6 Vegetation Responses to Climate Change in the Alps: Modeling Studies

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6.1 INTRODUCTION

High altitude plants are well adapted to their present environment (Körner 1992), but their ability to adapt to the changes in climate expected over the next century remains uncertain (Guisan, Holten, Tessier et al. 1995). Chapter 3 presented a few glimpses of plants and ecosystems' reactions to changing climates in the past. Chapter 5 reviewed the present knowledge about montane ecosystems and hypotheses for their possible responses to climate change in the Alps, based on experiments and field observations. In this chapter, we present a modeling approach for assessing climate change's impact on the vegetation of the Alps.

Our current understanding of the systems and processes that characterize natural vegetation offers a wide array of answers to the question of how vegetation will respond to expected climate change (Idso 1980a, 1980b; Körner and Arnone 1992a, 1992b). For example, the spectrum of predictions for forests ranges from severe diebacks (Neilson 1993) to a general increase in productivity due to elevated temperatures, precipitation, and atmospheric CO_2 concentrations (Blum 1991; Graybill and Idso 1993; Idso and Idso 1994; Kimball and Idso 1983). For montane forests, invasions of trees into areas above present timberline are predicted (Bugmann 1994; Kienast 1989, 1991; Kräuchi and Kienast 1993). For herbaceous or dwarf shrub species of the alpine zone (above tree line), predictions range from global vegetation shifts and species invasions or extinctions (Ozenda and Borel 1990) to local variations in species' abundances or community composition regulated by microhabitat distribution. However, except for the most extreme climate change scenarios, natural mosaic-like microtopography might provide refuges for species that would otherwise be threatened as a result of climate change (Körner 1995).

Different studies diverge in their assessments of climate change's effects because multiple processes can influence ecosystem dynamics in conflicting directions; for example, increased atmospheric concentrations of CO_2 may enhance potential productivity (Eamus and Jarvis 1989; Morison 1987; Robinson 1994), whereas superoptimal temperatures and drought may

reduce it. Moreover, these processes and their typically nonlinear responses to climate work at different temporal, spatial, and organizational scales, also impeding a direct assessment.

One way to integrate our current knowledge of the ecosystem processes' effects to evaluate climate change impacts is to use simulation models of vegetation occurrence or dynamics (Guisan, Holten, Spichiger, et al. 1995). Not only do such models help improve our understanding of the processes taking place at the interface between climate and ecosystems, but they also allow a preliminary assessment of climate change's potential impacts on vegetation by comparing simulation results under present and future climate.

In addition to conceptual models (Romme and Turner 1990), numerous computer-based simulation models have been developed for assessing terrestrial ecosystems' response to anticipated climate change. They differ in their spatial scale and resolution, in the level of detail at which they work, and also in whether and how they treat vegetation's variability and temporal development. Solomon and Leemans (1989) Walker (1990) and Kirschbaum and Fischlin (1996) review these models, which assess environmental change's ecological impact, and detail their advantages, drawbacks, spatiotemporal-scale requirements, limitations, and applications.

Dynamic models describe how vegetation changes with time, even when input values are constant. Process rates in these models usually depend explicitly or implicitly on climate.

Dynamic ecophysiological process models (Bossel 1987, 1991; Bossel et al. 1991) describe in detail many ecophysiological processes contributing to plant growth, birth, and death. These models' complexity confines them to the local scale and to relatively short time windows.

Succession models, such as the forest gap or patch dynamics models like JABOWA (Botkin, Janak, and Wallis 1970, 1972a, 1972b), FORET (Shugart and West 1977) or FORSKA (Leemans and Prentice 1989), are less detailed and offer the advantage of mimicking vegetation dynamics' long-term characteristics. They work at the local to regional scale and at the level of individuals. The forest patch models FORECE (Kienast 1989, 1991; Kienast and Kräuchi 1989; Kienast and Kuhn 1989), FORSUM (Kräuchi 1993; Kräuchi and Kienast 1993) and FORCLIM (Bugman 1994, 1996; Fischlin, Bugmann, and Gyalistras 1995) all apply in the Alpine region, because their species sets contain most of the dominant tree species found in this region. Recently, several gap models have been simplified to more efficient structured population models (Fulton 1991; Kohyama and Shigesada 1995; Lischke, Löffler, and Fischlin 1998).

Also many nondynamic models or modeling procedures are used to assess possible impacts of climate change. Global biogeography models (e.g., BIOME (Prentice et al. 1992), TVM (Leemans and van-den-Born 1994), BIOME2 (Haxeltine, Prentice, and Cresswell 1997), MAPPS (Neilson 1995), and DOLY (Woodward and Smith 1994; Woodward, Smith, and Emanuel 1995)) are static equilibrium vegetation models that can be driven by tran-

sient input variables and are sometimes coupled with dynamic nutrient cycling models. Vegetation is considered in terms of plant functional types, vegetation complexes, or biomes. Potential vegetation composition is determined empirically or causally from ecophysiological constraints, such as yearly day-degree sum, and from dominance tables or maximum net ecosystem production (NEP) or the leaf area index that can be reached under the given moisture and nutrient conditions.

Many models of vegetation or single species are based on statistical analyses of interactions between species and their ecological environment. Such models are more descriptive and often noncausal, although they increasingly include ecophysiologically meaningful variables. Busby (1988, 1991) applied his BIOCLIM approach (a fitted, species-specific, p-dimensional environmental envelope) to alpine vegetation of southeastern Australia using 0.1 degree latitude-longitude grid cells. As an improvement, Carpenter, Gillison, and Winter (1993) developed the DOMAIN model to map potential distributions of species. It is based instead on a point-to-point similarity metric (measure of multivariate distances) and has been proven more suitable to applications where available records are limited.

As an alternative, a large range of regression methods (least square, nonlinear regressions, regression trees, generalized linear or additive models (GLMs, GAMs); Nicholls 1989; Yee and Mitchell 1991; see also section 6.2) have been developed for modeling species' distributions and ecological tolerances (realized niches). Numerous such studies have been successfully applied to climate change ecological impact assessment (Austin 1992; Brzeziecki, Kienast, and Wildi 1994; de Swart et al. 1994; Hill 1991; Huntley et al. 1995).

Thus, overall, there are many distinct ecological models or approaches, and each has its particular advantages and drawbacks depending on the particular application's goals. However, for our purpose not all of these models are adequate. In our studies, we wanted to focus on the level of individual plant species. This excluded the use of biogeography models, which aggregate species to plant functional types or biomes. We were also interested in assessing climate change impacts at a scale between local and regional (1– 1,000 km), however, with the fine resolution (1–100 m) required for dealing with the rugged microtopography typical of the Alps as well as the associated high ecological complexity. This excluded models either restricted to single locations because of too great computing time and input value demands, such as detailed ecophysiological models, or those working at too large a resolution, such as the biogeography models already mentioned.

We were also interested in two different aspects of vegetation responses: We wanted to predict the potential future distribution of alpine species in large areas, particularly those of rare species, for reasons such as conservation or biodiversity management. At the same time, we were interested in the dynamics of dominant forest species during the next century to assess local impacts of climate change, such as that on the regulation of water run-

off, or to explore montane forests' potential role in the future global carbon cycle (see chapter 5). Therefore, we chose two different modeling approaches, each suitable for its specific application and working on comparable spatial and hierarchical scales.

The first model aims to assess the potential future distribution of alpine plant species (sensu stricto, those above tree line). To include many species, including rare ones, this approach has to be simple, because detailed species-specific information about ecological processes is not available for all species. It is therefore a static model similar to those Brzeziecki, Kienast, and Wildi (1993, 1994) and Kienast, Brzeziecki, and Wildi (1994) developed for forest communities but focusing on herbaceous and dwarf shrub species above forest limits. It is empirical and comparative, in that it uses statistical analyses to relate present plant distributions to environmental covariates (e.g., climate) and predicts probabilities of plant species occurrence in geographic space (section 6.2).

The second model focuses on the temporal development of a limited number of dominant species, in this case forest trees. A static approach is not appropriate and also not required, because rather detailed information is available about forest tree species' ecological processes. Therefore, we chose the mechanistic (i.e., more causal) and stochastic forest patch dynamics approach, which explicitly simulates birth, growth, and death of individual trees and is suitable for site-specific, realistic simulations of the mid- and long-term temporal development of tree biomass and species compositions for the coming century (section 6.3).

Our two models differ from those few existing models that combine both static and dynamic aspects (Solomon and Leemans 1989). The static model used here is clearly spatially based, working at a regional scale with a fine resolution and depending on the resolution of the available digital elevation model, yet it lacks a time dimension. The dynamic model, in contrast, is temporally explicit but deficient regarding the spatial dimension, that is, for each site a separate simulation has to be run. Both models, together with their development and validation, are discussed in terms of their respective properties, advantages, and drawbacks, particularly with respect to their application to climate change (Brzeziecki, Kienast, and Wildi 1995; Fischlin 1995; Guisan, Theurillat, and Spichiger 1995).

6.2 THE STATIC ASPECT: MODELING THE POTENTIAL HABITAT OF ALPINE PLANTS

6.2.1 Static Plant Modeling

Static modeling procedures are not new. In fact, as long as ecologists have tried to relate vegetation or plant distributions directly to the physical environment, they have made static analyses based on assumptions of pseudo-

equilibrium. Static modeling is now being reconsidered in studies of global climate change as one possible method for obtaining rapid primary impact assessments over large areas.

Since the 1980s, many bioclimatological studies have considered the distribution of plant species in both environmental and geographical spaces (Hill 1991). A species' environmental space corresponds to its realized ecological niche (the combination, or envelope, of ecological conditions that a species can tolerate in a multidimensional environmental space); its geographical space is its actual geographical distribution (dependent, for instance, on historical factors and human influences). Both spaces were judged to be necessary for assessing climate change impacts on plant species distributions (Hill 1991). Many examples of such bioclimatic studies exist, but almost all are concerned with low elevation areas (Guisan et al. 1998). Few bioclimatic studies have been conducted in high-altitude areas (alpine and snow belts), whose rugged topography requires a much higher spatial resolution to obtain reliable results. Fischer (1990) used topographic factors, radiation, land use, precipitation, and snow cover (which integrates temperature, precipitation and microrelief in time and space) to predict the distribution of plant communities, including alpine communities, in the region of Davos (Switzerland) and achieved a rather high (70 percent) correspondance with actual vegetation maps. Brzeziecki, Kienast and Wildi (1993) applied another vegetation model to all of Switzerland; the model included the seventy-one forest community types described by Ellenberg and Kiötzli (1972). More recently, Zimmermann and Kienast (in press) improved the model to include alpine plant communities. They performed quite successful modeling experiments in the Swiss alpine region of Grindelwald and recently generalized their model to the whole country (see figure 6.3b). However, no model has yet focused on specific alpine plant species distributions in Switzerland.

Such a static approach is primarily based on statistical methods (such as multiple regression, decision trees) and focuses mainly on determining the potential present and future distribution of plant or animal species or communities. The range of possible applications includes biodiversity and endangered flora management as well as primary, short-term assessments of climate change impacts over specific areas. In particular, such an approach could enable researchers to identify species or communities that might be particularly threatened by a change in climate and those that might be favored. It assumes, within the resolution and time frames of interest, that current vegetation outside of areas of intense human impact is in a quasi-stationary equilibrium. This postulate is considered true for alpine areas, where any kind of modification to the local climate could break such a fragile ecological equilibrium and modify the composition and structure of ecosystems (Galland 1982).

At the scale of the whole Alpine arc, the distribution of plant species can be described, at best, by indicating presence or absence within broad biogeographic units (Welten and Sutter 1982), within political entities (see

Aeschimann et al. in press) or within relatively large grid divisions (Hartel et al. 1992). Such macroscale information indicates clearly the overall biogeographical and historical distribution trends but does not allow for an accurate ecological description of species' specific habitats (Theurillat 1995).

Modeling at a finer resolution requires knowledge of a species' ecological requirements at the microscale level (for instance, along a mountainside or within a small alpine catchment). For Switzerland, knowledge about alpine species' environmental requirements is summarized by ecological indices for species (Landolt 1977). However, in practice, such ecological values are difficult to include in phytogeographical models because of their semi-quantitative nature, and because their reliability is too limited geographically. Our study thus required us to undertake our own intensive field sampling to obtain more reliable data on the ecology of species.

Most models and results presented in this section are related to the ALPLANDI project, which is part of the wider Ecocline coordinated project (Theurillat et al. 1997) developed in the framework of the Priority Programme Environment of the Swiss National Science Foundation (Guisan, Theurillat, and Spichiger 1995; Guisan 1997; Guisan et al. 1998).

6.2.2 Model Construction and Calibration

The modeling of alpine plant distributions involves many successive steps and also requires many different analytical techniques and associated tools. As an illustration, the methodology we are following requires the use of a triangulated constellation consisting of a geographical information system (GIS), a statistical package, and a database package (see figure 6.1). The basic kernel of all our modeling procedures is a 25-meter resolution Digital Elevation Model (DEM) covering the whole study area (see figure 6.1).

The following sections describe some important practical and theoretical aspects involved in constructing a static alpine plant distribution model (see also Buckland and Elston 1993 for a more general review). They are illustrated with concrete examples from the ALPLANDI project.

6.2.2.1 Data Sources The data set used for calibrating the model was sampled in the field during a three-year summer campaign (1993–95). Classical Braun-Blanquet *relevés* (measure of abundance-dominance of species) were made at each point of the sampling design in a four-square-meter plot. The first two years (1993–94) were devoted to sampling points to be used for calibrating the model. An additional summer (1995) allowed us to sample independent *relevés* for validating the model.

Spatial variations in environmental factors within the area were determined by modeling procedures on the DEM (for example, solar radiation, annual mean temperature, permafrost; following Hutchinson and Bishof 1983 and Brown 1994) by digitizing existing maps (geology, hypdrology, lithology) and through derivation from aerial photographs or satellite scenes
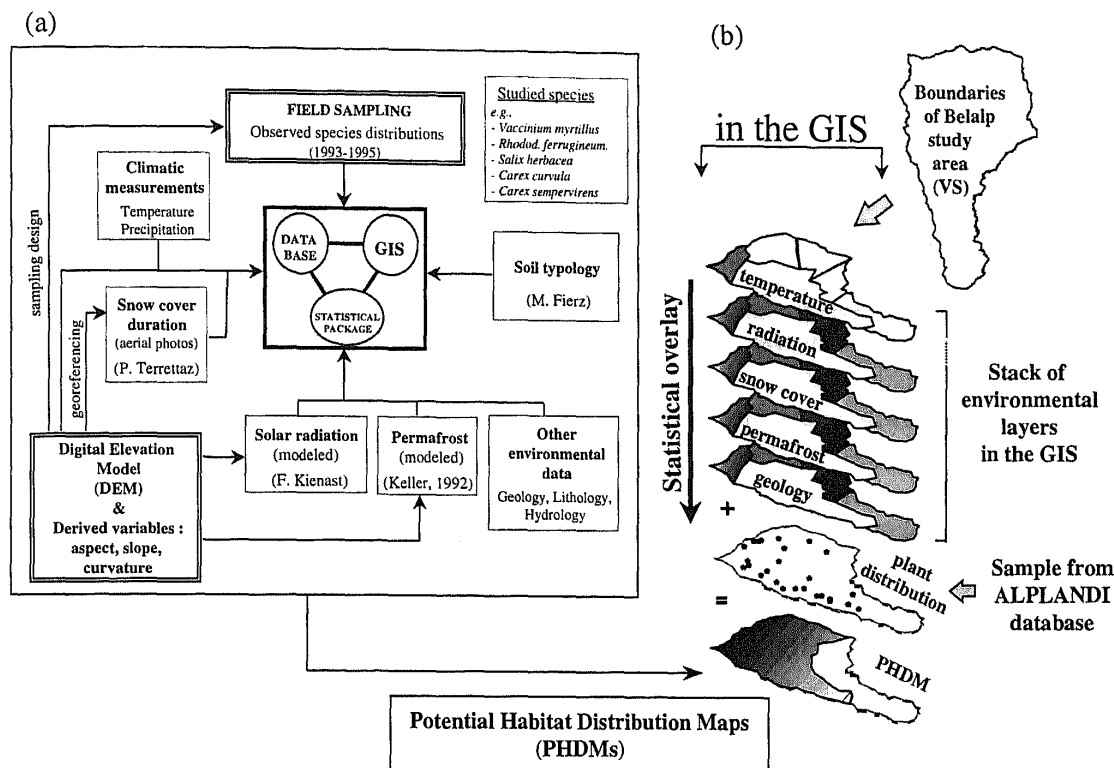
Figure 6.1 Structure and organization of the data and tools used in the ALPLANDI methodology, clearly showing the central role of the 25-meter digital elevation model (DEM) regarding sampling design, variable derivation, and data georeferrencing. Shading on the Gis maps is for illustrative purposes only.

(snow cover, vegetation cover, unmapped hydrology). These variables were stored as environmental layers within the Geographical Information System (see figure 6.1).

6.2.2.2 Spatial Scale and Autocorrelation In formulating a statistical model, selecting the spatial scale is a crucial decision, because of the scale dependency of most statistical relationships in ecological studies (Greig-Smith 1983; Jongman, Ter Braak, and van Tongeren 1987). In particular, if spatial autocorrelation (AC) is observed for the dependent variable (that is, at a measured spatial distance, pairs of observations take more (positive AC) or less (negative AC) similar correlation values than would be expected if pairs were randomly associated), then correlations and estimation of model parameters can change with scale (Anselin and Getis 1992). From a purely statistical point of view, the optimum scale for modeling should preferably be "just small enough" to avoid spatial AC. However, when observed at the level of species distributions, spatial AC can also be considered an indicator of spatial processes such as dispersal and be used to incorporate dispersal functions into classical analyses of the distribution of species abundance (Malanson 1985). At the scale of this study, that is, one point sampled every 250 meters, no autocorrelation was observed in the data.

6.2.2.3 Ideal versus Reasonable Sampling Strategy

In a single spatially limited study area, it is very difficult to sample the broad range of ecological conditions that a species can tolerate. A sampling limited to a part of the actual range of conditions the species experiences can make the species' observed response to an environmental variable appear different from what it actually is, thus "truncating" its environmental profile (see section 6.2.2.5).

Efficient sampling strategies therefore aim to give complete and accurate information on species' responses along an identified environmental gradient. However, the problem becomes much more complex when, as in our case, numerous species must be sampled using the same sampling strategy (in a global survey), because the position of their maximum occurrence may differ along the main gradient (in our case, elevation), and because other environmental features also determine their distributions. In fact, setting up an efficient random-stratified sampling for more than one species is, in practice, very difficult. For all the species in a region, it becomes unrealistic.

Given these limitations, a grid-sampling scheme was considered the best alternative. Our set of calibration points was obtained by sampling all points (208) of a 250 m × 250 m DEM (the only one available at that time) covering the study area. The set of 100 validation points was sampled randomly at a later date among the points of the newly aquired 25 m × 25 m DEM.

6.2.2.4 Selection of Environmental Variables

The next step in model construction entails retaining, from a broad set of environmental variables, those most highly correlated with the species distribution pattern. To keep the model statistically valid, the potential problem of multicollinearity between these variables should first be managed. That is, each variable or combination of variable should ideally be independent of the others. This can be achieved by selecting them on the basis of the degree of correlation between them or, in some cases, by combining them linearly to obtain artificial orthogonal factors explaining most of the variance (Franklin et al. 1995). With the latter operation, however, ecological interpretation of the new principal components remains problematic unless they are strongly correlated to simple combinations of the basic variables.

Furthermore, Austin, Cunningham, and Good (1983) demonstrated that many of the so-called environmental variables (or combinations of variables) used in vegetation modeling had no direct physiological impact on plants. Because static plant distribution models' basic aim is clearly not to analyze cause-and-effect relationships but rather to obtain reliable final predictions validated by actual field data, nonexplicit environmental variables can be used in principle. However, in such a case, no physiological interpretation should be derived from the results. Therefore, if possible, physiologically meaningful environmental variables should be preferred to noncausal variables (for example temperature values rather than altitude).

In particular, solar radiation and snow cover are important variables for alpine landscape modeling (Brown 1994; Fischer 1990). They can be derived

simply for wide areas from a DEM and satellite images (e.g., Parlow and Scherer 1991). As synthetic factors, they integrate several single variables (e.g., slope, aspect, microtopography and altitude), thus limiting the number of variables included in the model. Moreover, they are physiologically important for most high-altitude plants (solar radiation budget is directly related to photosynthesis and snow cover to the duration of the growing season). Snow cover presents the additional advantage of being directly related to climate. This is particularly interesting if climate change scenarios must be derived, as in our case. Other important variables in alpine landscapes are geology (the nature of bedrock, acid versus basic influences), rocky cover (form of substrate: e.g., moving or fixed screes, cliffs), hydrology (proximity of mountain streams, marshes, or springs), permanently frozen soils (permafrost), microclimate, and human-induced or natural disturbances (e.g., grazing, fire). Soil is a more problematic component, as most soil types result primarily from the underlying geology and are probably secondary, as much influenced by vegetation as an influence upon it. Moreover, in alpine regions, their typology remains too understudied to include them in the present ecological models (see chapter 5).

The final set of quantitative environmental variables retained were: solar radiation index (obtained by extracting the first axis of a principal component analysis on nineteen individual days of solar radiation), snow cover index (derived from aerial photographs), slope and curvature (a scale going from concave to convex) of the sample point, and mean annual temperature (derived from elevation using field measurements). In addition, three classes of nominal variables that proved, from exploratory analyses, to have an important power for discriminating species distributions were also retained: two classes of lithology (screes and cliffs) and a class of geology (moraines). Because it is not a physiological variable and because it is highly correlated with solar radiation index, slope aspect was not included in the set of input variables for the specific models to be developed. Precipitation was not included either because, to our knowledge, no reliable spatial extrapolation of precipitation could yet be made in an alpine landscape and because precipitation information is already partly included in snow cover information. A second step used permafrost (Keller 1992), and a water accumulation index (derived from the DEM and the hydrological layer in the GIS) as filtering factors of the preliminary maps (i.e., species once observed or not in the corresponding factor class).

6.2.2.5 Ecological Responses of Species As a next step, a species' physiological response to a given environmental variable should ideally be identified and integrated into the model (Huisman, olff, and Fresco 1993). However, a species' actual response to an environmental variable (that is, its ecological response curve) may not follow its physiological response obtained from laboratory experiments under controlled conditions, because inter- and intraspecific competition and other biotic factors influence physio-

logical responses in the natural environment. Thus, the response cannot be considered solely physiological but, rather, at a higher level of ecological complexity. This exemplifies the overall problem of incorporating results from laboratory experiments into such static ecological models.

In plant ecology, the debate about the form of plant response curves remains partly unresolved. Whittaker (1956) proposed that most response curves approach a normal distribution (i.e., Gaussian: bell-shaped and symmetric), and most plant ecologists accepted this as typical of species' response to ecological variables (Brown 1984; Ter Braak and Gremmen 1987; Ter Braak and Looman 1986). However, the evidence remains equivocal. There is no a priori reason to assume that such response curves need to be symmetrical or indeed that any ideal or ubiquitous response curve exists (Austin, Cunningham, and Good 1983; Austin and Gaywood 1994; Huisman, Olff, and Fresco 1993; Jongman, Ter Braak, and van Tongeren 1987). Austin (1979) showed that bimodal and even more complex responses of species to a single environmental variable are common. He felt that many of the statistical techniques commonly used in vegetation modeling were inappropriate, given such complex responses. Austin, Nicholls, and Margules (1990) discussed observations of skewed responses to changes in variables such as temperature, organic matter content, or total nitrogen in soils. More recently, Austin and Gaywood (1994), using beta functions (measures of shape: skewness and kurtosis), tested and confirmed two hypotheses: Species response curves differ significantly from Gaussian-shaped curves, and the direction of skew is a function of the species' position along the environmental gradient. They showed that a great variety of response types exist depending on the organisms and variables considered. Such knowledge should now be better integrated into static model construction.

As discussed in section 6.2.2.3, the type of response also depends strongly on how the sampling is undertaken along the environmental gradient (Austin 1987; Green 1979; Mohler 1983). For example, curved responses may appear linear or close to linear if only one side of the mode is sampled (Jongman, Ter Braak, and Tongeren van 1987).

As an example, figure 6.2 shows different species' empirical response curves along a temperature gradient. In this case, response curves were drawn using techniques for smoothing histograms (with a large smoothing parameter) as an exploratory method for approaching the response's shape. Unimodal species' responses were observed (bell shaped, skewed, or even more complex ones, as for *Salix herbacea*), suggesting the need for at least a second-order term in the model. The use of simple responses, including an additional second-order term, was first investigated by running exploratory univariate GLMs including various-order terms of the same variable $(x, x^2, x^3, \ldots)$. Cubic terms were not retained because they always generate sinusoidal curves, which are not subject to simple ecological interpretation. This approach enabled us to develop satisfactory models for some species (see section 6.2.3). More complex responses (e.g., using beta functions) were
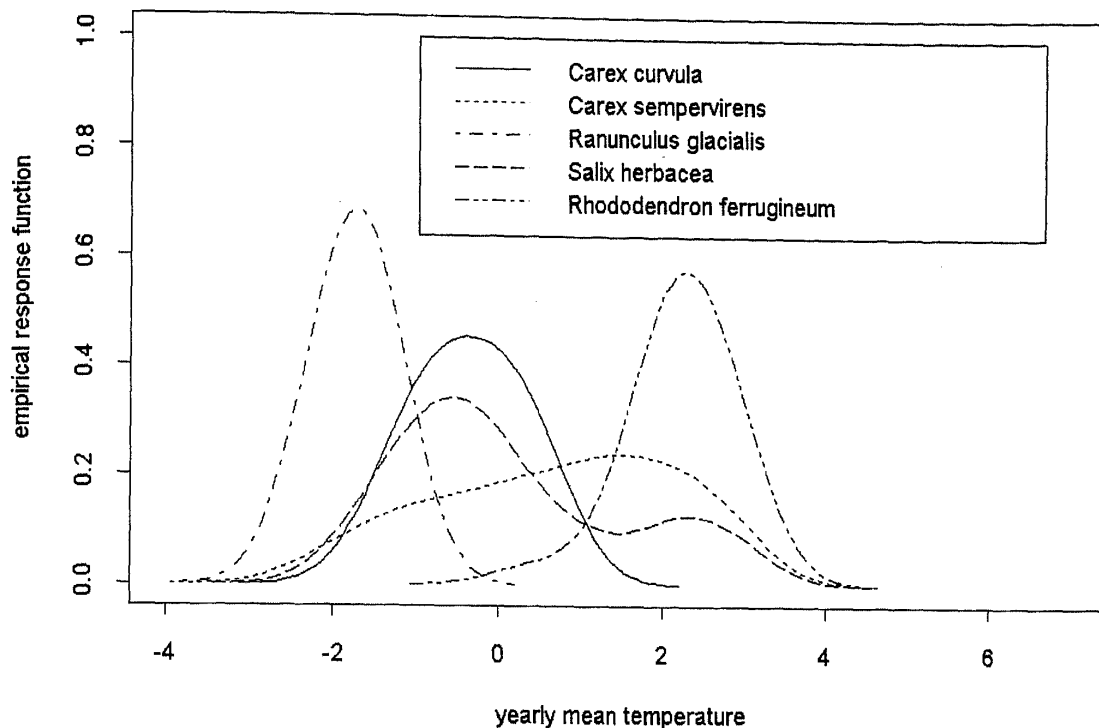
Figure 6.2 Empirical curves of various alpine plant species, ecological response to yearly mean temperature. The aim here is merely to explore possible shapes of response curves, here obtained by techniques for smoothing histograms. The abscissa's scale is in density function units (the curve's surface area must be unity).

considered for species for which model results were not satisfying (e.g., *Carex sempervirens*).

6.2.2.6 Statistical Models As discussed previously, curves of plant response to environmental regimes are not generally Gaussian. In this case, ordinary least-squares linear regression models are unlikely to have Gaussian residuals, and so they cannot be applied. Alternative methods of regression are thus more likely to produce representative results. The use of GLMs (see McCullagh and Nelder 1989) is a possible alternative when the response function's distribution family is known, because GLMs allow nonnormal response distributions to be modeled by transforming them to linearity.

GLMs rely on the following principles. If y is the dependent variable (i.e., response variable), with a known (but not necessarily Gaussian) frequency distribution, and $x_1, \ldots, x_n$ are the n explanatory variables, it is assumed that in a GLM, these variables can influence the distribution of y only through a single linear function called the *linear predictor*. The mean of y is thus a smooth, inversible function of the linear predictor, and its inverse function is called the *link function*. Hence, a multiple regression is made between the linear predictor (LP) and the explanatory part of the equation; for example,

$$LP = a + b_1 x_1 + \cdots + b_n x_n,$$

where a, b_1, ..., b_n are the different regression coefficients to estimate, using, for example, the maximum likelihood principle. The probability of species occurrence, in response to a single environmental variable x, can then be expressed simply as a function of the linear predictor. More complex models including quadratic and interaction terms can similarly be considered. Common examples of GLM families include Gaussian, binomial, Poisson, inverse Gaussian and gamma response distributions and their most current associated link functions: identity, logit, log, 1/2, and inverse (see McCullagh and Nelder 1989 for details). Such GLMs have been successfully used in many recent ecological studies (Austin 1992; Austin et al. 1994; Austin, Nicholls, and Margules 1990; Brown 1994; Ferrer-Castán et al. 1995; Yee and Mitchell 1991) and are also applied in our study.

6.2.2.7 GIS: A Necessary Tool for Modeling Potential Habitat

The analyses of geographical data in this study differ somewhat from those in other ecological studies where the exact geographical location of observations in not important (e.g., when focusing on a particular ecological factor and species without aiming to make predictions from the results). When the aim is to predict the spatial distribution of species' potential habitat, that is, when a large amount of geographical data has to be handled simultaneously, a GIS provides both an analytical and a cartographic tool (Haslett 1990). Examples of GIS approaches applied to plant or animal species are numerous (Davis and Delain 1986; Jensen et al. 1992; Lancia, Adams, and Lunk 1986; Leninhan 1993; Lyon et al. 1987; Mille, Stuart, and Howell 1989; Ormsby and Lunetta 1987; Pereira and Itami 1991). These systems have been conceived in such a way that they are able to handle data of different geographical types (vector versus raster, empirical (field) versus derived data, digitized maps versus satellite scenes or aerial photographs). This is particularly useful when studying relationships between plant species and ecological factors, which often need an approach combining both field data and existing data (from herbaria and from the literature; Rhoads and Thompson 1992). Every specific set of data constitutes a single, monovariate layer in the system (see section 6.2.2.1).

In addition to producing a nice cartographic output to classical statistical analyses, GIS also enables particular analyses of geographical data to be performed that could not be performed in another way (neighboring analysis, for instance). Such GIS-specific handling of data can allow the derivation of new layers (synthetic factor) by modifying elements (e.g., slope, aspect, or curvature from the DEM), by combining layers (e.g., Gams index; see chapter 5) or by modeling new ones (e.g., permafrost, temperature, solar radiation). Once the model is developed and potential maps are calculated and stored within the GIS, geographical information from the newly generated map (for model evaluation, for example) can be accessed quickly.

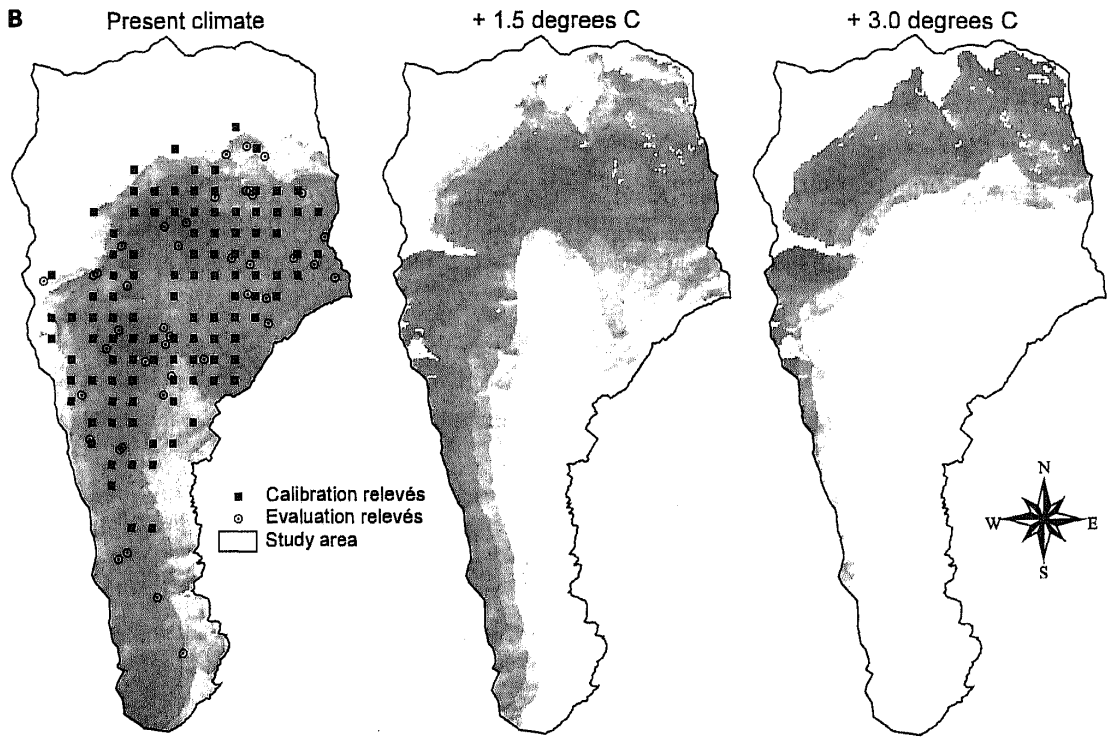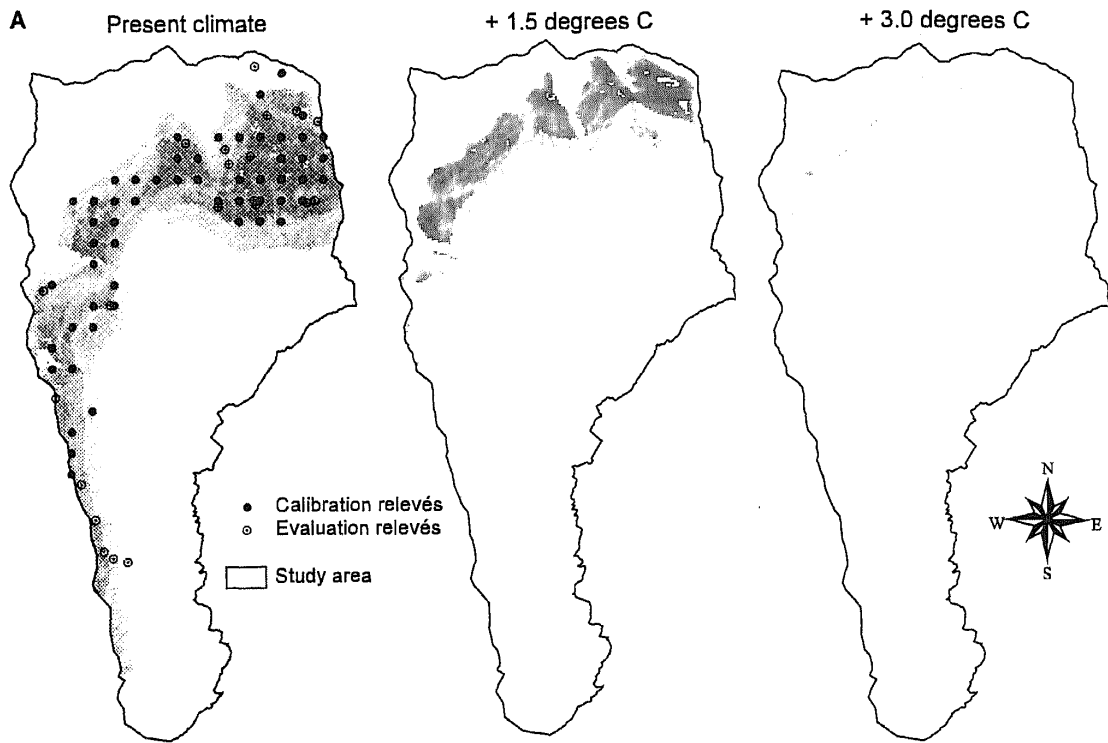### 6.2.3 Model Results: Potential Habitat Distribution Maps

Once the species' multiple response (i.e., its global ecological profile) is derived by statistical and geographical modeling, its associated potential distribution within the modeled area can be determined. As previously stated, modeling plant species' potential distribution is equivalent to modeling their potential habitat (in the sense of Whittaker, Levin, and Root 1973) and it is relevant to speak about Potential Habitat Distribution Maps (PHDMs; d'Oleire-Oltmanns 1995; Schuster 1990). PHDMs correspond to probability maps (figure 6.3) and are cartographic representations, for all points of the DEM, of the probability of finding the species. Figure 6.3 provides examples of PHDMs for *Carex curvula*, *Carex sempervirens*, and *Rhododendron ferrugineum*. An example of a similar static potential distribution modelling is given by Zimmermann (1996), who predicted the distribution of most alpine plant communities under present climatic conditions (see, e.g., fig. 6.3d).

6.2.4 Model Evaluation

The procedure's next stage is testing the model's quality. The study should be initiated (started) with two distinct data sets, one for building the model and another for its evaluation. In addition to the primary visual comparison of predicted and actual distributions in the study area, a more reliable model evaluation is conducted by checking the predictions over the set of evaluation points.

The quality or the model's robustness, also varies according to the species modeled. As an example, more than 66 percent of the predictions made for *Carex curvula* or for *Rhododendron ferrugineum* (over the set of 100 validation points) fell within a 10 percent interval around the actual values; for modeling in plant ecology, this is considered a rather good result. The models for *Carex sempervirens* reached only 25 percent agreement. However, as the choice of this interval is subjective, considering a slightly larger interval would increase by far the model's quality. Given the present results, the methodology was considered successful for the prediction of some alpine plant distributions. Including data on moisture potential, however, would greatly improve it, because this variable has proven its importance as a latent environmental gradient in exploratory analyses of the species data (correspondence analysis) and could help determine distributions for less successfully modeled species.

As a rule, static presence-absence or abundance models, especially at high spatial resolution, rarely explain more than 60–70 percent of the variance in the distribution of plant species, communities (Brzeziecki, Kienast, and Wildi 1993; Zimmermann 1996) or vegetation boundaries (Brown 1994). Indeed, explaining 50 percent of the variation is sometimes considered a good result (e.g., Brown 1994). However, these models are sufficiently valid with regard to the purpose for which they were constructed: to permit comparative studies.

A Present climate   + 1.5 degrees C   + 3.0 degrees C

- Calibration relevés
- Evaluation relevés
- Study area

N
W · E
S

B Present climate   + 1.5 degrees C   + 3.0 degrees C

- Calibration relevés
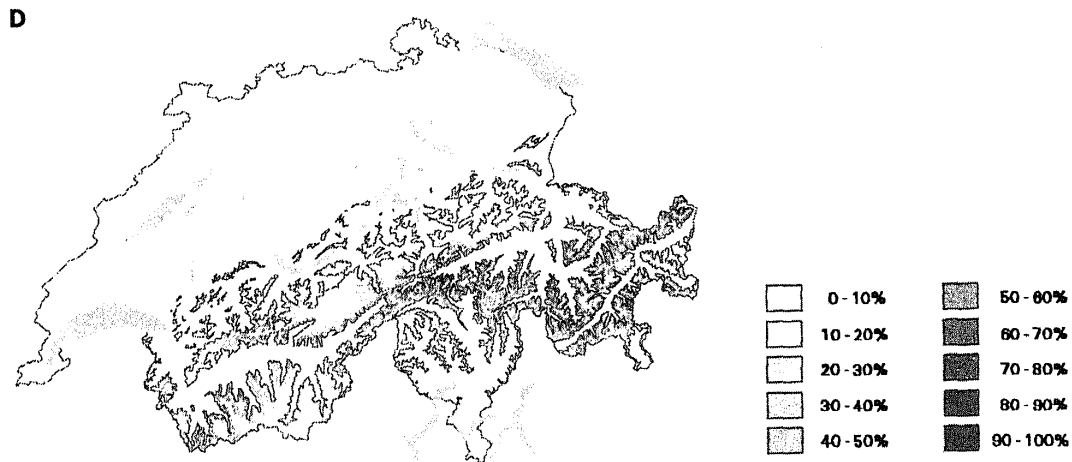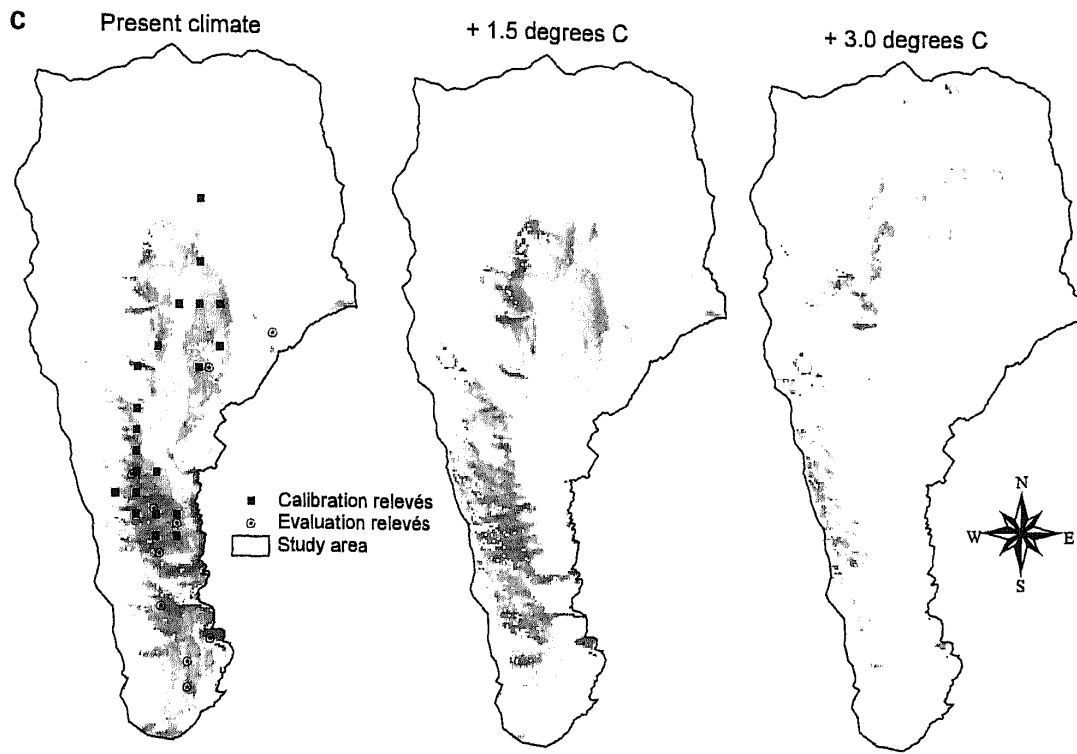- Evaluation relevés
- Study area

N
W · E
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Figure 6.3 Three-paneled Potential Habitat Distribution Maps for (a) *Carex curvula* All., (b) *C. sempervirens* Villars and (c) *Rhododendron ferrugineum*. L., under present climatic conditions and with a + 1.5 and a + 3.0 degree increase in yearly mean temperature (ymt). Gray scale: probability of presence of the species. Black: probability = 1 (100%). White: probability = 0 (d) Potential distribution maps (kindly provided by Klaus Zimmermann (1996)) of the alpine plant community *Caricion curvulae* (characterized, among others species, by a high density of the sedge *Carex curvulae*).

The numerous uncertainties involved in this kind of modeling explain why the models show a relatively low level of correspondence with the data. First, it is difficult to gather complete environmental information at a high resolution and to follow an adequate multispecies sampling scheme (see section 6.2.2.3). Second spatial studies superimposing external and GIS-derived environmental layers in a GIS have a high risk of error propagation. The error accumulation probably starts during data collection, when species can be misobserved, grazed, not yet in flower, or simply not present at the time the *relevé* is made. Third, the possibility of coexistence of species with similar niches, and thus the existence of processes of competition and nonuniform seed dispersal (Shmida and Ellner 1984), adds another error component to species distribution.

However, we still believe that increasing the spatial resolution to one meter and using the most powerful global positioning systems (GPS), now reaching an accuracy of one centimeter, to locate the sampling points in the study area should greatly enhance the models—one aim of the second stage of our project.

6.2.5 Deriving Climate Change Impact Scenarios

Deriving accurate climate change impact scenarios for alpine regions requires two main products: a good climate change scenario, reliable at the local scales used for modeling, and the ecological model itself, including the same driving variables (which should be physiologically meaningful for the species) as predicted by the climate change model. However, good climate models at the local scale are not yet available. Predictions for some locations are derived by downscaling procedures (Gyalistras et al. 1994; Wanner and Beniston 1995), but their results cannot yet be extrapolated to the local spatial scale. Thus, provisional climate change impact scenarios for this study were simply built by including mean annual temperature in the model as a function of elevation and calibrated from actual field measurements. The two climate change scenarios considered (CC1 and CC2) (obtained from Gyalistras and Fischlin 1995, chap. 4) did not include any precipitation change, likewise because of lack of availability and accuracy of precipitation change scenarios and the difficulty of introducing such changes into the snow index used in the model (instead of precipitation). They were

• *CC1:* a mean annual temperature change of +1.5°C; downscaled climate under ECHAM1/LSG 2 × CO_2 (344 to 720 ppmv; Cubasch et al. 1992; see chapter 4), and

• *CC2:* a mean annual temperature change of +3.0°C; downscaled climate under CCC GCMII 2 × CO_2 (Boer, McFarlane, and Lazare 1992).

The predicted probabilities of finding the species were then divided into five categories of prediction: A (absent), I (improbable), P (probable), V (very probable) and S (sure). Table 6.1 gives the number of sites falling into each category (over a total of 32,000 sites).

Table 6.1 Results of climate change simulation on the distribution of three alpine species

Counts	Categories				
	A	I	P	V	S
Present					
cc	22,000	2,800	2,900	2,800	1,500
cs	82,00	3,100	4,800	12,800	3,100
rf	21,900	5,400	2,700	1,400	600
CC1					
cc	26,400	1,600	1,700	1,700	600
cs	10,200	4,200	5,200	9,200	3,200
rf	23,250	4,800	2,100	1,400	450
CC2					
cc	30,500	600	400	400	100
cs	19,200	2,400	2,000	4,800	3,600
rf	28,500	1,800	700	700	300
Relative differences	(percentages)				
CC1					
cc	+20.00	−42.86	−41.38	−75.00	−60.00
cs	+24.39	+35.48	+8.33	−28.13	+3.23
rf	+6.16	−11.11	−22.22	0	−25.00
CC2					
cc	+38.64	−78.57	−86.21	−85.71	−93.33
cs	+134.15	−22.58	−58.33	−62.50	+16.13
rf	+30.14	−66.67	−74.07	−50.00	−50.00

Note: cc—*Carex curvula*; cs—*Carex sempervirens*; rf—*Rhododendron ferrugineum*. The five categories of prediction are: A (absent), I (improbable), P (probable), V (very probable), and S (sure). PRESENT: present climate; CC1: +1.5°C warming; CC2: +3°C warming. Counts are number of pixels with associated probability class, estimated from a histogram of the probability maps in the GIS. The table's lower section gives precentages of changes from current levels under the two climate change scenarios and for each species.

The results (figure 6.3) clearly show that strong decreases in occurrence are to be expected for two of three species studied (excluding *Carex sempervirens*). Under both scenarios, the number of sites where *Carex curvula* is predicted to be absent increases, and those where the species is predicted to be present decreases, with a stronger decrease observed for the most probable categories. The pattern is similar for *Rhododendron ferrugineum*, although the distribution of predicted decreases is not the same within categories. For all three species, distribution declines are predicted (i.e., more sites where the species will be absent). For *C. curvula*, 20% disappearence is predicted under CC1 and 38.64% under CC2; for *C. sempervirens*, 24.39% (CC1) and 134.15% (CC2); and for *R. ferrugineum*, 6.16% (CC1) and 30.14% (CC2).

6.2.6 Discussion

Specific models were built for alpine species that assessed more particularly the species' bioclimatological space to allow the derivation of climate change impact scenarios. Driving variables were mean annual temperature, solar radiation, snow index, slope, and a class of lithology (screes). The water accumulation index and permafrost were then used as posterior filtering factors. The preliminary results from these models indicate that under both low (CC1) and middle (CC2) IPCC climate change scenarios, tremendous change could be observed in the potential distributions of species. In particular, the present range of strictly high-alpine species (see figure 6.3(a) for *Carex curvula*) could become more suitable for lower-elevation alpine species (see figure 6.3(b) for *Carex sempervirens*). Because their competitive abilities would probably be lowered, and because higher elevation becomes decreasingly suitable for vegetation establishment and growth (as greater surface area is covered by sterile screes, permanent snowy area, and permafrost), the range of high-alpine species could diminish.

However, at this stage of the discussion, we should mention some important limitations. First, the results from static modeling indicate changes in species' *potential* distribution. These potential distributions have been successfully evaluated for present situations, but no evaluation is possible for future scenarios. Because of the model's nondynamic nature, results must be considered with care. In particular, soils' reaction to climate change is very uncertain (see chapter 5). Because soils are very closely related to the establishment of new species and soils in turn developed through plant establishment, the time for which the responses are predicted could well be delayed (ecological inertia). Second, new situations could also alter competitive relationships, potentially in favor of the indigenous high-altitued species. These species sometimes form dense underground networks of roots (as observed with populations of *Carex curvula*) and might not allow invader species to establish. Third, many species in the high-alpine zone are not in a climatic climax but rather in a site-specific climax (see chapter 5 for a definition of both types of climax). This could greatly postpone their reaction to climate change. Moreover, in such sites where species can be independent from the general climate, only primary successional species can develop, thus limiting again the number of invader species that can establish themselves. Fourth, the fact that a precipitation change was, in this first step, not included in the scenario, owing to the lack of reliability of climate scenarios in alpine regions and to the difficulty in obtaining spatial distributions in such complex landscapes, also limits the results. Precipitation change should be factored in as soon as climatologists provide reliable downscaled scenarios for precipitation change in alpine landscapes.

6.3 THE DYNAMIC APPROACH: EVALUATING THE FATE OF FORESTS

Even in comparison with alpine plants (chapter 5, section 6.2), forest trees are characterized by long generation times and life spans on the order of several decades to millennia. As a result, forest ecosystems respond slowly to changing environmental conditions before reaching a new equilibrium, if they reach it at all. Thus, a static, that is, an equilibrium-based approach is inappropriate for predicting forest responses to continuously changing climatic conditions in the coming centuries. An approach is required that can simulate forest ecosystems' temporally changing (transient) behavior. In addition, forest dynamics' large timescales hinder an empirical approach; experiments studying the responses of entire forests are exorbitantly expensive and limited in scope.

Dynamic forest models are appropriate tools to overcome these problems. They can integrate knowledge about forest ecosystems and simulate both transient and equilibrium behavior of the forests.
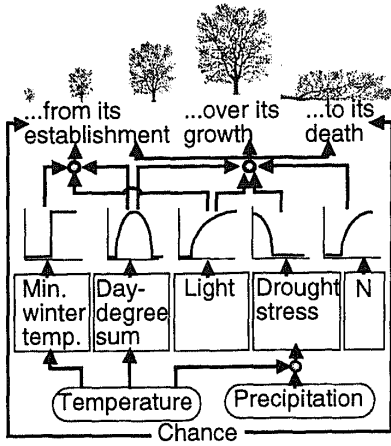
We made use of one such dynamic forest model, FORCLIM (Bugmann 1994, 1996; Fischlin, Bugmann, and Gyalistras 1995), which we briefly present here. Methods and problems of model validation, as well as case studies of quantitative assessments of possible forest responses to climate change scenarios, are demonstrated by means of this model.
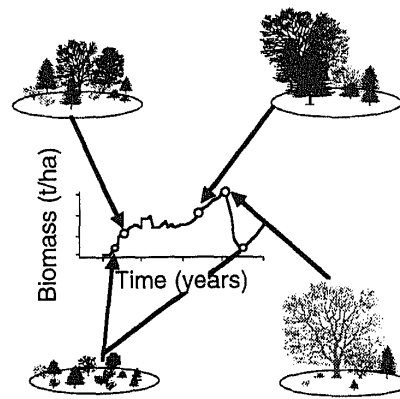
6.3.1 The Forest Model FORCLIM

The model FORCLIM focuses on trees, neglecting other biota found in forests. Trees dominate the ecosystem "forest" in two respects. First, trees (in general, not species specific) strongly influence the other biota, for example, by shading and microclimatological effects, whereas the feedback from other biota to the trees is much smaller. Second, forest trees are more important for carbon sequestration (or fixing), both at a local and global level (see chapter 5), than nontree components of the ecosystem.

FORCLIM is a patch model, that is, it simulates the fate of individual age classes of trees, called cohorts, (panels (a) and (b) of figure 6.4) within small (1/12 ha) patches by mimicking establishment, growth, and death processes. The growth submodel is deterministic; the growth rate depends nonlinearly on environmental conditions (panel (a) of figure 6.4), such as the yearly day-degree sum; nitrogen; light, which is controlled by the shading of the trees; and drought, which is affected by monthly temperatures and precipitation. Climate input fluctuates stochastically around mean values. Establishment and death are formulated as stochastic processes, with mortality influenced by the same abiotic factors as growth, and with establishment depending on minimum winter temperature, yearly day-degree sum and light availability on the forest floor. Other abiotic forcing factors such as forest fires or flooding, which in the Alpine region play only a minor role, are implicitly included
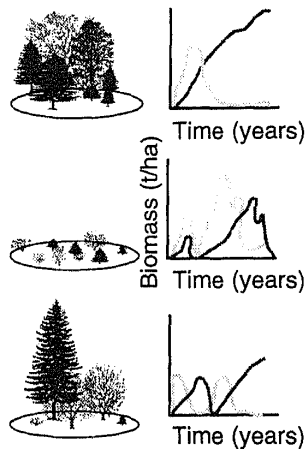
a) FORCLIM simulates the stochastic, climate-dependent fate of each individual tree...

...from its establishment ...over its growth ...to its death

Min. winter temp. | Day-degree sum | Light | Drought stress | N

Temperature Precipitation
Chance

b) The dynamics of the trees on one small patch are determined by the individuals and their competition.

Biomass (t/ha)
Time (years)

c) Many patches...

Biomass (t/ha)
Time (years)
Time (years)
Time (years)

...form the forest

...and determine its dynamics.

Biomass (t/ha)
800
600
400
200
0
0   400   800   1200
Time (years)

Ulmus glabra
Quercus robur
Quercus petraea
Populus nigra
Fraxinus excelsior
Fagus silvatica
Castanea sativa
Betula pendula
Acer pseudoplatanus
Acer platanoides
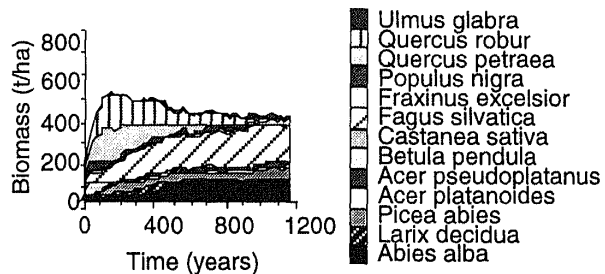Picea abies
Larix decidua
Abies alba

Figure 6.4 Principal functioning of the forest model FORCLIM (Bugmann 1994; Bugmann 1996; Fischlin, Bugmann, and Gyalistras 1995): (a) Climatic parameters drive a weather generator, which is used to determine values of bioclimatic variables. Species-specific functions of response to environmental factors (only qualitative shape is shown) influence process rates of individual trees living on a small patch (1/12 ha). (b) Because the model is stochastic, its behavior over 1,200 years needs to be sampled repeatedly (Monte Carlo simulation). (c, left) In this study, we always sampled 200 patches and used mean abundances to describe the changes in species compositions (c, right).

in the stochastic mortality rate. Seeds of all tree species are assumed always to be present. Genetic adaptation is not taken into account, partly because of trees' long generation times, which render an adaptation by mutation and selection improbable, and partly because information about intraspecific genotypic variability is lacking. Given the site characteristics such as climate parameters and field capacity, FORCLIM is typically used to estimate the average temporal evolution of a forest (panel (c) of figure 6.4) by simulating 200 forest patches for 1,200 years using a Monte Carlo simulation. Typically, such simulation averages reach a quasi-stationary state (equilibrium) after about 1,000 years (Bugmann and Fischlin 1992). As the input data for forest patch models describe the characteristics of a single specific site, these models act at the local scale. Covering larger heterogeneous areas requires a large number of simulations.

6.3.2 Validation in the Present and in the Past

Prior to its application, a model as complex as FORCLIM should be evaluated (figure 6.5) for its ability to predict a set of observations independent of those used for structuring the model and estimating its parameters. Two sources of independent data are required: first, a record of the input data the model requires (e.g., temperature and rainfall parameters), and second, measurements of those variables that the model calculates (e.g., plant species composition). Then the measured variables can be compared quantitatively with the calculated ones.

Model validation, or at least plausibility tests, should be performed for a range of conditions (for example, for the climatic input) similar to the range of conditions expected for the planned model application to test not only the model's precision but also its general applicability. For a climate-driven forest model like FORCLIM, such a range of conditions may be defined by climate gradients in space (validation at different locations in the present, panel (a) of figure 6.5) and time (paleoecological validation, panel (b) of figure 6.5).

Data used to evaluate dynamic forest models may come from many sources. There exists a potential wealth of observations on past and current forests, such as yield tables, forest inventories, long-term data from permanent plots, tree ring chronologies, pollen records, remote sensing data, and phytosociological *relevés*. However, most of these data either do not cover a long time span (e.g., forest inventory and remote sensing data), lack the temporal aspect (e.g., phytosociological descriptions), or are available at only a small number of sites and do not adequately cover climate gradients (e.g., permanent plots, tree ring chronologies, and pollen records).

Therefore, the validation must rely on a combination of several data sources. Two, phytosociological descriptions and pollen data, are used below to illustrate the potential benefits and pitfalls of validating a complex ecosystem model such as FORCLIM.
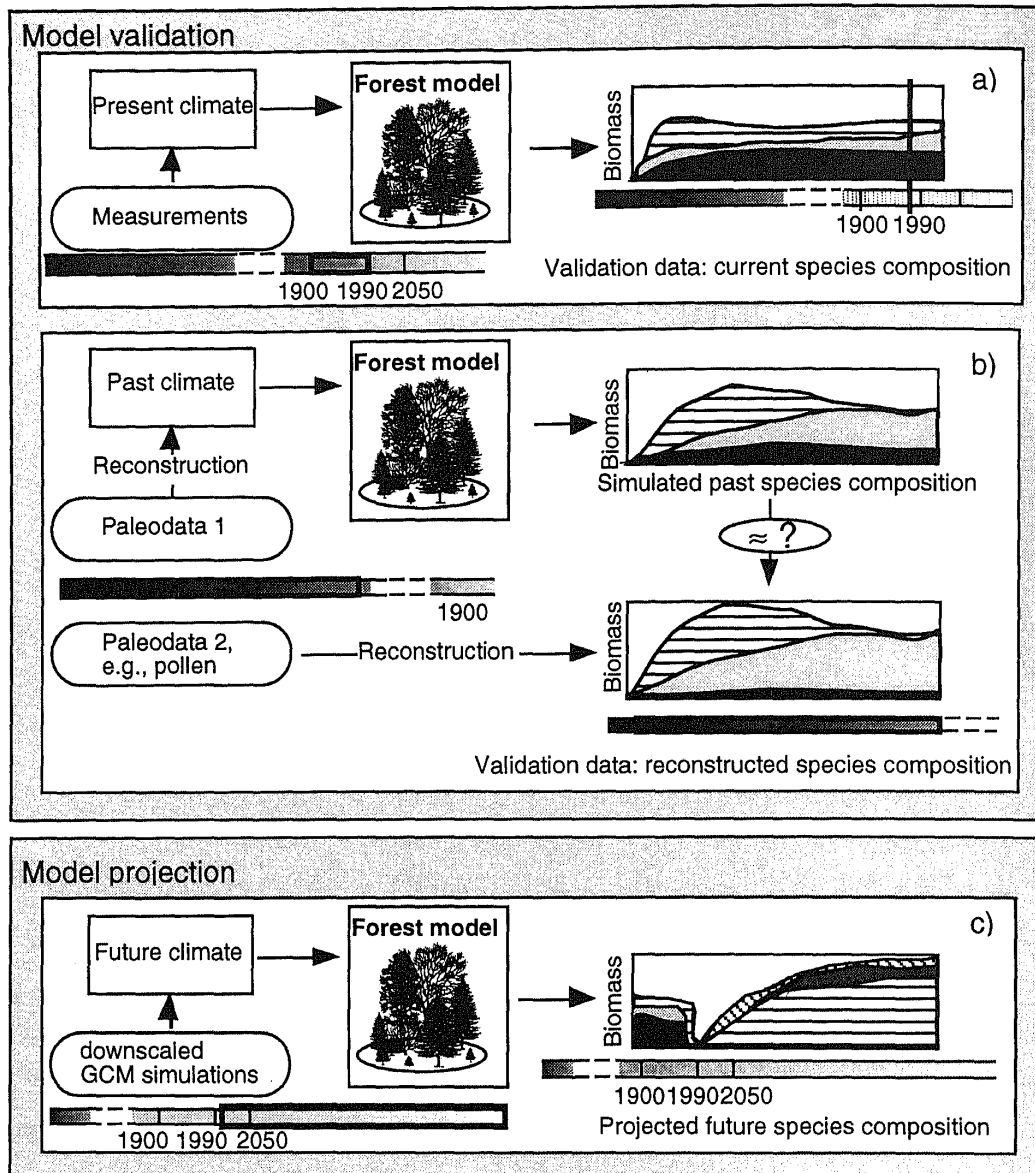
Figure 6.5 (a) Validation with present data: The forest model is validated with today's climate as input by comparing the equilibrium species distribution with that of modern forests. (b) Paleoecological validation: The model's transient behavior must be validated with past data. Here both climate input and comparison data are reconstructed from paleodata, such as ice cores and pollen data. (c) Model application: The model aims to project the impact of a future climate change as derived from GCM simulations. The black frames and the black vertical line in (a) indicate the time window of data and simulation.

6.3.2.1 Data from the Present FORCLIM's behavior was tested along transects through the European Alps and through eastern North America. The required input data were monthly expected values, standard deviations, and cross correlations of temperature and rainfall for climate parameters, and species-specific parameter values (e.g., maximum height or shading tolerance) of the most abundant tree species in the respective subcontinents. In most cases, the simulated equilibrium species compositions and the total above-

ground biomass along the transects corresponded to the observed near-natural forests (Bugmann 1994; Bugmann and Solomon 1995).

However, this kind of model validation presents several difficulties. In the first place, the simulations do not include natural disturbances such as fire and windstorms, although these effects introduce additional stochastic variability that can strongly shape natural vegetation. Second, most of the forests in the simulated regions are at best near-natural; that is, they have been more or less intensively managed during the last 1,000 years. Thus, the simulated natural species' composition rarely mirrors that observed in today's landscape. Third, it is not sufficient that the simulated species' biomass and composition correspond with observed data in an equilibrium state. To study the impacts of transient climate change, it is also necessary to assess the model's transient (i.e. time-dependent) behavior.

6.3.2.2 Paleoecological Data
Validating a dynamic forest model's transient behavior requires long time series of input data and independent validation data from natural forests. Both can be obtained from paleoecological proxy data sources (figure 6.5b). However, these data must meet certain requirements that can be problematic to fulfill.

First, no direct data source exists for the required temperature and precipitation variables. Instead, these data have to be reconstructed (e.g., from ice core or lake level data; see chapter 3), usually by using another model. Such data reconstruction models may contain errors of their own and have limited precision (Bradley 1991). Moreover, the reconstruction's temporal resolution is often restricted to annual or seasonal values, and it is therefore not possible to reconstruct the full annual cycle (Guiot, Harrison, and Prentice 1993). Hence, to arrive at a resolution of monthly intervals, it is necessary to make additional assumptions, which add to the uncertainties of the reconstruction itself.

Second, forest patch models simulate the abundance or biomass of tree species. Information about such variables in the distant past must be derived from proxy data (e.g., pollen found in lake or peat bog sediments). Pollen data usually are converted into relative biomass per tree species using the Iversen factors (Faegri and Iversen 1975; Lotter and Kienast 1992), which only estimate roughly the amount of pollen deposited per unit tree biomass.

Third, the reconstructed temporal sequence of data must be mapped onto the ecosystem model's time axis. However, the dating of proxy records may be inaccurate or biased because of coarse temporal resolution in the record as well as uneven sedimentation rates. Thus, differences between proxy data and model output are difficult to interpret, because they may stem from a system-intrinsic time lag or a dating error.

Finally, the pollen accumulated in lake sediments represents the plants of at least a whole catchment area. However, catchments are not homogenous. Therefore, a given pollen record represents the differential contributions of different areas within the catchment, each with their distinct site characteristics (in, for example, soil water-holding capacity, slope, aspect, and climate)

and hence forest types. A forest model like FORCLIM, however, simulates a forest only at one particular site with a well-defined set of specific characteristics. Therefore, the site characteristics used in the simulation are implicitly assumed to represent a mixture of all the sites within the whole pollen source area.

In general, at least three models with all their inherent uncertainties are involved in paleoecological validation of an ecosystem model: the ecosystem model itself and two auxiliary models to convert proxy data into the form needed for input and comparison data. Together with the uncertainty of dating and of the pollen source area, these issues complicate the validation of a model using paleoecological data.

6.3.2.3 Pollen Data from Soppensee
To compare tree species succession as simulated by the forest patch model FORECE with documented pollen sequences, Lotter and Kienast (1992) used an annually layered pollen stratigraphy from Soppensee (Swiss Plateau, elevation 596 m) covering about 4,000 years of the early Holocene (Lotter 1989; panel (a) of figure 6.6). We repeated this experiment by using the model FORCLIM to illustrate the potential and the limitations associated with such a study (Bonan and Hayden 1990; Solomon et al. 1980; Solomon and Tharp 1985; Solomon, West, and Solomon 1981).

An optimal scenario to be used as climate input in such a study should yield reliable information about the transient climate in a high temporal and spatial resolution (e.g., seasonal values at the specific study site). Additionally, it should be as much as possible independent from pollen data. However, since no data were available to fulfill all these requirements one at a time, we had to rely on a compromise consisting of transient, nearly pollen-independent, seasonal temperature and precipitation anomalies in small to medium temporal and spatial resolution.

The scenario used was based on the current climate at Huttwil (SMA 1901–90) near Soppensee, assuming that anomalies in annual precipitation and seasonal temperatures changed over the entire simulation period (table 6.2). It was constructed from temperature anomalies obtained by GCM simulations for the Holocene (Huntley and Prentice 1993) with the Community Climate Model (Kutzbach and Guetter 1988) and from precipitation anomalies reconstructed by Guiot, Harrison, and Prentice (1993) based on Holocene pollen and lake level data. Furthermore, we assumed a mesic soil with a field capacity of 30 cm water (Bugmann 1994). The simulation was run for 4,000 years, and the pollen record was assumed to start around 10,000 BP.

Although the GCM simulations used must be interpreted with caution and their spatial and temporal resolution was coarse (about 500 km and 3,000 years), we got an indication of transient seasonal temperature anomalies, which were obtained independently from pollen data. The precipitation scenario in turn was originally derived from pollen data but corrected with data about Holocene lake levels and can therefore be considered more or less in-
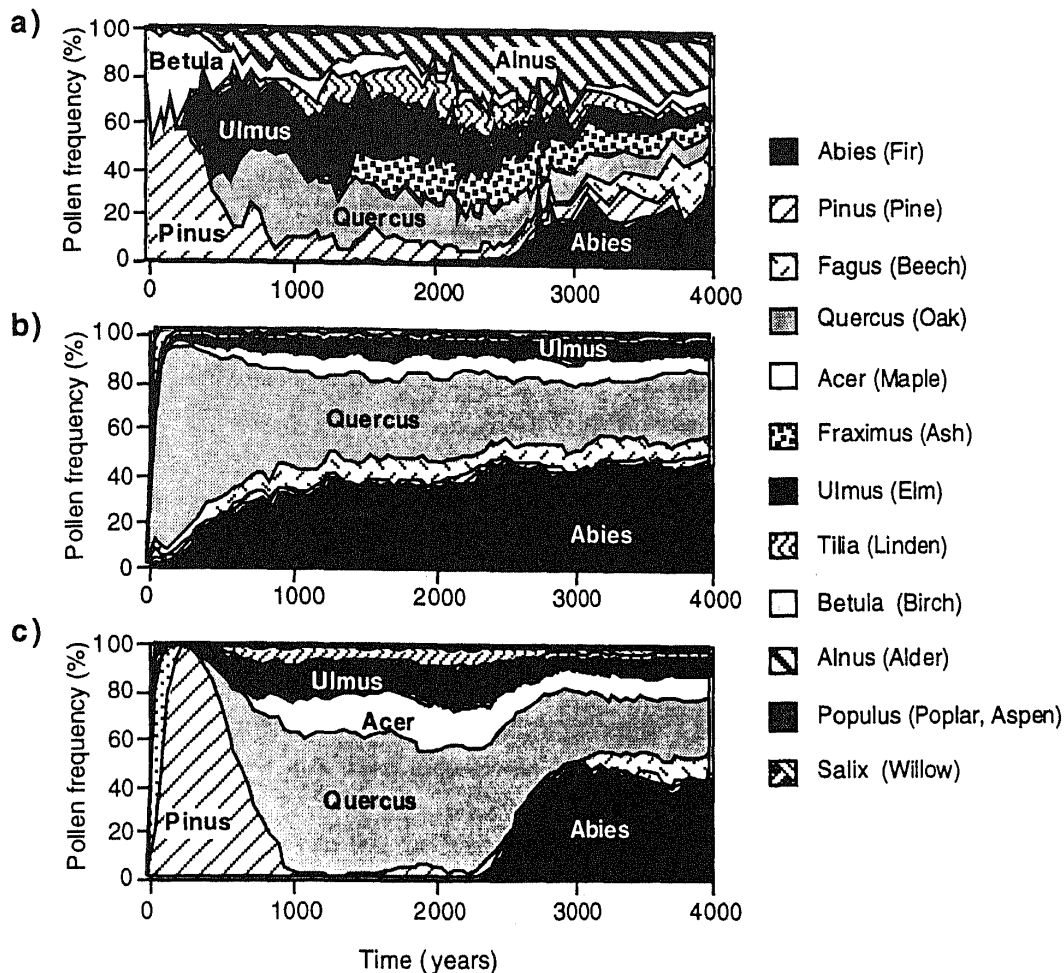
Figure 6.6 Comparison of the 4,000-year pollen record (a) reconstructed from a stratigraphy from Soppensee and (b and c) redrawn from (Lotter and Kienast 1992) with the vegetation simulated by FORCLIM (Bugmann 1994, 1996; Fischlin, Bugmann, and Gyalistras 1995) during 4,000 years. Climate input scenario (table 6.2): Seasonally varying and transient temperature anomalies and negative precipitation anomalies. (b) All species assumed present from start of simulation. (c) All species assumed to be present when reaching more than 1 percent in the pollen record. In all cases, the pollen sum includes only arboreal pollen without *Corylus*. The biomass values simulated by FORCLIM were converted to pollen frequencies using inverted pollen representation factors (Faegri and Iversen 1975) and summed to genera.

Table 6.2 Paleoclimate scenario used for paleovalidation of FORCLIM

Time (years BP)	Temperature anomaly (°C)		Precipitation anomaly (cm/month)
	Winter	Summer	
10,000	−1.17	1	−3.33
9,000	0	2	−3.33
6,000	−2	1	−0.83

Note: The scenario is obtained by interpolation between the given anomaly values. After 6,000 BP, climate was assumed to remain constant. Temperature anomalies are from Huntley and Prentice (1993) and Kutzbach and Guetter (1998), and precipitation anomalies from Guiot, Harrison, and Prentice (1993).

Vegetation Responses to Climate Change in the Alps: Modeling Studies

dependent from pollen. Futhermore it was available at a spatial resolution of one degree. The simulated species-specific biomass values were converted to pollen percentages using inverted Iversen factors of pollen representation (Lotter and Kienast 1992) and summed to genera.

The first simulation studies based on the above experimental setup (panel (b) of figure 6.6) yielded a forest dominated by species of the genera *Quercus* (oak) and *Abies* (fir) toward the end of the first 1,000 years, sharply different from the known pollen record. Thus, the model cannot explain the pattern found in the pollen record under the given paleoclimate scenario.

In the following, we tried to evaluate the influence of another boundary condition. To a certain degree, the pollen record reflects the immigration history of tree species into the Swiss Plateau after the last Pleistocene glaciation; for example, *Abies* appears rather late in the pollen record. Such a late arrival of tree species at the pollen source area might have resulted from insufficient migration rates, or from long distances between glacial refugia and available sites for colonization or from geographic or climatic barriers between them, such as high mountain ranges. Therefore, the subsequent simulation assumed that the complete absence of a genus in the pollen diagram was due not to competition, but to delayed immigration. This was simulated by allowing the tree species to establish only after they had attained more than 1 percent in the pollen record.

The results of these simulations (panel (c) of figure 6.6) show a more satisfactory agreement with the pollen record (panel (a) of figure 6.6). The model simulates the transition from the early *Betula-Pinus* birch-pine forest (years 0–500) to a *Quercus-Ulmus* (oak-elm) forest (years 500–2,700) followed by a mixed deciduous forest where *Abies* becomes important as well as *Fagus* (beech) (years 2,700–4,000). Major quantitative discrepancies are an overrepresentation of the pollen percentage of *Quercus* and *Acer* (maple) and an underestimation of the pollen percentage of *Tilia* (linden), *Fraxinus* (ash), and *Alnus* (alder).

The fact that in the simulation the region was regarded as uniform with regard to field capacity, where a mean value was used throughout the region, which favors species adapted to this mean field capacity, may explain the remaining differences between model results and observations from the pollen record. From present conditions we must assume that the pollen source area consisted of various soil types, including very wet soils, where flood-resistant species such as *Alnus* and *Fraxinus* probably had a competitive advantage. Furthermore, the simple empirical model for pollen-to-biomass conversion can lead to deviations, because a relatively small change in the pollen representation factors can dramatically change the relative values of the pollen record.

Inferring the time of species immigration from the pollen record violates the requirement that the input data be independent of data used to evaluate model behavior. However, at least for *Abies* and *Fagus*, we can assess from the pollen maps of Huntley and Birks (1983) that in actuality their absence is

probably due to delayed immigration. For example, presumably the high elevations of the central Alps formed both a topographic and a climatic barrier for the immigration of *Abies* from its glacial refuge in northern Italy. Finally, it would be desirable to estimate the points in time when species immigrated by the explicit modeling of tree migration. By taking into account the climatic conditions on the migrational path, the specific reasons for delayed immigration could be evaluated.

For other species, such as *Quercus*, the pollen maps do not support the hypothesis of delayed immigration; their premature appearance in the first simulation can be attributed to uncertainties in the climate input scenario, which was derived from GCM simulations on a coarse scale, or in the dating of the pollen record as well as to uncertainties in the model.

Therefore, the validation of the model's transient behavior can be judged neither successful nor unsuccessful unless the uncertainties in the input scenario or the boundary conditions can be narrowed. One approach for further validation could be to determine a plausible set of input scenarios and boundary conditions with which the simulation matches pollen proxy data at one specific site, then to validate the model with data from other sites, using this specific set.

6.3.2.4 Potential and Pitfalls of Model Validation Evaluating the performance of dynamic forest models requires a combination of approaches that test models' transient and equilibrium behavior under a range of conditions. From the case study of model validation using the Soppensee pollen proxy data, we conclude that paleoecological validation of forest ecosystem models has potential but also limitations.

Paleoecological proxy data offer time series of adequate length of unmanaged forest dynamics and mirror forest changes under a climate that was fluctuating at various rates, thereby increasing our confidence that the model behaves realistically under scenarios of future climate change. However, a paleoecological model validation has several limitations. First, it requires a high quality, highly resolved and independent record of past climatic input conditions. Such data will potentially be available soon (cf. chapter 3). Second, a number of uncertainties are introduced in addition to the potential errors in the ecosystem model. To reduce these uncertainties, further ecological models are needed: a process-oriented model of pollen production, transport, and sedimentation is required that could replace the transfer functions often used to reconstruct past vegetation compositions. In addition, models of tree migration are needed, because migration potentially plays a key role in transient forest responses to climate change, especially during phases of extreme climate change such as at the end of the last glacial period, and as is projected for the next century.

6.3.3 Responses to Future Climates: Surprises and Inertia

The Soppensee case study indicates that a final validation of the model's transient behavior is still problematic. However, even with this remaining uncertainty, simulations with a dynamic model such as FORCLIM are still useful for projecting transient forest responses under climate change (if one keeps in mind this uncertainty), in particular because such models are the only ones available for this purpose. FORCLIM makes it possible to study forests' sensitivity at various sites to an identical climate change scenario and to examine the the variability's effect within climate change scenarios.

6.3.3.1 Different Responses at Different Sites For several sites at a range of altitudes, we used the site-specific monthly temperature and precipitation anomalies obtained from semiempirical downscaling of transient GCM simulations (cf. chapter 4, Gyalistras et al. 1994) as input data for simulations with FORCLIM. These scenarios were derived from the same GCM simulations (Cubasch et al. 1992) and based on the IPCC "Business-as-Usual" CO_2 scenario A (Houghton, Jenkins, and Ephraums 1990). The simulations were run for 1,000 years with present climatic conditions to allow the simulated forests to reach an equilibrium state. The climate then was assumed to change instantaneously in 2080 and held constant afterward. The simulated forests were again allowed to adapt to the new climatic conditions for 1,000 years to assess the new equilibrium vegetation (Bugmann and Fischlin 1994).

These step response simulations demonstrated that a large range of possible responses can be expected from the same projected global climate change depending on the climatic characteristics of the site and the forests simulated for present conditions (figure 6.7). At midaltitudes, represented by the simulations for Bern, on the periphery of the Alps, the forest appears to be well buffered against the projected climatic changes, because the model predicts no extreme changes in species composition (panel (b) of figure 6.7). However, at high altitudes, such as at Bever in the central Alps, the model predicts that the species composition responds strongly (panel (a) of figure 6.7). A forest similar to those currently found in the montane zone would replace the subalpine forest simulated for the present, thereby reflecting an altitudinal shift of the forest belts. These predicted changes are drastic, and the associated transient forest diebacks might cause problems ranging from soil erosion to slope destabilization in vulnerable areas. Finally, the model predicts surprisingly strong responses at the low altitude site of Sion (panel (c) of figure 6.7) in a central part of the Alps, where none of the tree species present in the model would survive. Here the projected warming in combination with a relatively small change in the precipitation regime so increase the water pressure deficit in the simulation that an enduring drought stress prevented the survival of all trees (Fischlin, Bugmann, and Gyalistras 1995).
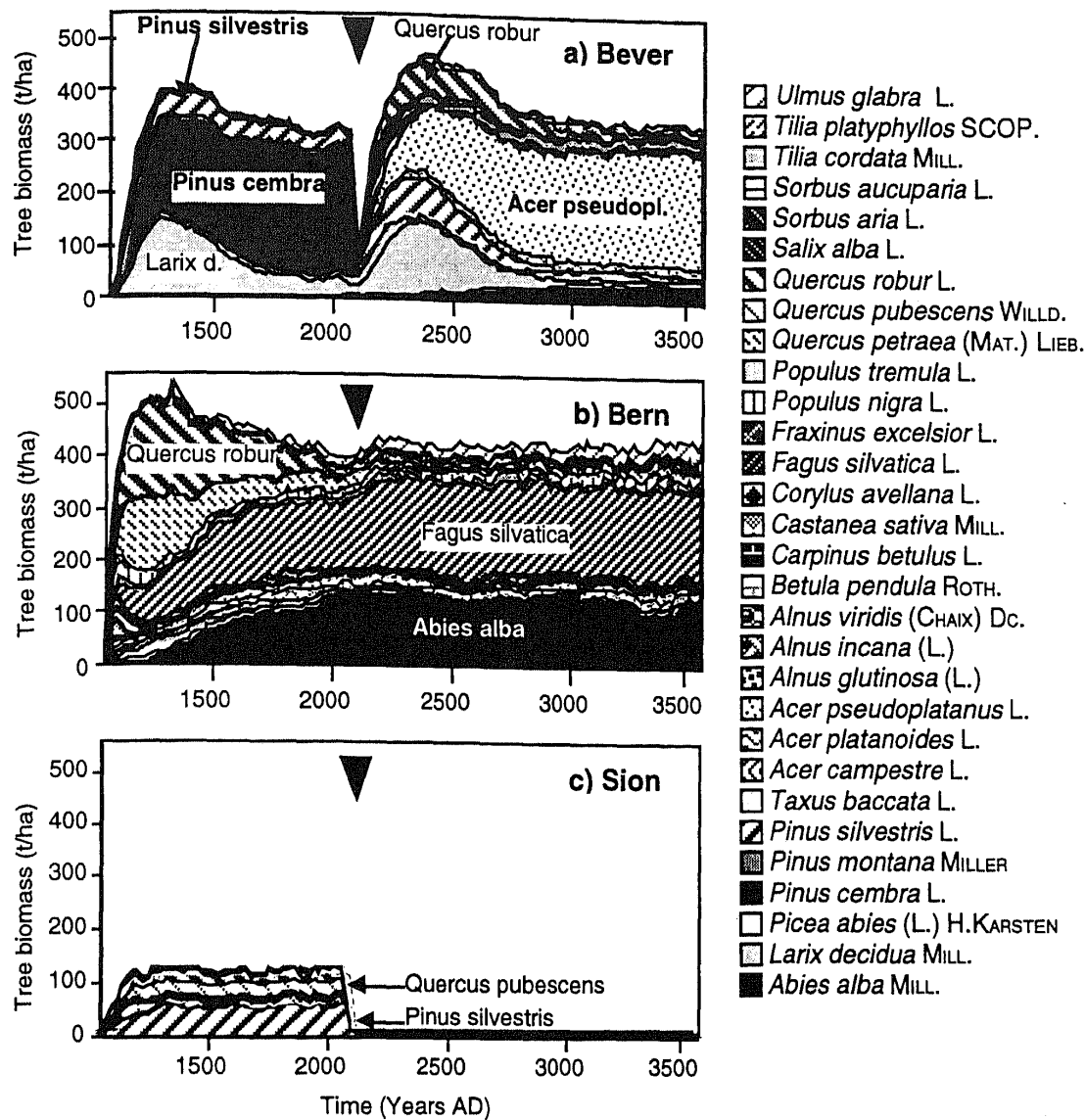
Figure 6.7 Projected step responses of forests at selected sites in the Alps to a climatic change as downscaled separately for each month from a transient IPCC Business as Usual GCM run (Gyalistras and Fischlin 1995, Gyalistras et al. 1994) for the year 2080. All simulations were made with the forest model FORCLIM (Bugmann 1994, 1996; Fischlin, Bugmann, and Gyalistras 1995) assuming the climate remains constant after the year of climate change (step at arrow). (For common English names of genera, see figure 6.6.)

6.3.3.2 Sensitivity of FORCLIM to Different Climate Scenarios

The chain of assumptions, methods, and models used to obtain regionally differentiated climate change scenarios contains many uncertainties. Principal sources of uncertainty range from CO_2 emission scenarios over GCM simulations to the downscaling of their results to the regional scale.

We tested the effect of these uncertainties on the forest model's behavior by simulating step responses for a set of climate scenarios at Bever (figure 6.8). All simulations were run with ECHAM-GCM results (Cubasch et al.
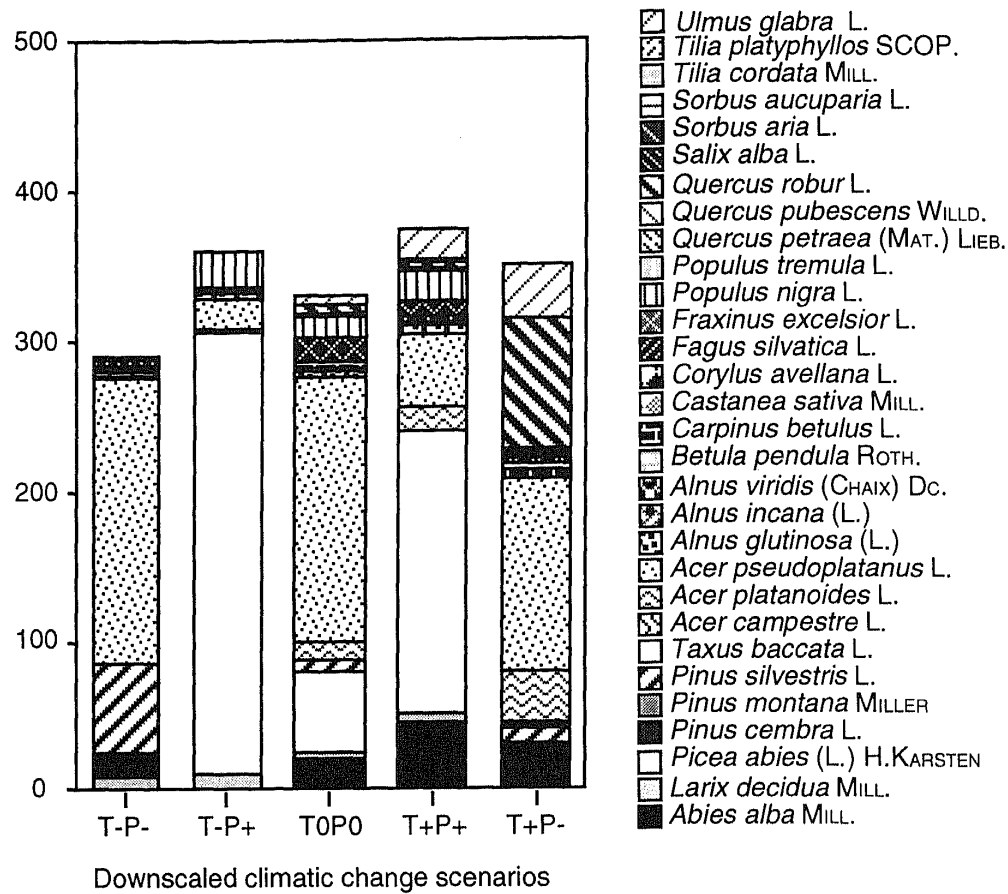
```
500 ┬

400 ┤

300 ┤

200 ┤

100 ┤

  0 ┴───┬────┬────┬────┬────┬──
      T-P-  T-P+  T0P0  T+P+  T+P-
```

Legend:

▨ *Ulmus glabra* L.
▨ *Tilia platyphyllos* SCOP.
▧ *Tilia cordata* MILL.
▤ *Sorbus aucuparia* L.
▨ *Sorbus aria* L.
▨ *Salix alba* L.
◪ *Quercus robur* L.
◪ *Quercus pubescens* WILLD.
▨ *Quercus petraea* (MAT.) LIEB.
▨ *Populus tremula* L.
▥ *Populus nigra* L.
▨ *Fraxinus excelsior* L.
▨ *Fagus silvatica* L.
◪ *Corylus avellana* L.
▨ *Castanea sativa* MILL.
▨ *Carpinus betulus* L.
▧ *Betula pendula* ROTH.
▨ *Alnus viridis* (CHAIX) DC.
▨ *Alnus incana* (L.)
▨ *Alnus glutinosa* (L.)
▨ *Acer pseudoplatanus* L.
▨ *Acer platanoides* L.
▨ *Acer campestre* L.
□ *Taxus baccata* L.
◪ *Pinus silvestris* L.
▨ *Pinus montana* MILLER
■ *Pinus cembra* L.
□ *Picea abies* (L.) H.KARSTEN
▨ *Larix decidua* MILL.
■ *Abies alba* MILL.

Downscaled climatic change scenarios

Figure 6.8 Simulated sensitivity of species compositions at equilibrium to uncertainties within the climatic change scenarios. All climate anomalies wree downscaled (Gyalistras et al. 1994, Gyalistras and Fischlin 1995) separately for winter and summer from the ECHAM-GCM (Cubasch et al. 1992) simulations based on the transient IPCC Business as Usual global CO_2-emission scenario A (Houghton, Jenkins, and Ephraums 1990) for 2080. Simulations were made with the ecosystem model FORCLIM (Bugmann 1994, 1996; Fischlin, Bugmann, and Gyalistras 1995). T—Temperature; P—Precipitation; TøPø—Best estimate; T−P−, T+P+—respectively, the minimal and maximal estimated changes (95 percent confidence intervals). (T—Temperature, P—Precipitation; TøPø—Best estimate, T−P−, T+P+—respectively the minimal and maximal estimated changes, *T−P+ and T+P− the combinations of minimal temperature and maximal precipitation change and vice versa* (95% confidence intervals). (For common English names of genera, see figure. 6.6.)

1992) which were based on the IPCC "Business-as-Usual" global CO_2-emission scenario (Houghton, Jenkins, and Ephraums 1990) and downscaled separately for winter and summer half year to the Bever site (Gyalistras et al. 1994). We show only the simulated species composition at equilibrium. The center represents the best estimate TøPø obtained by the downscaling procedure for the changes in temperature (T) and precipitation (P). The left and the right sides represent, respectively, lower estimates (T−P−, T− P+) and higher estimates (T+P+, T+P−) for temperature, where T+ and P+ represent the upper estimated limits of the 95 percent confidence interval and T− and P− the lower limits. This study reveals that forests in the Alps, such as

the subalpine forest at Bever, may show strongly differing responses depending on which climate change scenario is assumed.

6.4 CONCLUSIONS

Ecosystems are highly complex (see chapter 5), which renders a simple, direct extrapolation of their behavior to future climatic conditions impossible, even if deterministic predictions of climate were possible. For the same reason, and because of the slow reaction times and high inertia of forest and alpine ecosystems, it is likewise difficult to learn experimentally about their responses. In this situation models are indispensable, despite all their drawbacks, especially when we attempt to assess the ecosystems' future behavior under a changing climate. Two models have been presented: a static, equilibrium-based distribution model for high-alpine plant species and a dynamic succession model for montane forests.

Because no model can capture the full complexity of the system it simulates, both models focus on a limited number of key components and features of the ecosystems at the expense of others. The forest model simulates the dynamics of dominant tree species at single sites, neglecting other forest species. The climate input variables of temperature and precipitation drive the forest model, which describes the processes determining the dynamics of forests such as climate-dependent stochastic tree growth or death. In turn, whereas the static, equilibrium-based, alpine plant species model can take into account many species, including rare ones, in an entire area, and include more abiotic factors, it does not include information about specific processes.

The major difference between these models is in the way they treat the temporal development of the ecosystems or biological entities they model. The static alpine species distribution model considers only equilibrium or climax states of vegetation. The alpine ecosystems modeled are assumed to be currently in equilibrium. Moreover, future potential species distributions are predicted as though ecosystems could rapidly reach a new equilibrium. Although the first assumption seems justified for high-alpine meadows (i.e., "it is estimated that, without climate change, the present state of the vegetation would not evolve in a significant manner" (Galland 1982)), the second is certainly debatable, because the alpine species' dynamics tend to be gradual in any case (see, e.g., chapter 5), notwithstanding time scales for soil dynamics on the order of millennia (see section 5.2). Thus, alpine vegetation will likely not be able to reach a new equilibrium as long as climate is changing.

Therefore, such static models do not provide a specific answer to the question of how climate change would affect future species' distributions, and they must not be taken as predictions. Rather, they attempt to explore possible ranges of vegetation change and thus offer a basis for discussion about, for example, species' potential to reach new habitats. Moreover, they constitute the basic layers for future spatiotemporal vegetation models (Halpin 1994; Solomon and Leemans 1989).

The time constants of forest dynamics are so large, probably exceeding those of alpine vegetation, that here the transient behavior clearly must be simulated to assess consistently the response to a transiently changing climate in the coming centuries. The forest model's dynamic approach accomplishes this.

However, this model's dynamic nature results in comparably long simulation times, which its stochastic nature further increases. The stochastic simulations enable us to capture forests' intrinsic variability. Yet many replicates of the stochastic process must be calculated to obtain reliable results (Bugmann, Fischlin, and Kienast 1996). These long simulation times impede spatial applications at a fine resolution, which would require a prohibitive number of simulation runs.

The application of all models, particularly those developed in a particular region, to a combination of conditions outside the range used to obtain the parameter values (by model calibration, as in the static model, or from empirical and experimental studies of single processes, as in the forest model) can cause problems. The mechanistic forest model offers some hope that the formulation of its process functions will still be valid under changed conditions, although a higher uncertainty due to its larger number of parameters might outweigh this. Therefore, models should not only be calibrated but also thoroughly validated, that is, tested by comparing their results to vegetation data under a broad range of conditions of an amplitude at least similar to that expected for the next century's putative climate change.

The evaluation of the plant distribution model is mainly limited by data requirements, that is, the gathering of supplementary species abundance data and associated environmental covariates. Therefore evaluation has been possible only in a small alpine area. Because the results were satisfying within the usual range of uncertainties encountered in such studies, we anticipate extending this model to other areas. Ideally, if input data about species, climate, and other abiotic factors were available at the same fine resolution, simulations could be conducted for all alpine regions of Switzerland or even at the scale of the entire Alps and results compared to vegetation data.

Both the equilibrium and the transient behavior of the dynamic forest model need to be further tested, which requires data from gradients in space as well as in time. Paleoecological data offer promising opportunities for model validation, but at the same time they introduce new problems, such as the many incertitudes in their interpretation. In particular, problems associated with tree species migration pose an unpleasant obstacle to our process of model testing, but they also point clearly to tree species migration's potential importance to future ecosystem adjustment to climate change.

Given a thorough validation under a larger range of climatic conditions as was performed in part for the forest model and planned for the alpine plant distribution model, both models should succeed in generating more valuable scenarios of vegetation responses to a changing climate. However, the two

models presented already allow preliminary glances at future potential vegetation and at the associated uncertainties. Based on both simulations, we can draw some general and tentative conclusions for the potential responses of montane forests and alpine herbaceous species' distributions to future changes in climate.

Although some forests might profit slightly from the envisaged climate changes or would be completely unaffected, some might suffer drastically. No uniform, simple response of the mountain forests to a climatic change could be expected. Moreover, the mountain forests might prove sensitive to climatic features that remain very uncertain in the regional climate change projections. The major sensitivities were found in subalpine conditions and in areas that border on having a continental climate already, as is typical for some of the large Alpine valleys. When we contrast these findings with what we have learned about the peripheral forests at lower altitudes, we conclude that mountain forests are especially sensitive to climate change.

Both a low and a medium IPCC climate change scenario predict tremendous changes in the potential distribution of species of herbaceous and dwarf shrub alpine plants. However, these results must be interpreted very carefully, because great uncertainties remain associated with the postulate of the future equilibrium of alpine ecosystems: uncertainties in alpine soils' potential reaction to climate change (see chapter 5), in the future competitive relationships among plant species, and in the interaction of these factors. Hence, the prediction of plant species distributions mainly indicates that a changing climate would displace present locations of ecological optima and tolerance limits of plants geographically. It does not say whether plants will be able to reach and colonize new habitats or to adapt to such modifications of their present environment.

A sound assessment of alpine ecosystems' potential vulnerability beyond these first steps demands, first of all, full validation of both models. Toward this goal, the alpine plant distribution model should be calibrated using data from additional, ecologically distinct regions. Validating the forest model's transient behavior requires paleoclimatic scenarios that were reconstructed independently from past vegetation (see chapter 3).

In both models species' ability to migrate under altered climatic conditions turned out to be crucial. Many factors affect the facility of migration, such as seed dispersal capacities, climate-dependent vegetation dynamics along the path of migration, natural and human barriers, and suitability of substrates. Explicitly modelling migration as a combination of seed dispersal and climate-dependent community dynamics along the migrational path could reduce the uncertainty concerning species migration.

Another uncertainty remains concerning the plants' potential to adapt to changing conditions in ways other than migration, that is, through natural selection or through physiological and phenological adjustments or other kinds of phenotypic plasticity. These traits are currently not captured by the

presented models and would require further experimental and modeling efforts.

The responses of both alpine herbaceous or shrub vegetation and forest ecosystems for the entire Alpine region could be systematically evaluated either by covering the entire Alpine arc with a grid of point simulations or by subdividing the Alps into "representative" regions, as defined by the most frequent combinations of abiotic factors, and performing simulations for each of these regional classes only. This would require spatially highly resolved data for abiotic input variables, in particular local climatic change scenarios, such as changes in monthly temperatures, monthly precipitation, annual distribution of precipitation, or snow cover duration, such as those that other researchers within the CLEAR project are currently developing (Gyalistras et al. 1994; Wanner and Beniston 1995).

In the long term, both ecosystem modeling approaches might converge to spatially highly resolved, species-based, dynamic vegetation models. Such models would provide the necessary basis for people within the Alpine region, in particular decision makers, to assess the possible consequences of policy decisions made today, either by them or by people from other parts of the globe. Despite all their deficiencies and drawbacks, vegetation models offer indispensible means of glimpsing the possible future plant covers of the Alpine region. Of course, local as well as global environmental changes, not all covered to the same extent by a particular model, might affect vegetation. But global changes like those anticipated for climate pose a particular challenge and call strongly for means of projecting the future as precisely as possible, especially because of the intrinsic, lengthy time delays between the decisions made today and their consequences. These decisions' impact on the vegetation may lie as far as centuries into the future. A manifestation of just such "vegetational pictures" begins to emerge from efforts like those presented here.

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