadwood differ in terms of their origin, decaying processes and colonization (Stöcker, 1998). Additionally, dimensional diversity considerably enhances species diversity (Schulz, 1998; Stöcker, 1998). Stöcker (1998) argues in favour of standing dead trees with large diameters, because the benefits of such material for invertebrates cannot be replaced by fallen logs. Deadwood is usually quantified on a volume per unit area basis in different decay and diameter categories. However, the calculation of dispersion indices (e.g. Clark and Evans, 1954) or diversity indices (e.g. Shannon index) may be used. At the genetic level the presence of genetic variants within a given species induces additional phenotypical variability. A commonly used indicator of genetic structure is heterozygosity at genetic marker loci (Nei, 1987).

**TABLE 2**  
**ATTRIBUTES OF ECOSYSTEM STRUCTURE, RELATED INDICATORS,**  
**NUMERICAL INDICES AND DATA REQUIREMENTS**

*Atributos de la estructura de los ecosistemas, indicadores relacionados, índices numéricos y datos necesarios para su cálculo*

| attribute              | indicator  | selected numerical indices   | data requirements  |
|------------------------|--|--|--|
| horizontal structure   | individual distribution                              | Clark and Evans (1954)<br>Kotar (1993)<br><br>mingling index (Füldner, 1995)<br>Pielou's segregation index | coordinates of each tree<br>tree density [ $p=n/A$ ], coordinates of each tree<br>species and coordinates of each tree<br>species and coordinates of each tree   |
| tree size              | tree size differentiation                            | diameter differentiation index (Füldner, 1995)<br>range of heights<br>range of diameters                   | diameter and coordinates of each tree<br><br>height of each tree<br>diameter of each tree  |
| vertical structure     | profiles of vertical structure                       | vertical species index (Pretzsch, 1996)<br>foliage height diversity (MacArthur and Horn, 1969)             | species, height of each individual<br>leave area per canopy stratum or individual tree   |
| stand diversity        | stand diversity index (Jaehne and Dohrenbusch, 1997) | species diversity<br>distance differentiation<br><br>height differentiation<br>crown differentiation       | proportion of species with min. and max. abundance<br>n minimal distances between neighbouring trees, n max. distances between neighbouring trees<br>n diameter <sub>max</sub> and n diameter <sub>min</sub><br>max. crown-width of n trees, min. crown width of n trees |
| age                    | diversity of age states                              | —  | tree age   |
| architectural elements | architectural complexity                             | —  | number and abundances of architectural elements (e.g. bark, buds,...)  |
| deadwood               | snags  | volume   | volume per decay state and diameter category   |
|                        | coarse woody debris (CWD)                            | volume   | volume per decay state and diameter category   |
| genes/alleles          | genetic structure (allelic/genotypic)                | heterozygosity   | alleles, genotypes   |



*Functional aspects of biodiversity: dynamics in space and time*

Structural and compositional changes of a forest in space and time are the result of tree growth, tree mortality due to competition and extrinsic reasons (e.g. disturbances) and the regeneration of trees. Within a forest ecosystem, disturbances may result in a significant change from the normal pattern and can be characterized by their spatial extent (Oliver and Larson, 1990), frequency (Canham and Loucks, 1984) and the effect on biological elements (i.e. intensity). Thus, the ability of forest models to mimic these processes is of particular interest for biodiversity assessments.

Functional phenomena can be divided into an array of processes such as photosynthesis, transpiration or the flow of energy and matter through a forest ecosystem, which are mainly driven by the abiotic environment (e.g. sunlight, temperature). In this context silvicultural interventions can be considered as a controlled disturbance to favour certain parts of the population (e.g. individuals, tree species, etc.) or processes (e.g. tree growth) within a forest ecosystem. In addition the functional component of biodiversity includes all forces that affect diversity at the genetic level. These forces may act either at the molecular level or at the population level. At the molecular level mutation may produce new variants within a population, and recombination may «re-shuffle» genetic diversity along the chromosomes of a sexually reproducing organism (Lewin, 1994). At the population level, evolutionary forces such as gene flow, genetic drift or selection may affect genetic structures within a stand (Hartl and Clark, 1997).

## CLASSIFICATION OF FOREST MODELS

Numerous approaches to classifying forest models have been proposed (e.g. Korzhukin *et al.*, 1996; Mohren and Burkhart, 1994; Dale *et al.*, 1985; Shugart, 1984). The criteria which have proved useful in the classification process are the general modeling approach taken and the spatial resolution of the model. However, additional criteria have to be considered if the applicability of forest models for biodiversity assessments is the subject of interest.

Most discussions about approaches to forest modeling distinguish between two main concepts: empirical and process modeling (Kimmins *et al.*, 1990; Bossel, 1991; Mohren and Burkhart, 1994). Process-based models incorporate a mechanistic description of the interaction of the modeled phenomena with the environment. The objective of process models is to define the rules which determine forest structure and behaviour and to describe the data using the current understanding of the underlying key mechanisms (Korzhukin *et al.*, 1996; Battaglia and Sands, 1998). Consequently process models are responsive to changes in environmental conditions. Empirical models seek to describe statistical relationships based on a limited number of driving variables with limits regarding the modelled object's internal structure. One major disadvantage of statistical models is that projected results may be incorrect if the models are applied beyond the range of conditions represented in the calibration data (Goulding, 1994).

Though numerous reviews use the terms «process» and «empirical» to differentiate among models, a continuum exists between the two approaches (Korzhukin *et al.*, 1996). This simple classification is misleading because process-based models also include em-

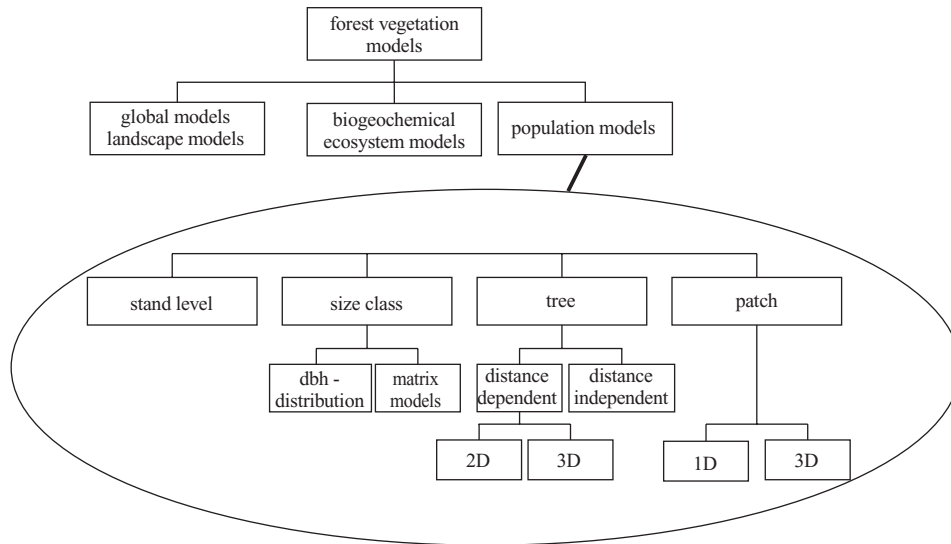


pirically gained knowledge based on regression analysis and hypothesis testing. Kimmins and Scoullar (1981) introduced a further category, hybrid models which try to combine the useful features of both modeling approaches by using rather elementary processes to increase biological realism.

According to Sharpe (1990) a model should meet the requirements of precision (i.e. degree of exactness in predictions), generality (i.e. applicable over a wide range of conditions) and reality (consideration of true cause and effect relationships). However, different modeling approaches tend to satisfy different aspects of these requirements (Sharpe and Rykiel, 1991). Consequently the requirements for a particular question are important. Models for long-term scenarios use lumped parameters to represent average properties of processes operating at finer scales or ignore dynamic feedback loops (Titak and van Grinsven, 1995). They meet a high degree of generality but are rather imprecise. Usually the opposite holds for models developed for short- to mid-term projections. Thus, the user is confronted with a trade-off situation, where the preference for a certain aspect will depend on the problem he wants to address.

### Structural organization of forest models

Principally all types of modeling approaches can be developed over the entire range of spatial scales: tree level, size class level, stand level, ecosystem and landscape or even the global level. In this context it is important to note, that the temporal and spatial resolution of the output from a model can not be higher than those at which the model operates. Fig. 1 gives a classification of models according to their structural organization. Global models and landscape models are either primarily ecology-based or integrate sociological and economical phenomena (integrated models) (Picket *et al.*, 1994). Though there are attempts to develop dynamic models of vegetation at that scale, most existing models of this class are static equilibrium models and thus not feasible to project transient responses of forests to forcing variables. Biogeochemical ecosystem (or «tissue» models) lump biomass into broad plant tissue categories and model the flows of matter (i.e. carbon, nitrogen) and energy through these compartments (e.g. Running and Gower, 1991). Recently the biogeochemical approach has been extended to population models (e.g. Bugmann *et al.*, 1997). Population models are the most relevant models for forest management applications. Thus, most of the existing forest models belong to this group. Within population models several variants can be distinguished. Stand-level models, such as the traditional yield tables (see Schwappach, 1890; Assmann and Franz, 1963) describe the development of even-aged pure stands by projecting the mean tree height and breast height diameter over time and the cumulative statistics for the total number of trees, basal area and volume growth. An extension of yield tables are size class and matrix models. Size class models split the tree population by different breast height diameter classes to predict the timber value as it depends on the diameter distribution within a given stand (see Clutter and Bennet, 1965). Matrix models describe the probability for a tree to move from one diameter category to the next (Vanclay, 1994; Leary, 1979). While the diameter distribution approach is mainly related to even-aged pure stands, the matrix model approach was successfully extended to uneven-aged multi-species stands (Solomon *et al.*, 1986).



**Fig. 1.—Classification of forest models with regard to structural resolution focusing on population models**

*Clasificación de los modelos forestales en relación a su resolución estructural, incidiendo en los modelos poblacionales*

Individual tree models seem to be the most relevant models for forest management applications. These models keep track of changes in individual trees using tree lists. They identify tree species and are specifically designed to address forest management demands. Distance-dependent individual tree models explicitly consider the position of an individual tree within the stand. For each tree a unique competition situation can be calculated to model the architectural arrangement of tree biomass in two- or even three-dimensions. This provides a very detailed structural representation of a forest stand which is particularly important for the application area discussed. In contrast, distance-independent tree models assume that competition among trees can be adequately described with some average measure of stand density per unit area for the modeled population. A variant of the distance-independent tree models are gap models (patch models *sensu* Shugart *et al.*, 1992). This type of model mimics the growth, death and reproduction of individual trees on small patches of forest land (ca. 100-1000 m<sup>2</sup>) where the position of an individual tree within a modeled patch is unspecified (Botkin *et al.*, 1972; Shugart, 1984). In spatially explicit 3D-patch models an array of patches is arranged on a grid and simultaneously grown as an interactive unit (Leemans and Prentice, 1989; Lexer and Hönninger, 1998).

### Considered phenomena

Most forest management models were developed for mid-term projections of volume growth in even-aged single species stands. While the growth of trees is well represented, only a limited number of models consider regeneration or recruitment of young trees (Vanclay, 1994; Golser and Hasenauer, 1997). An irregular stand structure and an ongoing steady natural regeneration process are key elements of a «close to nature» forest management (e.g. Kuper, 1996; Lähde *et al.*, 1999). Within such a management approach, forest models which do not consider tree regeneration are of limited value for biodiversity assessment. In intensively managed forests tree mortality induced by inter-tree competition may be of minor concern because stand treatments such as thinning replace natural mortality. In unmanaged forest stands, however, mortality due to competition is one of the key population dynamic processes (Shugart, 1984; Monserud, 1976). Unfortunately mortality is a highly stochastic event and thus extremely difficult to model (Lee, 1971). In addition tree mortality is affected by external disturbances such as windthrow and snow breakage. These impacts are even more difficult to model because such disturbances are rare events, and the occurrence of the risk agent per se is difficult to predict. Examples of forest models which include disturbance features are provided by Hasenauer *et al.* (1995) and Lexer and Hönninger (1998). In addition the sensitivity of modelled ecosystem processes to management practices is important if effects of silvicultural treatments have to be assessed. A classification of forest population models based on spatial resolution, structural attributes and phenomena considered is given in Table 3.

### COMPATIBILITY OF MODEL OUTPUT AND DATA REQUIRED TO CALCULATE BIODIVERSITY INDICATORS

By comparing the data requirements of biodiversity indices («demand») and output provided by models of different categories from Table 3 («supply») we can evaluate the extent to which existing forest models are able to satisfy the information needs for biodiversity assessment. Table 4 shows that the proportion of information needs satisfied increases with increasing spatial resolution of the models. Although ecosystem models (compare section on Structural organization of forest models) provide information on ecosystem processes, appropriate information on composition and structure is usually lacking. Hence this type of model currently does not have much potential for biodiversity assessments. Classical projection tools operating at stand-level resolution such as yield tables are unsuitable for assessing the impacts of different silvicultural treatments on biodiversity. The reasons are: (i) yield tables are designed for even-aged mono-species stands and (ii) often assume a particular management regime (v. Gadow and Hui, 1999).

Size class models provide substantially more information on stand composition and structure and enable the assessment of silvicultural effects on stand development (Solomon *et al.*, 1986). Single tree models are the most suitable tool for projecting parameters relevant for biodiversity assessments because they are explicitly designed to address forest growth response to a range of silvicultural treatments. Distance dependent tree models (e.g. Pretzsch, 1992; Hasenauer, 1994) with their detailed description of tree distribution

TABLE 3  
A CLASSIFICATION OF FOREST POPULATION MODELS WITH REGARD TO SPATIAL RESOLUTION,  
STRUCTURAL ATTRIBUTES AND FACTORS PREDICTED  
*Clasificación de modelos de poblaciones forestales respecto a su resolución espacial, sus atributos estructurales y los factores predichos*

| spatial<br>resolu-<br>tion | structural attributes |                  |                       | factors         |        |        |            | examples |   |
|----------------------------|-----------------------|------------------|-----------------------|-----------------|--------|--------|------------|----------|---|
|                            | age<br>structure      | compo-<br>sition | distance<br>dependent | dimen-<br>sions | G      | Mo     | R          | D        | Ma  |
| stand                      | even                  | mono             | no                    | 1D              | x      |        |            |          | Schwappach (1890) [-], Assmann and Franz (1963) [-],<br>Marschall (1975) [-]                                  |
|                            | even<br>uneven        | mono<br>mixed    | no                    | 1D<br>1D        | x<br>x | x<br>x | (x)<br>(x) |          | Clutter and Bennett (1965) [-], Burkhardt (1971) [-]<br>Solomon <i>et al.</i> (1986) [-]                      |
| tree                       | even/<br>uneven       | mono/<br>mixed   | no                    | 1D              | x      | x      | (x)        | (x)      | Burkhardt <i>et al.</i> (1987) [-], Nyyssönen and Mielikäinen (1978)<br>[-], Pukkala <i>et al.</i> (1994) [-] |
|                            | even/<br>uneven       | mono/<br>mixed   | yes                   | 2D              | x      | x      | (x)        | (x)      | Hasenauer (1994) [-], Nagl (1995) [-], Monserud <i>et al.</i> (1997)<br>[-], Miina <i>et al.</i> (1991) [-]   |
|                            | even/<br>uneven       | mono/<br>mixed   | yes                   | 3D              | x      | x      | (x)        | (x)      | Pretzsch (1992) [-]   |
|                            | even/<br>uneven       | mono/<br>mixed   | patch                 | 1D              | x      | x      | (x)        | (x)      | Botkin <i>et al.</i> (1972) [±], Bugmann (1994) [±], Bugmann <i>et al.</i> (1997) [±]                         |
|                            | even/<br>uneven       | mono/<br>mixed   | patch                 | 3D              | x      | x      | (x)        | (x)      | Urban (1990) [±],<br>Lexer and Hönninger (1998) [±]   |
|                            | even/<br>uneven       | mono/<br>mixed   | patch                 | 3D              | x      | x      | (x)        | (x)      |   |

G = growth, Mo = mortality, R = regeneration, D = disturbance, Ma = management; x = considered in current models, (x) = limited consideration in current models, Mono = single species stands.

**TABLE 4**  
**EVALUATION OF FOREST POPULATION MODELS WITH RESPECT TO BIODIVERSITY ASSESSMENT**  
*Evaluación de modelos de poblaciones forestales respecto a la evaluación de la Biodiversidad*

| Component   | attributes                 | stand models |                  | size class models |                | tree models  |              |          |          |     |
|-------------|----------------------------|--------------|------------------|-------------------|----------------|--------------|--------------|----------|----------|-----|
|             |                            | even/mono    | dbh-distr. model | matrix model      | dist.indep./1D | dist.dep./2D | dist.dep./3D | patch/1D | patch/3D |     |
| Composition | species                    |              |                  | x                 | x              | x            | x            | x        | x        | x   |
|             | abundance                  |              |                  | x                 | x              | x            | x            | x        | x        | x   |
| Structure   | genetics                   |              |                  |                   |                |              |              |          |          |     |
|             | individual dispersion      |              |                  |                   |                | x            | x            |          | (x)      | (x) |
| Structure   | diameter differentiation   |              |                  |                   |                | x            | x            |          | (x)      | (x) |
|             | range of tree dimensions   |              |                  |                   | x              | x            | x            | x        | x        | x   |
|             | vertical structure profile |              | (x)              | (x)               | (x)            | (x)          | x            | (x)      | x        | x   |
|             | deadwood (CWD, snags)      |              | (x)              | (x)               | (x)            | (x)          | (x)          | (x)      | (x)      | (x) |
|             | herb and shrub layer       |              |                  |                   | (x)            | (x)          | (x)          | (x)      | (x)      | (x) |
|             | architectural complexity   |              |                  |                   | x              | x            | x            | x        | x        | x   |
|             | genetic structure          |              |                  |                   |                |              |              |          |          |     |
| Function    | growth                     | x            |                  |                   |                |              |              |          |          |     |
|             | regeneration               |              |                  | x                 | x              | x            | x            | x        | x        | x   |
|             | tree mortality             |              |                  | (x)               | (x)            | (x)          | (x)          | x        | x        | x   |
|             | external disturbances      |              | x                | x                 | x              | x            | x            | x        | x        | x   |
|             | genetic processes          |              |                  |                   | (x)            | (x)          | (x)          | (x)      | (x)      | x   |
|             | management                 | (x)          | x                | x                 | x              | x            | x            | x        | x        | x   |

x = information provided, (x) = limited information provided.

and stand structure allow the calculation of an array of proposed structural indicators for various stand treatment scenarios. Nevertheless, some existing tree growth models fail to consider natural regeneration establishment and development and are therefore only suitable for assessing biodiversity for stand development phases without regeneration. Patch models include regeneration, but trade off precision against generality. Thus, this class of models is usually applied for long-term scenario analysis. Until recently, forest managers were mainly interested in timber yields whereas herb and shrub layers were of little interest. The COVER extension (Moeur, 1985) to the Forest Vegetation Simulator FVS (Wykoff *et al.*, 1982) and a patch model by Kellomäki and Väisänen (1991) are rare examples where herb and shrub layers are explicitly considered in a forest model. There are only a few attempts to incorporate dynamics of deadwood in a forest model (e.g. Beukema *et al.*, 1997). Obviously another weak point of practically all models is the non-consideration of external disturbances (but see Hasenauer *et al.*, 1995; Lexer and Hönninger, 1998). Finally, none of the available forest models considers genetic parameters.

## CONCLUSIONS

From our comparison of the data required for biodiversity assessment and the current range of model outputs we conclude:

- (i) Tree models adequately characterize stand structural attributes due to their «bottom up» approach in modeling stand development.
- (ii) With very few exceptions, prominent parameters for biodiversity assessment such as deadwood (snags, coarse woody debris; compare Beukema *et al.*, 1997) and understorey vegetation (e.g. Moeur, 1985) are currently not included in forest models.
- (iii) Mortality from windthrow and other abiotic and biotic agents substantially affects stand structure and composition. Such disturbances are rarely, if ever, included in forest models.
- (iv) Patch models which are an interesting tool to assess effects of changing environmental conditions on forest development have to be extended so that better representations of stand structure and management options are provided (Lindner *et al.*, 1997). Classical management-oriented tree growth models already offer the opportunity to apply various silvicultural treatment scenarios.
- (v) No current forest model considers attributes of genetic biodiversity.

These findings might be considered disillusioning. However, two important factors have to be considered: (i) although our analysis shows that individual tree growth models – especially the distance dependent approach – already provide a substantial proportion of the information needed to calculate a comprehensive array of biodiversity indices, it is important to recognize that none of the existing forest models were designed to address non-timber values; (ii) one alternative to the all-embracing approach of quantifying biodiversity *per se* is to define specific issues of interest such as habitat quality requirements for certain species (Southwood *et al.*, 1979).

It is important to note that different demands may exist between biodiversity assessments and forest growth modelling. While biodiversity measures are explicitly designed to express the distributional and structural diversity of a stand, most existing forest models are intended to produce reliable estimates of the mean stand development (Vanclay, 1998). An important exception is the family of distance-dependent individual tree models (see Pretzsch, 1992; Hasenauer 1994). This type of model calculates the competition situation for each tree within a given stand and is able to represent the vertical and horizontal diversity of a forest stand properly. Finally, if forest models include stochastic effects (e.g. snow breakage, fire) each simulation represents a unique situation and multiple simulation runs to cover the whole range of possible outcomes have to be performed.

Although some models meet the data requirements of compositional and structural indicators, other important biodiversity measures, such as genetic diversity and deadwood can not be accounted for sufficiently with current forest models. Furthermore, external factors which are highly relevant to forest stand development such as the impact of browsing by wildlife, are usually not considered explicitly in forest modeling although they may strongly influence future stand development (but see Kienast *et al.*, 1999; Jorritsma *et al.*, 1999).

Regarding the genetic component of biodiversity, it does not seem reasonable to view forest stands as isolated entities due to high levels of pollen flow from surrounding stands (e.g. Chase *et al.*, 1996; Dow and Ashley, 1996). A first attempt to integrate genetic processes into real-structure forest models is provided by Degen and Scholz (1996). The necessity to consider the landscape level as well may be inferred from the fact that a single silvicultural system may not be adequate to provide the entire array of desired stand attributes at larger scales. Consequently, planning at the landscape level is needed to optimize the maintenance of biodiversity (Greenough and Kurz, 1996). Geographical information systems are an essential tool to capture the spatial dimension at scales beyond the stand level and to analyse features such as habitat fragmentation.

Biodiversity attributes which are either difficult or expensive to assess (e.g. wildlife species, ecosystem processes such as nutrient cycling) might be inferred from more readily available model outputs. A first attempt to link environmental indicators and stand structural parameters recently was presented by Kolström (1998). However, the extrapolation of such empirical relationships is difficult because the correlation between environmental factors and stand structural parameters does not address the actual cause-effect relationships.

To study the effects of alternative silvicultural treatments on biodiversity of Scots pine forests in Europe, appropriate prediction tools are a prerequisite. For boreal and Central European conditions single tree models exist which can be considered an appropriate modeling approach. However, these models have to be enhanced to include regeneration modules and to allow for the simulation of mixed stands consisting of Scots pine and broadleaves such as oak (*Quercus* spp.) and birch (*Betula* spp.). Furthermore the development of reliable submodels for deadwood dynamics is a key issue on the way towards prediction tools which consider both timber and nontimber values. «Classical» stand-alone growth simulators will not be sufficient for forest management decision support within multiple purpose forestry due to the increasing complexity of the trade-offs involved between conflicting objectives. Additional modules designed for the evaluation of multiple-criteria problems coupled with growth simulators might be a promising approach. According to Rauscher (1999), the development of appropriate decision support



tools will probably be the most urgent and challenging task to turn concepts of multiple-purpose forestry and ecosystem management from quasi philosophical paradigms into operational resource management processes.

## RESUMEN

### El uso de modelos forestales para la evaluación de la biodiversidad al nivel del rodal

Existe una demanda creciente para incluir evaluaciones de la biodiversidad como una entrada adicional de gestión dentro de la toma de decisiones selvícolas. Existe un gran número de modelos forestales en uso para apoyar la planificación de la gestión forestal. Sin embargo, ninguno de estos modelos se diseñó explícitamente para considerar la biodiversidad del ecosistema forestal y como puede cambiar ésta bajo diferentes tratamientos selvícolas. En este trabajo se identifican medidas y atributos destacados de la biodiversidad y los datos requeridos para su cálculo, basándose en una revisión de la literatura. Los modelos forestales existentes se clasifican respecto al enfoque general de la modelización (es decir empírico vs. modelos basados en el proceso), los fenómenos y los atributos estructurales considerados. Después de comparar los datos requeridos para la evaluación de la biodiversidad y las salidas disponibles de los modelos forestales, se discute hasta qué punto los modelos existentes pueden satisfacer la información necesaria para evaluar la biodiversidad al nivel de rodal. La conclusión principal es que se necesita una extensión de los modelos existentes de crecimiento para incorporar los aspectos de la biodiversidad en la planificación de la gestión forestal. Probablemente el enfoque más prometedor consiste en el desarrollo de la familia de los modelos de crecimiento individual del árbol, porque pueden indicar explícitamente la diversidad estructural horizontal y vertical del rodal forestal. Una limitación importante es la carencia de información sobre la diversidad genética.

**PALABRAS CLAVE:** Biodiversidad  
Indicadores ambientales  
Modelos forestales  
Ecosistema forestal  
Evaluación

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