Up-scaling, interpolation and extrapolation of biogeochemical and ecological processes

Models
Predictability
Space
Time
Scale discrepanties

As regional and global scales become more important to ecologists, methods must be developed for the application of fine-scale knowledge to predict coarser-scale ecosystem properties. Scaling-techniques for aggregation, up-scaling, interpolation and extrapolation all have their specific constraints and possibilities. In this paper we address scale issues in ecological and landscape ecological research with special emphasis on up-scaling.
We conclude that in ecological modelling, limitations in data and their applicability for predictive modelling are more the rule than the exception, since collecting data on fine-grain patterns that are relevant at larger scales is generally costly and time consuming. Nevertheless, ecologically sound models can be obtained at the intermediate landscape scale (c. 100-10000 km^2) if they are based on a clear understanding of the scale at which relevant processes operate and serve as a template in choosing the appropriate scale in observation and modelling.

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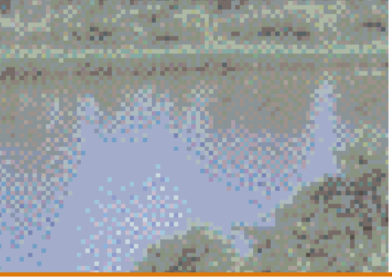
Although much progress has been made in understanding landscape processes, a thorough understanding of interactions between processes in and between landscape compartments and ecosystems is still largely lacking (Heymans *et al.*, 2002, Rietkerk *et al.*, 2002). This is partly due to discrepancies between the scales at which various processes operate, but more importantly, to discrepancies in scale regarding the questions asked, the models used and the data sources available (Gosselink & Lee, 1989). The scale of an investigation may have profound effects on the patterns one finds. Dynamic, statistical and spatial modelling are each used to integrate process information across scales. Such attempts have two directions. First, detailed studies carried out at finer scales can be integrated through dynamic models that can be used to study coarser scale processes. Typically, landscape models combine information on ecological processes with spatial information available through GIS (Arheimer & Brandt, 2000, Van den Bergh *et al.*, 2001, Pieterse *et al.*, 2002). A second approach to landscape analysis involves downscaling from studies that start at larger scales (e.g., entire river catchments) and work toward understanding relationships between geomorphology, geohydrology and land use patterns at smaller scales (see Burrough & Pfeffer, Whigham *et al.*, Mander *et al.*; this issue).

In this paper we analyse some scale issues in landscape science and we especially focus on up-scaling. After introducing some relevant definitions we address predictability in relation to space-time scaling. Next, we present three examples from the literature of scale-dependent processes each operating at a very different spatial and temporal scale. These examples are chosen to demonstrate that there are constraints in up-scaling approaches and they in fact show us that the problem of scale dependency is scale-independent. After discussing the implications of the scale of processes for data analysis and modelling we present two modelling studies: an empirical statistical model and a mechanistic model. In developing these models for up-scaling or aggregation we had to overcome several scale issues. Both approaches had their specific scale related constraints and possibilities, which may serve as general lessons. Finally, we formulate rules for application to avoid scaling errors.

Definitions

Generally speaking the scale of an object or process is its spatial or temporal dimension. In scaling studies the ability to detect patterns in space or time is a function of both the extent and the grain of an investigation (O'Neill *et al.*, 1986). *Extent* is defined generally as the overall area



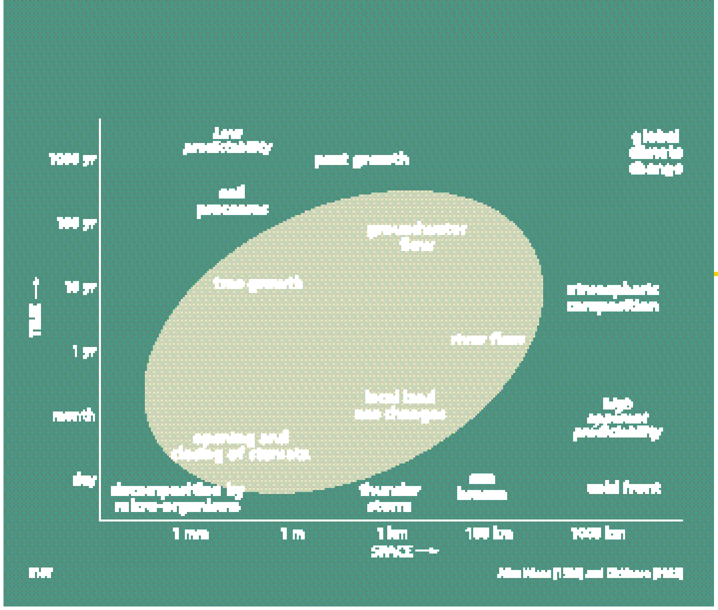
encompassed by a study or the duration of the study. *Grain or support* is the size of the individual units of observation (Wiens, 1989) and is usually the largest area or time interval for which the property of interest is considered homogeneous (Bierkens *et al.*, 2000). *Coverage* is the ratio of the sum of areas or time intervals for all support units and the extent (Bierkens *et al.*, 2000). Thus, in a spatial example coverage refers to the part of the research area that is covered by samples, and in a temporal example it implies the sum of time intervals of observations divided by the total study time. Loosely speaking, up-scaling means transferring information from a smaller scale to a larger scale. More specifically *up-scaling* or *aggregation* is defined as increasing the support of the research area or the research time. Changing the extent of the research area or research time usually involves going from a smaller to a larger extent. Increasing the extent is called *extrapolation*. Interpolation involves increasing the coverage of the research area or research time, which is in fact the reverse of sampling (Bierkens *et al.*, 2000).

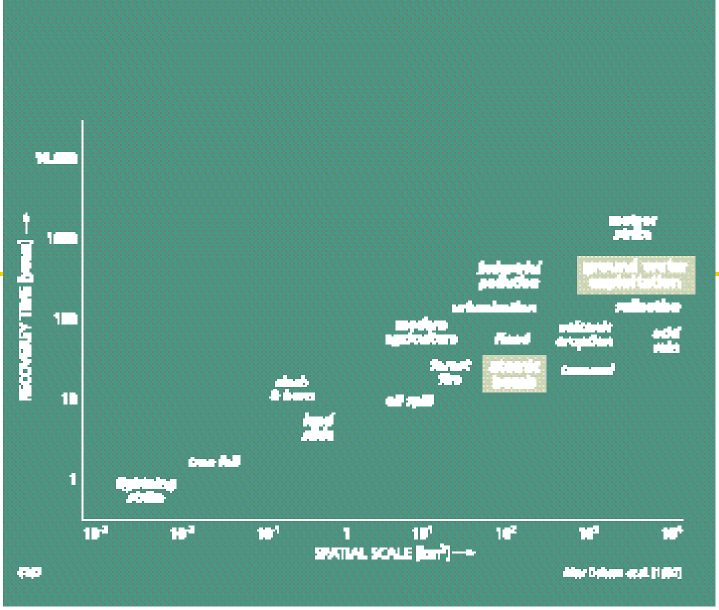
Note that MacArthur & Levins (1964) considered grain in a different way as we defined above. They defined grain as a function of how animals exploit resource patchiness in environments. The observational window of a consumer is then referred to as the grain at which a consumer perceives its habitat (O'Neill *et al.*, 1988, Milne, 1992, Ritchie, 1998). Differences in the scale of patchiness of the resource and the grain of observation by the consumer will affect the intensity of exploitation by the consumer. The size of the habitat that is covered by the consumer when searching for resource is then called the extent.

Predictability and space-time scaling

Our ability to predict ecological phenomena depends on the relationships between spatial and temporal scales of variation. Although there are no standard functions that define the appropriate units for space-time comparisons in ecology, with increased spatial scale, the time scale of important processes may also increase. This is because the relevant processes may operate at slower rates, their effects may involve time lags and their indirect effects may become increasingly important (Delcourt *et al.*, 1983, Clark, 1985). Thus, as the spatial scale of a system increases, so also may its temporal scale, although these space-time scalings differ for different systems. Studies over a long time and at a fine spatial scale have low predictive capacity at larger scales; they are simply too site-specific. Short-term studies conducted at broad spatial scales generally have a high apparent predictability but may be less capable of characterizing small-scale processes. This is pseudo-predictability since the natural dynamics of the system operate at much longer time scales than the period of study. It is as if we were to take two snapshots of a forest a few moments apart and use the first to predict the second (Wiens, 1989). The first photograph is a perfect predictor for the second, but it does not teach us anything about the relevant processes in a forest. Investigations that are designed to include a close correspondence between the time and space scales probably have the highest predictive power. In Fig. 1 we present a space-time diagram of ecological, hydrological and atmospheric processes illustrating the spatial and temporal scales that must be considered. Processes situated within the elliptic space are hypothesized to have a high predictability, whereas soil processes and peat growth are examples of processes with low predictability. Prediction of the activity of micro-decomposers or meteorological processes such as a thunderstorm event or the development of a cold front have a high apparent predictability over a wide range of scales.

In Figure 2 we depict the relationship between recovery time of events and scale (Dobson *et al.*, 1997). Remarkably,





according to these authors a groundwater system needs a longer time to recover after groundwater exploitation than it takes for a part of the land surface to recover after an atomic bomb explosion.

An important implication from Figures 1 and 2 is that the questions asked by policy makers rarely are directed to the dynamics of the system and to the means (both financially and in time) that are given to those studying these processes. Often, ecologists have been urged by resource managers to answer questions and make and test predictions on relatively short time scales (some years), regardless of the spatial scale of the investigation. Politicians are frequently only interested in time horizons related to their careers, and since most of them are not in powerful positions before their mid forties, fifteen years ahead is about the maximum time span still enabling them to harvest within their active career. Thus, policy is often based on relatively short-term studies regardless the extent of the area and the rate at which the important processes occur. Especially, predicting the effects of human interference in processes such as peat growth, groundwater flow, groundwater composition and global climate processes require long term monitoring data. In comparison, short-term studies conducted at broad spatial scales have a high apparent predictability, since the natural dynamics of the system are so much longer than the period of study.

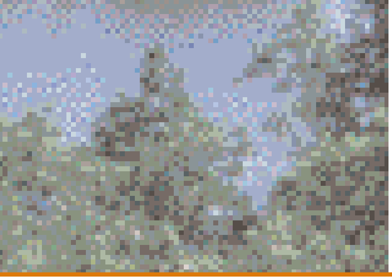
The difficulties in matching relevant scales in ecological modelling and the difficulties that they present in relating ecological information to policy decisions should be kept in mind when reading the three examples presented below. The examples illustrate that it is essential to identify the scale at which processes operate in order to design appropriate sampling schemes and perform sound analyses of data.

Figure 1. Predictability in relation to the space-time scaling of processes. (Left)

Figure 2. Recovery in relation to spatial scale. (Right)

Example 1: Denitrification in floodplains

Denitrification is the process in which micro-organisms use oxygen obtained from nitrate for their respiration. The process results in the conversion of nitrate to gaseous forms of nitrogen (primarily N_2 and N_2O) that are lost to the atmosphere. Since denitrification decreases NO_3 concentrations and produces N_2O, the concentrations of NO_3 and N_2O in groundwater should be inversely related. The absence of this relationship found in field samplings (Weller *et al.* 1994) suggests that the N_2O pool is controlled by processes in addition to denitrification. N_2O can be produced by nitrification and can both be produced and consumed by denitrification. In addition, dissolved N_2O can be carried through the soil in groundwater or lost to the atmosphere. So, instead of measuring concentrations of two variables related to the process, it makes more sense to measure the rate of N_2O emission. This can be measured in closed chambers, in which

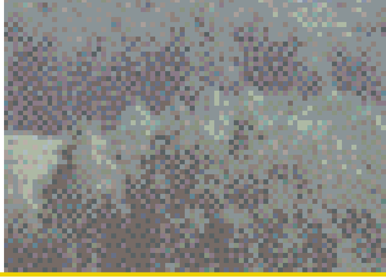


gasses emitted from the soil are measured. However closed chambers can only be used for short periods because temperature increase and gas buildup can change gas emission rates (Ryden & Rolston, 1983). Weller *et al.* (1994) used more than thirty chambers of 1x1 meter in a floodplain and did not find any obvious spatial pattern of N_2O emission rates nor any match with the pattern of N_2O or NO_3 in groundwater. Apart from N_2O emission rates being quite spatially variable, repeated measurements also showed big differences. Gas emission can also be measured using larger flow-through chambers. Larger chambers (20x1m) are more difficult to set up, but the constant flow of air minimizes temperature change and gas buildup over longer periods resulting in more useful data for monitoring emissions for days at a time (Jury *et al.*, 1982). Weller *et al.* (1994) installed two flow-through chambers in a floodplain, one on a low-lying, frequently waterlogged soil and one on a drier site. They observed a clear seasonal cycle with N_2O emission rates increasing from December to May and decreasing from September to December, paralleling seasonal temperature changes. They also observed diurnal variations in N_2O emission rates that correlated with temperature in the surface soil. The expected higher emissions in the low-lying floodplain site (having low redox status) were not observed, rather the reverse. Langeveld & Leffelaar (2002) modeled underground processes to explain N_2O profiles in the soil. Their model simulates several biological and physical processes. O_2 and CO_2 profiles were satisfactorily simulated indicating that the respiration rates used in their model were realistic. The N_2O profiles were less well simulated. They concluded that their assumption of homogeneity within soil layers was probably incorrect.

We conclude that it is hard to make realistic inferences about denitrification based on measurements that have high spatial and temporal variability. This is because it is a complex process operating on a fine scale in an environment where spatial heterogeneity of the factors influencing the process is large. This makes denitrification a difficult process to scale-up, to extrapolate and to model. Therefore generally valid estimates of NO_3 removal from groundwater by denitrification are lacking. An approach that might work for processes like denitrification is the search for so-called hot spots and hot moments, where the process is operating at a high rate (McClain *et al.*, 2003). These spots and moments probably cause the bulk of the nitrate removal in landscapes. They occur because at some points in space and time, an environmental factor that had limited the process is optimised. Denitrification requires low redox, pH>4, nitrate availability, carbon availability and a temperature higher than a critical minimum. Searching the conditions creating high rates in spatial data bases may help to identify such hot spots and moments.

Example 2: Biodiversity in ponds

Chase & Leibold (2002) tested Grime's (1979) hypothesis that local-scale species diversity first increases with slight increases of productivity, but then declines to low diversity when productivity is high. This so-called hump-shaped curve of species richness in response to productivity is supported by a wide variety of data and predictions of ecological models. This pattern is often seen in empirical studies at relatively small spatial scales (Waide *et al.*, 1999, Mittelbach *et al.*, 2001, Leibold, 1999, Dodson *et al.*, 2000). However, at regional spatial scales, species diversity often monotonically increases with increasing productivity instead of being hump-shaped (Curry & Paquin, 1987, Mittelbach *et al.*, 2001). Because studies performed at different spatial scales often consider different ecosystems and employ different methodology, it remains unclear if these relationships are scale-dependent or whether a single relationship holds across scales.



Chase & Leibold (2002) chose thirty ponds nested within ten watersheds. Each watershed had three ponds that were similar in productivity and total area. Local species richness within ponds was defined as the number of species in a pond, regional species richness as the total number of species observed in the three ponds within each watershed. At the local scale, both producer and animal species richness had a statistically significant hump-shaped relationship with primary productivity. In contrast, at the regional scale (among watersheds), species diversity linearly increased with productivity. An explanation might be that the differences in species composition among localities within regions increase with productivity. To test this hypothesis the authors calculated species dissimilarity of each watershed by quantifying the species compositional differences among the three ponds within a watershed. Species dissimilarity indeed increased with productivity; ponds within watersheds of low productivity shared the majority of their species, whereas ponds within watersheds of high productivity shared few.

Without going into the mechanisms causing these differences we may conclude that spatial scale dictates the productivity-diversity relationship. Species diversity, when viewed at different spatial scales, can respond in fundamentally different ways to the same environmental factor (productivity in the case of the ponds). Thus, straightforward up-scaling from local to regional scale is not appropriate in biodiversity studies.

Example 3: Variability in the feeding success of Sperm whales

Sperm whales (*Physeter macrocephalus*) feed on octopuses in the deep ocean at depths of 200-1000 meter. Large animals with a low reproductive rate and low mortality like the Sperm whale cannot react to environmental variation through changes in reproduction or mortality, thus they must possess mechanisms for surviving and averaging environmental variation over temporal scales less than their lifetimes and spatial scales less than their home-ranges. Whales come to the surface regularly to breath. When they dive again, their tail, the so-called fluke, is raised into the air. It is their habit to defecate at this particular moment, visible by a brown patch in the water. So the defecation rate is easy to observe and is defined as the proportion of fluke-ups at which the whale defecates.

Whitehead (1996) followed groups of Sperm whales in the Pacific and used temporal and spatial variation in defecation rates, which is a variation in feeding success, for assessing variation in octopus distribution in the deep ocean and the response of whales to this variation on a temporal and spatial scale. Mean defecation rates (per fluke-up), varied among years. When defecation rate is high (a high feeding success), the whales travel only short distances. If the variation in defecation rate is compared with the mean defecation rate, it appears that for time intervals of one day the coefficient of variation is somewhat less than the mean. For time intervals between 10 and 100 days variance is low and for intervals of years the variance is high compared to the mean.

Apparently, temporal variability in the deep ocean is dominated by features with wavelengths of years. If we look at differences in variance with distance, we see that the variance over distances of about 100 kilometers is the same as that over periods of few days: somewhat less than the mean. However, over several hundred kilometres the variance in feeding success is larger, and similar to that over time periods of several years. Over larger distances it is about the same as the mean.

What can we learn from this study in which a proxy (defecation rate of Sperm whales) is used to estimate variability in octopus distribution and density in the deep ocean? Temporal variability in the deep ocean is governed by low-frequency, inter-annual features, just as was observed in studies focusing on variability at the surface (Steele 1985). These features are found in the Pacific in the California Current, the Humboldt Current (Peru) and the Equatorial Undercurrent influenced by El-Nino effects. Spatial coherence of such phenomena is limited to scales of a few hundred kilometres. The Sperm whales anticipate this by using migration over ranges of 300-1000 kilometers as their principal strategy for surviving in an unpredictable habitat. Migration thus allows Sperm whales to survive in an environment with unforeseen periods of food shortage. In other words, migration allows them to maintain high biomass and low reproductive rates in an environment, which at any location contains long unpredictable periods of food shortage.

Implications of the scale of processes for data analysis and modelling

The three examples of processes operating at very different spatial and temporal scales illustrate that scale does matter and that it is essential to identify the scale at which processes are operating. More specifically, one needs to identify the spatial scale at which the main factors operate or are distributed: the resources or variables influencing

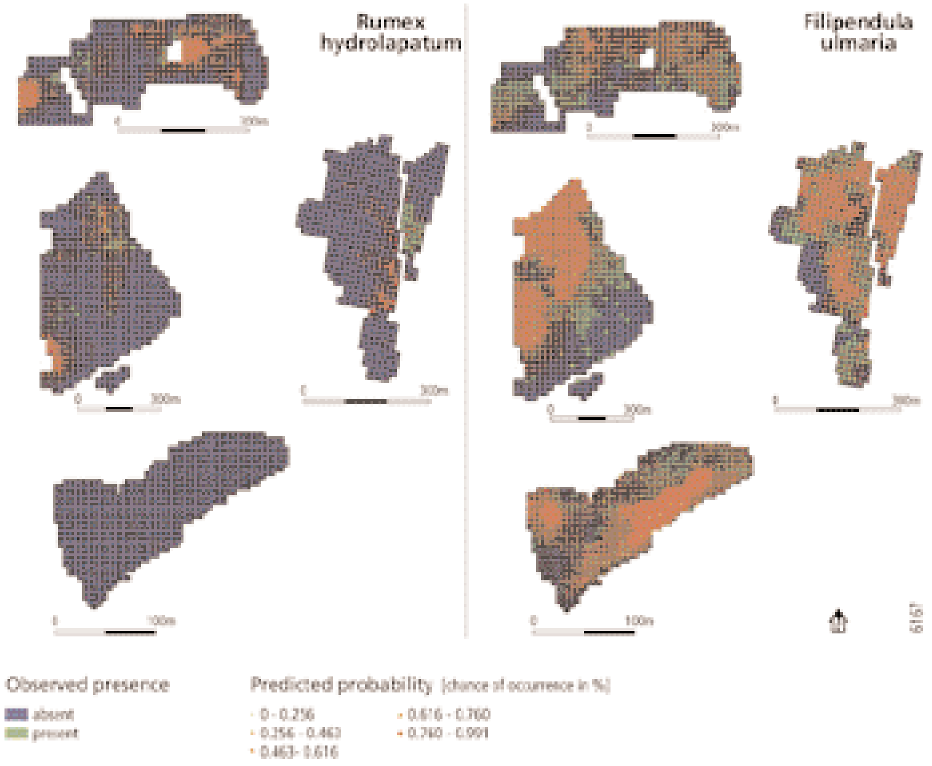


Figure 3. Performance of the empirical statistical species response model VLITORS. For 38 species the models discriminated satisfactorily between areas but poorly within areas (shown is *Rumex hydrolapathum*). For 37 species the models discriminated satisfactorily between areas and within areas (shown is *Filipendula ulmaria*). For 10 species the models discriminated poorly between areas (not shown). Dots indicate the predicted probabilities; the background color of the grid cells indicate the observed presence of the species (blue absent, green present) (after De Becker *et al.*, 2001).

them (for example temperature, the availability of water or mineral nutrients, the distribution of plant cover or prey) and the organisms consuming a certain resource (for example denitrifying micro-organisms, herbivores or predators). It is also important to identify the spatial scale at which the interaction between resource and influencing variable or consumer takes place, e.g., N-sources in the soil and redox conditions; NO_3 and denitrifying micro-organisms; plant growth and herbivores; predator and prey. Van der Koppel *et al.* (in press) provide a simple framework that explains how differences in the spatial scale at which consumers and their resources function affect food chain theory. Such a framework is useful to identify critical scale aspects and to assess the risks of anthropogenic changes for trophic interactions by interfering with their functional scales.

Both the denitrification example and the Sperm whale example also illustrated that the temporal scale at which processes are influenced can vary a lot. Denitrification is affected by temperature and redox-conditions that vary during the day and also among seasons and years. The migration of Sperm whales varied among years. The study of biodiversity in ponds supported the notion that considerable insight can be gained by increasing the scale, both spatially and temporally, in which species diversity is viewed. Straightforward up-scaling from pond studies to catchments seems inappropriate in this case, since it would lead to erroneous conclusions for biodiversity in catchments, because of the non-linearity between the local scale and the catchment scale.

In the process of up-scaling among fine-scale components (such as biodiversity in local ponds) to predict coarser-scale properties of the aggregate (biodiversity in catchments), one has to be aware whether or not the relationship between variables and attributes is linear. If the model is linear it does not matter if the values of the variables are averaged before calculation of the average attribute value or if the average attribute value is obtained from averaging the separate calculated attribute values. If the relationship were non-linear such a procedure would result in an aggregation error (Rastetter *et al.*, 1992). Such an aggregation error will increase as the concavity of the non-linear function increases. To avoid such an error, when dealing with non-linear models, one has to calculate the attribute values first (apply the model at all grains, i.e., locations where input variables are known) and next average the function values (Bierkens *et al.*, 2000). Examples of such non-linear up-scaling functions are up-scaling from individual-leaf photosynthesis to full-canopy photosynthesis, up-scaling from small scale variation of the phreatic surface to regional models, or up-scaling of measured daily precipitation to average precipitation for a decade.

Scale problems in empirical statistical versus mechanistic modelling in landscape ecology

Ecological models generally link abiotic information (like water availability and quality) to organisms. Mechanistic ecological models, containing causal relationships derived from experimental studies, are available for relatively simple and thoroughly studied ecosystems (e.g., Van Liere and Gulati, 1992, Janse *et al.*, 1992). Mechanistic model development is both time-consuming and expensive. For the restoration of regional landscapes like watersheds and river valleys, generally applicable models valid for a range of ecosystems are required. These ecosystems and their interrelations are so complex that deterministic knowledge fully covering all processes is often not available and laborious experimental studies are not feasible. The two examples presented below serve as case studies illustrating the constraints related to scale issues in both types of modelling approaches. What we can learn

from these examples is that the general principle that discrepancies between the scale of observation, dominant processes, and model calculations should be avoided is frustrated in practice by limitations in data. Both modelling studies focus on river valleys: one empirical statistical approach focused on the response of plant species on changes in site factors (De Becker *et al.*, 2001, Bio *et al.*, 2002) and one a mechanistic approach focused on geochemical flows (Van der Peijl, 1997, Van der Peijl & Verhoeven, 1999, 2000).

Empirical model for plant species

This case is an example of spatial ecological predictive modelling, within the limitations imposed by data availability and model purpose given by environmental policy makers. Policy makers, e.g., water and nature managers, wanted a generally applicable model for Flemish river valleys although data only were available for four specific valleys. The data, collected from 1993-1997 in four nutrient-poor Flemish lowland river valleys, consisted of presence and absence records for groundwater-dependent plant species and abiotic site conditions describing management, soil, groundwater level and several groundwater chemistry parameters. Biotic data, management and soil were mapped in grids of adjacent regular square cells (20 x 20 m). Data on groundwater tables and water chemistry were collected at a limited number of point locations within each grid; hence, at a much smaller sampling scale (or support) and with extensive un-sampled surface in between. This example thus deals with a number of specific scaling constraints: limited extent of the study versus the need for a wider geographical applicability of the model; differences in support between variables; spatial autocorrelation.

The differences in support were relatively easy to overcome. The variables sampled with less support were spatially interpolated and up-scaled (to grid-cell size) to match the other data. This was done by block-kriging following a semi-variogram model, since this gave a much better result than standard block-kriging (De Becker *et al.*, 2001). Next, spatial auto-correlation in vegetation field records and model residuals was assessed through empirical semi-variograms; the residual semi-variograms indicated spatial structure not accounted for by the model's explanatory variables (cf. Albert & Mc Shane, 1995). Multiple logistic regression modelling was performed using two modelling frameworks. Generalized Linear Models - GLM- (Nelder & Wedderburn, 1972, McCullagh & Nelder, 1989) have been successfully applied in numerous ecological studies (e.g., Austin *et al.*, 1984, Margules *et al.*, 1987, Zimmermann & Kienast, 1999). Generalized Additive Models - GAM - (Hastie & Tibshirani, 1990, Yee & Mitchell, 1991) have been applied in more recent studies (e.g., De Swart *et al.*, 1994, Huntley *et al.*, 1995, Austin & Meyers, 1996, Bio *et al.*, 1998). Both enable ecologists to model species response to a wide range of environmental data using a link function (i.e., *logit*) between response and predictor variables. Generalized Additive Models form an extension of GLM. While GLM fit functions linear in their parameters, allowing for linear and polynomial response shapes, GAM are more flexible permitting both linear and complex additive response shapes, as well as a combination of the two within the same model (Hastie & Tibshirani, 1990). More than half of the species were modeled more accurately by GAM with data driven smooth response shapes instead of second-order polynomials. Model evaluation and comparison was based on cross-validation and model discrimination (Bio *et al.*, 2002). A factor coding for the four sampled valleys was most of the times very significant when added to the final regression model. This points at regional differences (between the valleys) in species distribution that are not ex-

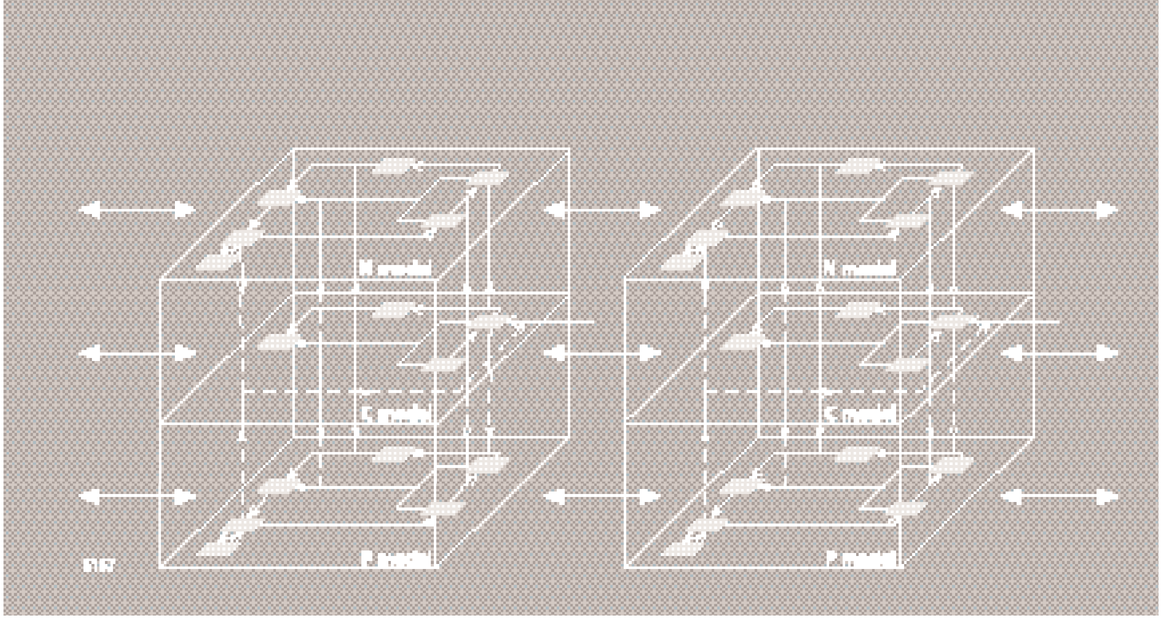


Figure 4. Conceptual diagram of a site-model consisting of two unit-models. Each unit-model consists of a nitrogen sub-model, a carbon sub-model and a phosphorus sub-model. Within these sub-models there is internal cycling. Landscape geochemical flows are shown between the unit-models (after Van der Peijl & Verhoeven, 2000).

plained by the models. There may be differences in species response to the explanatory variables due to valley-specific pseudo-correlations with non-modeled variables.

Overall, the regression models seemed ecologically sound and predicted species distribution in Flemish river valleys adequately, despite discrepancies between data quality and model assumptions. Figure 3 shows two examples illustrating model performance. The model of *Rumex hydrolapathum* only predicted well between areas and not within. The model for *Filipendula ulmaria* predicted observed distribution well both within and between areas. This study demonstrated that predictive modelling using standard statistical regression procedures can be reasonably successful with GLM or GAM in the presence of data with the following characteristics: non-homogeneous aggregated data; data that are spatially auto-correlated; partly interpolated and partly measured explanatory variables; explanatory variables and response variables collected at different scales; and correlated explanatory variables. However model application and inference should be handled with care, as assumptions of independent, error-free explanatory variables and independent errors are clearly not met. We observe that, in practice, models have to suit model purpose as well as possible even if data do not fully support model assumptions. Shortcomings, if not removable, should be assessed and, at least, communicated to the final user, just as model applicability and credibility. The models presented are, for instance, valid for nutrient poor river valleys only, as model input data do not include nutrient rich situations. So far, the predictive power of these models could not be examined on other regions. Validation against data collected elsewhere - i.e., an extrapolation in space - is a next step to be taken to see how far the applicability of these empirical models reaches (Bio *et al.*, 2002).

Mechanistic model for biogeochemical flows in wetland ecosystems

An example of a model describing carbon, nitrogen and phosphorus dynamics at the ecosystem level is the one developed by Van der Peijl & Verhoeven (1999) for river marginal wetlands. This model was developed in the framework of a European project on Functional Assessment in European Wetland Ecosystems (Maltby *et al.*, 1996) to analyse nutrient-related processes and their importance for ecosystem functions. In this case the constraints are: choices to be made in spatial and in temporal extent of the study in relation to the needed general applicability of the model and limited extrapolation possibilities.

The model is a dynamic simulation model in STELLA and has three layers, one for each element under investigation, i.e., carbon, nitrogen and phosphorus (Figure 4).

Each layer has a basically similar set-up with a number of plant and soil compartments with mass flows between them. Carbon fixation, nutrient uptake, grazing by large herbivores, decomposition, mineralization and denitrification are important processes described in the model. One of the main features of the model is a factor associated with soil redox potential, water table and soil oxygen content, which influences most process rates. The most important connections between the three model layers are the control of carbon fixation by nitrogen and phosphorus availability, and the control of mineralization by the litter C:N and C:P ratios.

The purpose of the model was to investigate the nature of the interactions between the C, N and P cycles, to assess what consequences these interactions have for water quality flowing through the wetland, for carbon sequestration and for greenhouse gas emissions. Further, attempts were made to quantitatively assess nutrient-related functions in river marginal wetlands and to simulate the effects of management and other human influences in (or outside) the wetland on these functions.

After the initial calibration and validation of the model with data collected in river marginal wetlands in England (Van Oorschot *et al.*, 1997), the model was used to test the nutrient transfers between two connected ecosystems, i.e., a wet, groundwater-fed slope and a floodplain along the river Torridge, SW England (Van der Peijl & Verhoeven, 2000). The hydro-geomorphic unit (HGMU) concept was used for defining a separate, complete unit-model for each of the two HGMU units within the wetland (Figure 4). These unit-models were connected by defining the flows of nitrogen and phosphorus between them. These flows, also called landscape geochemical flows, usually consist of flows of water containing N and P. The two units at the study site, Kismeldon Meadows, slope and floodplain, were separated by a ditch, which caught most of the run off and shallow groundwater flows from the slope. Only an estimated 1% of the N and P that left the slope unit in the water outflow reached the floodplain unit; the rest was caught in the ditch, which prevented the geochemical flows from taking their natural course. To examine the influence of this ditch, the model was run for the same site, but without the ditch. This is comparable to a situation of a restored site, where run-off and shallow groundwater containing nutrients can freely flow from the slope to the floodplain.

The computer simulation experiment reconnecting the slope and floodplain showed that this (1) increased the nutrient input into the floodplain, causing a higher biomass production, and (2) increased the wetness of the floodplain, causing slower decomposition, which together (3) led to a faster soil organic matter accumulation in the floodplain. Nutrient inflows became relatively more important compared to atmospheric deposition, especially for phosphorus. By connecting the slope and the floodplain, 20 % more nitrogen and 18% less phosphorus flowed into the river.

This model has a great level of detail with respect to the various biogeochemical processes involved and requires the availability of field data such as C, N and P stores in plants, soil organic matter, and other soil pools. It also requires many environmental parameters, such as climatic data, soil characteristics, water level fluctuations, etc. It has been shown to be effective in describing C-N-P interactions in wetland ecosystems, and has been sufficiently robust to implement a two-unit model in a landscape with two hydrologically connected wetland ecosystems (Van der Peijl & Verhoeven, 2000). Further spatial expansion of the model would be possible, although there is not much opportunity for modelling small-scale hydrological patterns in multi-unit (or grid-based) approaches.

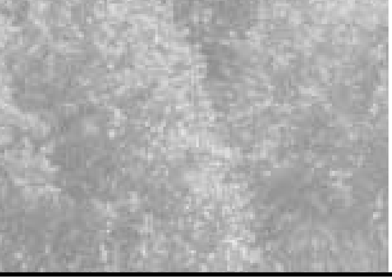
Discussion

Empirical ecological models are often based on available data that were not explicitly collected for that purpose or on limited data sets especially collected for the purpose of model development (see De La Ville *et al.*, 1997, Ertsen *et al.*, 1998, Bio, 2000). Therefore, quantity and quality of data is of utmost importance. An ideal data set for ecological modelling contains a sufficient number of samples that are representative of and well distributed in the modeled geographical and environmental ranges, and that satisfy model assumptions. Unfortunately, such ideal data sets are rarely found, and the urgent need for swift restoration measures presses modelers to do with less than ideal data (see Olde Venterink & Wassen, 1997).

Classical statistical inference is based on the assumption of independent observations collected at randomly chosen locations (De Gruijter & Ter Braak, 1990). However, records of spatial dependence in ecological data are numerous (e.g., Rossi *et al.*, 1992; Tilman, 1994, Fielding & Bell, 1997), as neighboring samples tend to be more similar than samples further apart. Using standard statistics, the presence of spatial autocorrelation in data and in model residuals may render error estimates and associated significance tests unreliable. It may also affect model choice, as variable selection is generally based on explained and residual variance. Nonetheless, these data are generally treated as independent, random samples and modeled using classical statistical procedures (e.g., Nicholls, 1989, Hill, 1991, Buckland & Elston, 1993).

Recently, methods have been developed for the modelling of spatial dependence, or auto-correlation, in regression using, for instance, neighborhood information (Sokal & Oden, 1978a, b, Smith, 1994, Wu & Huffer, 1997). Geostatistical modelling of residual spatial dependence is an alternative approach under development (Pebesma *et al.*, 2000). However, for prediction at other sites or in different conditions, the use of spatial autocorrelation as model term or residual information has serious drawbacks. On the one hand, neighborhood or other spatial dependence information is not directly available, and the assumption that levels of spatial dependence for new sites or conditions are similar to those found at the modeled sites may not be valid. On the other hand, a spatial dependence term in the model will act as an indirect variable accounting for—and, possibly, masking part of—the effect of several direct, ecologically relevant variables. Vegetation records and records of abiotic site conditions tend to be auto-correlated too, and an explanatory variable defining the neighborhood of a site in terms of a species' occurrence will combine biotic (e.g., species' dispersal ability or inter-species competition) and abiotic (favorable or non-favorable site conditions) information. This will render robust but less informative and, possibly, less generalizable models. Only part of the spatial autocorrelation in the response variable is likely to be explained by the explanatory variables in the regression model. Assessment of the residual spatial variance can aid model evaluation, and highlight shortcomings in explanatory variables or model structure (e.g. Robertson & Freckman, 1995, Begg & Reid, 1997, Gotway & Stroup, 1997, Köhl & Gertner, 1997, Bio *et al.* 2003).

The main problem with empirical statistical species models is that there is little cause-effect knowledge incorporated. Of course, the choice of certain site conditions as potential predictor variables is based on knowledge of how these conditions affect species, but for the rest the model is merely statistic. The potential danger of pseudo-predictions is larger when less predictor variables are included, when the model is spatially extrapolated and especially when the short time scale of a study is not balanced to its large spatial scale. Van der Rijt *et al.* (1996) developed a model for predicting vegetation zonation in



dependence of flooding in outer dike areas. They coupled several maps in a GIS and incorporated vegetation response regression models (based on a geographically small area) to these spatial data. The model was used for evaluation of the effects of different sluice management schemes on outer dike vegetation zonation in a wider area. There is nothing wrong with such predictions as long as flooding frequency and duration are the causal factors for vegetation zonation in all areas where the model is applied (Wassen *et al.*, 2003). The fact that we have to be cautious with extrapolation in time with this category of models is ironic, since this is what these models were developed for: extrapolations into the future.

High-detail (in terms of many processes incorporated) dynamic simulation models such as the one developed by Van der Peijl & Verhoeven (1999, 2000) have the advantage of integrating a strong knowledge base on biogeochemical interactions in order to analyze or predict the effects of major environmental drivers such as water level fluctuations and nutrient inputs in run-off on overall ecosystem performance, such as the water quality improvement function in wetlands. The drawback of the approach is that large data sets of site conditions are needed to implement the model. These would normally only be available if the site would have been intensively studied. Another limitation of the model is the coarse grain of study - it assumes homogeneous site conditions within certain hydrogeomorphic units. Such units subdivide the landscape in a discrete way, comparable with the 'ecotope' concept. Coarse-scale spatial variation in terms of multi-unit wetland landscapes can be tackled by running the model in every unit separately and using extra algorithms to describe the hydrological connections between the units. The model would be easier to apply if it would be simplified and implemented in a raster-GIS. There have been some first attempts to do this, and much simpler dynamic models simulating C-N-P interactions have been generated, which still kept their original level of predictability. If coarse-scale data for other units are unavailable, a statistical description of the fine-scale components across the extent of the coarser scale should be acquired. The fine-scale attributes can then be ranked by their contribution to the aggregation error. In such a way the important sources of error can be detected (Rastetter *et al.*, 1992). To detect scale-dependent processes and patterns, one depends on observation sets or model calculations of fine grain and large extent. Collecting data of fine grain and large extent is costly and time consuming. Therefore, an *a priori* choice of a certain scale of observation and/or modelling is often unavoidable. Clear understanding about the scale at which relevant processes operate is essential when choosing the appropriate scale of observation and modelling. A general guideline in choosing an appropriate scale of study is that discrepancies between the scale of observation, dominant processes, and model calculations should be avoided (Rietkerk *et al.*, 2002). Since in most environmental studies such discrepancies are a given and thus cannot be avoided, they should be explicitly acknowledged.

Although we have identified a whole range of pitfalls and possible sources of error involved in attempts to scale up patterns and processes from small-scaled site studies, we can identify several promising approaches, which can be further developed. A first approach is the use of statistical regression of spatial data, with attention for spatial autocorrelation including assessment of spatial variance. It is important that statistical correlations found with these models are validated with knowledge on cause-effect relations. If such knowledge does not exist for the specific relations found, these should be interpreted with care and should ideally still be studied in a causal-analytical way. A second approach is the implementation of simplified mechanistic models of biogeochemical and population ecological processes in a raster-GIS, with simultaneous modelling of the spatial relationships between raster cells in a hydrological model. The mechanistic model should be parameterised and calibrated with data from studies in one or two spatial cells in the study area. Only a limited number of sensitive parameters for the model have to be measured in all the raster cells.

We advocate a combination of approaches, empirical models for species response and mechanistic modelling of biogeochemical processes, in order to gain insight into regional landscapes and to allow for some form of prediction of environmental and management effects on these systems. Van den Bergh *et al.* (2001), Pieterse *et al.* (2002) and Gielczewski (2003) provide good examples of attempts of such integrated models. Although these models also suffer from scale discrepancies, they at least provide an explicit framework revealing them, since the questions asked have to be translated into spatial scenarios and subsequently into input maps whereas the models provide output maps and for all of these steps the spatial and temporal scale is clear.

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Abstract

Inquiries into the issue of scale become increasingly important in the field of landscape ecology and natural resource modelling and analysis. Scales of observation and modelling are often pre-set based on the *a priori* description of the system of study. In this paper we focus on upscaling approaches. We emphasize that predictability depends on the relation between the spatial and the temporal scale of study. Three examples of scale dependent processes illustrate the importance of identifying the scale at which processes operate to avoid erroneous conclusions. Two modelling studies show a number of scale related bottlenecks in data, interpolation, extrapolation and modelling. In statistical modelling of spatial data spatial dependence should be examined, truly independent validation data sets should be available and spatial extrapolation should be done with care. In mechanistic modelling of processes spatial up-scaling requires information on landscape heterogeneity and how this influences the modelled processes. Although a general guideline in choosing an appropriate scale of study is that discrepancies between the scale of observation, dominant processes and model calculations should be avoided, in most landscape ecological studies such discrepancies are a given. They should be explicitly acknowledged and the information in this paper may help in recognizing them and dealing with them.

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