Toward a Predictive Understanding of Ecosystem Processes at the Scale of Landscapes

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In this paper we stress the importance of considering patterns at the regional-scale in global change studies. Ultimately, the assessment of how ecosystems processes (e.g. water and carbon fluxes) respond to future changes relies on plot level process studies. However, logistics or limited resources restrict the direct estimation of processes at larger spatial scales. Describing examples from studies in four different biomes, we show how process-level studies may be integrated with information gained from spatial analyses and outline the need to consider the spatial variability of environmental conditions to make realistic estimates for larger regions. We conclude that understanding the underlying causes of spatial patterns is essential for assessing the response of ecosystems to climate change. Vegetation models can be used to identify those driving variables that are likely to dominate the future responses of the ecosystem.

1. Introduction

Global change research and resource management both require the prediction of ecological responses at large spatial scales. However, process-level ecological studies are invariably conducted at much smaller spatial and temporal scales. Thus, the degree to which scaling-up is possible and how it can be best achieved are of great practical importance. To address the question of how ecosystems respond regionally to environmental changes, it is necessary to conduct detailed studies and to identify how representative these locations are for a broader regional context.

At the regional scale, there is always some degree of environmental heterogeneity. This makes the direct estimation of processes at larger spatial scales cumbersome, if not impossible. Simply increasing sample size (i.e. number of plots) to reduce the error margin of spatial averages is often impractical. Direct measurement of large areas may be possible using airborne sensors, but variables of interest may not be amenable to remote sensing or sufficient time series may not be available. The choice of the number and location of sites needed to allow regional conclusions from plot level studies is difficult and a systematic approach is lacking.

In this paper we argue that the analysis of observable spatial patterns at regional or landscape scales plays an important role for gaining a predictive understanding of spatial processes. We describe four spatial studies as examples (Fig. 1). The first (Arctic Tundra) is furthest developed and illustrates most strongly how a failure to consider regional spatial variability may lead to erroneous conclusions for the interpretation of ecosystem processes in a larger regional context. The second and third (Spruce forest, Alpine meadows) provide further evidence, and the fourth (Tropical rainforest) illustrates how the principles outlined below might be applied to a region of high biodiversity.

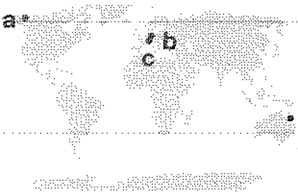

Figure 1: Location of study sites (a- Arctic tundra, b Spruce forest, c Alpine meadows, d Tropical rainforest)

2. Essential steps for scaling up

Scaling up processes from experimental field study sites to the regional scale requires the following steps:

A: Identification of significant environmental factors operating at the larger scale

Vegetation patterns are probably one of the most easily observable landscape properties. They can provide relatively fine-grained information (scale of meters) for large regional areas (extent of hundreds to thousands of square kilometres). These scale and extent ranges are most important for scaling-up between processes at plant and plot scales to integrated regional processes. Those variables most predictive in vegetation models will most likely generate the strongest system response if changed. If we understand the reasons for the distribution of vegetation, we have the key to predicting a wide range of potential ecological responses at large scales.

Topography influences all spatial climatic and hydrological gradients, and hence provides another rich source for the computation of spatial environmental conditions. Software packages such as ANUCLIM [McMahon et al. 1995] allow the generation of spatial climate information from point measurements. Topographic analysis further enhances the suite of environmental variables for quantitative analysis of spatial pattern e.g by providing information about horizontal water flow and patterns of water confluence. A comparative analysis relating vegetation to topography-based environmental conditions may provide insights into the most important spatial controls of ecosystem processes.

B: Quantification of the systems response

Ecosystem functioning at small scales is the fundamental base for our understanding of the impacts of environmental change. Much research is currently conducted at this scale. Models, however, should also reflect the heterogeneity of environmental conditions that were identified in the first step and care should be taken in case the main factors influencing processes in plot-level studies differ from regional influences. For example, wind velocity undoubtedly plays a major role in short term gas-exchange processes at the plot level, but may be relatively unimportant at larger spatio-temporal scales where other variables may be more important controllers of the system's response.

C: Linkage of information from observable pattern with process models

This step is necessary to answer many questions related to resource management. Yet, often this step is not taken. This is possibly because the effects of spatial variation are seldom considered in plot-level studies. Alternatively, researchers involved in spatial studies fail to integrate their results with process level research.

3. Case studies

3.1 Arctic Tundra

The first example examines the role of arctic ecosystems in the global carbon cycle. These pristine ecosystems are important due to the large carbon storage frozen in their soils. The work reviewed here was conducted in Northern Alaska. The 22 km^2 study site lies between 765-982 m altitude. Detailed models have been developed for a small catchment (Imnavait Creek, 2.2 km^2) within the area. Maps were generated with a resolution of 10m from aerial photography.

Step A: Water is a strong controller of pattern and process in the region. Quantitative vegetation models have clearly demonstrated that hydrological processes control the distribution of vegetation in the area [Ostendorf and Reynolds 1993, 1998]. The spatial pattern of water flow and retention has important influences on landscape heterogeneity (Figure 2) allowing the prediction of vegetation pattern with a goodness of fit of 78% [Ostendorf and Reynolds 1998].

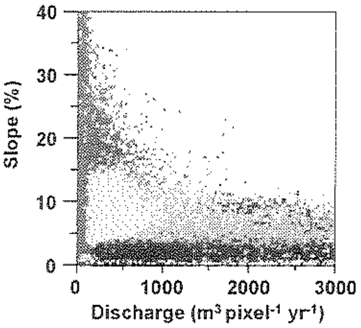

Figure 2: Distribution in environmental space as expressed by slope and discharge rates of tundra vegetation types (indicated by different shades of grey) (after Ostendorf and Reynolds [1998])

Step B: Extensive ecophysiological studies of leaf-level gas exchange led to a parameterization of the Farqhuar-Model [Farquhar et al. 1980] for three functional vascular plant types. Detailed structural vegetation data allowed a parameterization of GAS-FLUX, a physically-based canopy model [Tenhunen et al. 1994] for the three major vegetation types in the area. Oberbauer et al. [1992] measured carbon efflux from soils throughout the landscape and developed a regression model using soil temperature and water table depth.

Step C. The same variables which were found to control spatial pattern of vegetation were used in the catchment hydrological model TOPMODEL [Beven and Kirkby 1979] to compute an index of hydrological similarity across the landscape. The spatial vegetation pattern could therefore be linked directly with the spatial variables in the hydrological model [Ostendorf et al. 1996]. TOPMODEL, with GAS-FLUX, was able to predict discharge with 94% accuracy. This is notable since the catchment scale transpiration rates were generated by scaling-up leaf gas-exchange measurements.

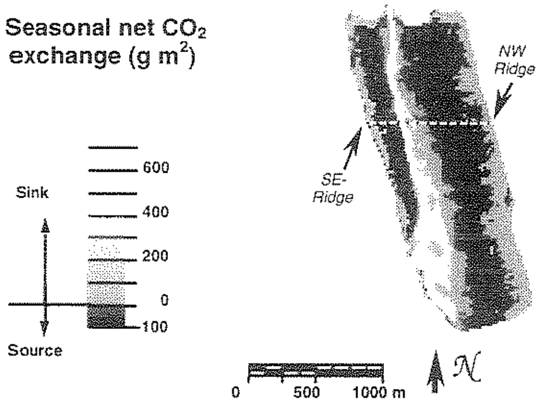

Figure 3: Seasonal net CO_2 exchange of the Imnavait creek catchment. The darker grey shades indicate source areas, the lighter areas are sinks for atmospheric CO_2 (after Ostendorf et al. [1996]).

Application: The hydrological model allowed an estimate of the spatial distribution of water table depths which could be fed into the soil respiration model to estimate the spatial pattern of seasonal carbon balance. The map (Figure 3) identifies patches of positive and negative seasonal carbon flow. The catchment as a whole is in a delicate balance between acting as a source or a sink for atmospheric carbon. However, point estimates from field data may be very misleading because areas in the mid slopes, that would intuitively be considered average (neither too moist nor too dry), are atypical of the catchment's CO_2 exchange [Ostendorf et al. 1996]. These areas exhibit a net efflux whereas the catchment as a whole takes up a small amount of carbon. The model also shows a strong influence of precipitation on the carbon balance through its effect on the watertable. In addition, increased irradiation increases soil respiration through a decrease of the water table caused by an increase of transpiration rates [Ostendorf 1996]. Such results clearly illustrate the necessity of understanding spatial patterns and processes in order to base regional predictions of ecosystem processes on a detailed process-level understanding.

3.2 Managed Spruce Forest

Forested headwaters influence water resources for large regions and the consequences of environmental change are a major concern. The Lehstenbach catchment is located in South-East Germany (see Alsheimer et al. [1998] for a site description). The 4.7 km^2 area is between 620-870 m elevation and is used for wood production and tourism. Most of the area is covered by variously aged spruce forest.

Step A: The most obvious spatial pattern relates to stand age. Stands are even aged with age reflecting past forest management decisions. Therefore, stand age does not identify environmental controls and consequently, the distribution of understorey plants was examined. Most variability of the understorey can again be explained by age class and the density of the tree canopy, but slope and drainage, the variables that explained most of the variability in the arctic region, also showed a moderate effect [Scharfenberg, 1996, Köstner et al. in press]. A different source of spatial information is a map of site conditions, originally generated for forest management. Using slope and drainage, this map could be predicted with a pixel by pixel accuracy of 43%, indicating a strong influence of spatial hydrological processes on ecosystem processes [Ostendorf and Tenhunen, 1995] as in the tundra example.

Step B. Estimates of stand level canopy transpiration derived from scaled xylem sap flow measurements (see Köstner et al. [1998]) showed large spatial differences. At all sites, canopy transpiration revealed similar relationships with climatic conditions. Single-variate regression models (2nd order polynomial) using vapor pressure deficit could sufficiently predict daily canopy transpiration within a stand (r^2=0.85-0.92). However, canopy transpiration rates at the six individual sites varied by almost 100% (maximum daily rates 1.4-2.6 mm day^{-1}, seasonal rates 109-208 mm season^{-1}). For all sites, soil moisture was high throughout the season and temporal reductions of transpiration rates during the driest part of the season were not observed. Despite this, the highest rates were measured in a topographic location with a high soil moisture status indicating that spruce stands acclimate to long-term site conditions.

Step C. Canopy transpiration per leaf area declined with stand age (r^2=0.65) from 40- to 140-year-old stands. The best correlation (r^2=0.89) was found with stand density ranging from 320 to 1680 trees ha^{-1} for the six sites. It follows that the estimation of catchment scale transpiration rates can be substantially improved by including the spatial distribution of stand age [Ostendorf and Manderscheid 1997]. Such data is available from the forest service in high detail. Further improvement can be expected from using catchment scale stand density information and spatial differences in water availability.

3.3 Alpine Grassland

The alpine meadow site in Northern Italy is located close to the alpine dividing range. The site is located on a south-facing slope with an elevation range between 1112 and 2353 m. With slopes around 60%, these areas are difficult to harvest and they are increasingly being abandoned. A big unknown is how land-use and climate change will affect water resources and biodiversity of the region. Even water from small creeks with flow rates of as little as 2-3 $l\ s^{-1}$ during much of the summer season is currently used for irrigation purposes. In contrast to many other regions in the world, high biodiversity has been maintained through moderate management converting higher elevation forests into hay meadows. This historic low intensity hay production has reduced the tree line by 250-300m to roughly 1700m.

Step A: Vegetation models of the Passeier Valley hillslope demonstrated that land-use history is the main factor determining today's vegetation pattern [Tasser et al. 1998, Tappeiner et al. 1998]. Predictive modelling of vegetation pattern using climatic and topographic variables yielded a map with a pixel by pixel accuracy of 55%. Adding land-use history increased the classification accuracy to 78%. Of the topographic and climatic variables included in the models, elevation and slope exerted the strongest influence on vegetation pattern, whereas water flow and curvature patterns appear uncoupled from the vegetation pattern. Elevation relates mainly to gradients of temperature and season length, whereas the processes leading to the strong influence of slope are difficult to judge. Slope relates not only to hydrological processes (water flow velocity), but is also strongly related to snow cover (season length) and management intensity since steep areas are not accessible with machinery and therefore are less intensively used.

Analysis of soil depth pattern allows additional information about spatial environmental patterns. Statistical analysis of a total of 711 soil cores revealed that next to vegetation and soil type, only slope and elevation contribute significantly to the spatial variance of depth to the C-horizon [Tasser et al. 1998]. Thus, a strong soil vegetation continuum exists, with small effects of horizontal material flow.

Step B: Detailed plot and species level ecosystem process studies (e.g. Wohlfahrt et al. [1998]) have been undertaken for three adjacent meadow patches with different management intensity and a forest site. Differences of transpiration rates and CO_2 exchange were found as a function of management. Results from the spatial studies however indicates that a more detailed consideration of elevation should be considered before estimations of the regional response to change may be attempted.

Step C: A linkage between landscape level patterns and small-scale process studies has been initiated. Details about the most important aspects of future change at species and plot levels have been collected. It seems possible to combine species level process information into the framework of canopy models (as was done for the arctic site), that can then be parameterised for sites in the various elevation zones. All indications are that horizontal exchange processes are of much less importance in this alpine area than they were in the tundra and forest systems, and that elevation/management classes may be fully sufficient to characterise the spatial heterogeneity.

3.4 Tropical Rainforest

The study region encompasses the largest contiguous rainforest in Australia including the "Wet Tropics World Heritage Area". The challenge for the region is the conservation of biodiversity and an assessment of the ecosystem goods and services related to the water and carbon balance in Australia's most significant rainforest region. The region encompasses about 20000 km^2 with an elevation range from sea level to 1586 m. A GIS has been generated at a spatial resolution of 1 ha. The landscape is very complex and the vegetation mosaic reflects the region's steep environmental gradients and complex substrate differences.

The high biodiversity (with approx. 800 tree species occurring in the region) prohibits scaling up from the species-level. Hence, research in this region cannot follow the lines of the previous three examples. However, much progress towards a predictive understanding of the region's ecosystems has been made because of the manner in which the vegetation has been mapped.

Step A: The region's forest types have been classified as environmental/structural types based on leaf size, the occurrence of vines or deciduousness and a number of other characteristics [Webb 1959; 1968, 1978, Tracey 1982]. An artificial neural network (ANN) model using 15 environmental variables generates a map with an exceptionally high accuracy of 75% [Hilbert and van den Muyzenberg in press]. Since the vegetation classification has such a strong relationship with environmental variables, it can be assumed that it might also represent spatial differences of processes very well. Other vegetation models, which identified the major environmental controls, show clearly that precipitation and temperature exert the strongest effects on vegetation. Using these two variables alone, the complex vegetation mosaic can be reproduced with a pixel/pixel accuracy of 60%.

Steps B and C are being undertaken currently. The need to consider spatial differences for regional assessments is obvious. Results from the spatial models have clearly demonstrated that mean annual temperature and precipitation gradients should be major factors in spatial process study design. The results also indicate, that for climate change studies, detailed regional precipitation models are needed to accurately represent the environmental boundary conditions. Precipitation, however, is currently the least predictable variable in regional climate models.

4. Concluding Remarks

The spatial studies of landscapes from four biomes illustrate differences in mechanisms controlling the spatial patterns of ecosystem processes. Although the objectives of these studies and hence the details of processes differ, some general conclusions can be made.

The results show that ecosystems differ substantially in their response pattern to current environmental conditions and hence also in their expected response to changes. The water relations of the different ecosystems serve as a good example. Whereas the spatial re-distribution of precipitation (rather than differences in amount) has the dominant influence in the arctic and to a lesser degree in the spruce site, it may have little effect in the tropical sites and seems absent in the high mountainous region of the Alps. The alpine landscape is most strongly influenced by temperature, the tropical forest vegetation pattern relates best to precipitation and temperature. Such information may be essential for the development of a spatial scheme for locating experimental plots. Regional process models should be individually constructed to account for peculiarities of different regions. But the results also clearly illustrate that the main variables influencing the distribution of current vegetation pattern can be identified and that it may be possible to systematise spatial influences within the global context to narrow the gap between field evidence and global change predictions.

In the pristine arctic tundra and rainforest, vegetation patterns appear to document the strongest spatial driving variables. As management intensity increases, vegetation's power to explain spatial differences declines. This was most apparent in the Lehstenbach catchment where even the presumed "unmanaged" understorey vegetation was more strongly related to the managed tree canopy than to any other variable. [Scharfenberg 1996]. But even in those systems, where the influence of man largely determines patterns and processes, spatial information such as site conditions or a spatial collection of a large number of soil cores can be collected. Such information provides the means to classify the natural heterogeneity of landscape and thus improves the assessment of landscape scale response to change.

Regional and global models of energy and material fluxes ultimately rely on field measurements to quantify the basic controls. The arctic tundra and the spruce examples are the most complete up-scaling exercises presented here. Both sites show that one can not assume that "a few" (restricted by manpower) responses and driving variables measured and identified at a small scale are representative at the larger scales. However, both examples also show that scaling-up across several scales is possible, but that careful planning of the spatial arrangement of plot level data is required to successfully achieve this goal.

5. Acknowledgments

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