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Spatio-temporal Gradients between High Mountain Ecosystems of Central Norway

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Abstract

Spatio-temporal gradients between ecosystems of the central Norwegian high mountains are analyzed. Complex landscape ecological site analyses combined with intensive pitfall trapping are carried out in four investigation areas in two regions. Key questions are addressed for the differences among ecosystems along a broad-scaled oceanic-continental gradient. The answers are based on ecological process analysis and mapping of zoocoenoses in small catchments of two alpine altitudinal belts. A comparison of four ridge sites is presented by analyzing water and temperature balance and activity of arthropods during the driest summer month. The results do not implicate summer drought and heat as limiting factors; summer wetness and cooling are most decisive. Landscape ecological processes, like the accumulation of snow during winter, snow melting, freeze-thaw action, percolation, soil moisture variation, and temperature regimes are exemplified by long-term measurements throughout the year in a small catchment in continental eastern Norway—the driest mountain region in Scandinavia. To learn about the organization and diversity of zoocoenoses, epigeic arthropods (Araneae, Carabidae) are investigated along spatial gradients. Interrelations between distribution patterns of animals and spatio-temporal dynamics of the environmental conditions are presented. The results are framed by gradient theory in landscape ecology. Finally, the complexity of spatio-temporal gradient determination between ecosystems is discussed and summarized by a scheme of gradient principles for the Norwegian mountains.

Introduction

This paper seeks to explain the relationships between topography, snow cover, soil moisture, temperature, and arthropod abundance. Thus, investigations on spatio-temporal gradients in high mountain landscapes are a great challenge for ecological research where steep meteorological as well as topographical gradients are found and altitudinal zonation of ecosystems is well pronounced. The topography best determines climatologic and hydrological conditions which, in turn, affect soil development, nutrient fluxes, vegetation patterns, and animal distribution (Köhler et al., 1994; Löffler et al., 2001). Those gradients are complex, and their ecological impact on the high mountain environment is not fully understood (Körner, 1999).

Extensive data have been available on Norwegian high mountain ecosystems for a century, especially on plant life and vegetation organization (Gjærevoll, 1990; Dahl, 1998; Wielgolaski, 1998; Moen, 1999; Wielgolaski, 2001). During the 1970s and 1980s, the Norwegian high mountains were involved in the International Biological Programme, studying ecosystem functioning at different sites for a global comparative synthesis (Rosswall and Heal, 1975; Wielgolaski, 1975; Bliss et al., 1981). Locally, research has been done on spatial dynamics and functioning of alpine ecosystems in Norway (Mosimann, 1985). Although some early studies have led to a detailed understanding of the complexity within the high mountain environment (Nordhagen, 1927; Dahl, 1956; Gjærevoll, 1956), the scientific challenge in Norwegian high mountain geography is still to intensify knowledge about large-scale temperature and snow cover differentiation as well as superior gradients between the oceanic and continental regions (Fægri, 1972).

Several investigations deal with epigeic arthropods from the high mountains of Norway (Hauge and Refseth, 1979; Hågvar et al., 1978), but analyses of fine-scale distribution patterns of the invertebrate fauna have been carried out locally (Ottesen, 1995). In general, there is a lack

of investigations that integrate animals into ecosystem analyses, considering them as factors with respect to their functions within the system (Holtmeier, 2002).

The studies by Mosimann (1984a, 1984b, 1985) used important new methodology to analyze the function of sub-arctic and alpine ecosystems. Based on this concept of the *landscape ecological complex analysis*, a lot of improvements evolved (Rempfler, 1989; Leser et al., 1990; Potschin and Wagner, 1996; Potschin, 1998; Döbeli, 1995, 2000). Several local examples brought detailed knowledge within the framework of comparative high mountain research. Regionalization of Norwegian high mountain ecosystems functions, from the micro- to the meso-scale, succeeded by using the temperature balance of near-surface layers (Löffler and Wundram, 2001; Pape and Löffler, 2004).

The adaptation of the process-oriented approach within the spatial analysis of different scales follows current principles and paradigms used in European landscape ecology (e.g., Billwitz, 1997; Haase et al., 1991; Leser, 1997; Bastian and Steinhart, 2002). Ultimately, these investigations have contributed to a characterization of Norwegian high mountain landscapes on a regional scale, emphasizing the interaction between spatial patterns and ecological process dynamics resulting in causes and consequences of spatial heterogeneity across a range of scales (Turner et al., 2001).

Overall aims of this approach are to examine the gradients of structure, function, and dynamics of the central Norwegian high mountain ecosystems. Besides geoecological studies (including vegetation studies), zoological analyses are a basis for this contribution to biotic aspects. Especially mobile organisms are regarded as very important in order to address the differentiation and dynamics of different sites. The project aims are:

- Spatial investigation of fine-scaled ecosystem patterns within small catchments (Löffler, 2002);

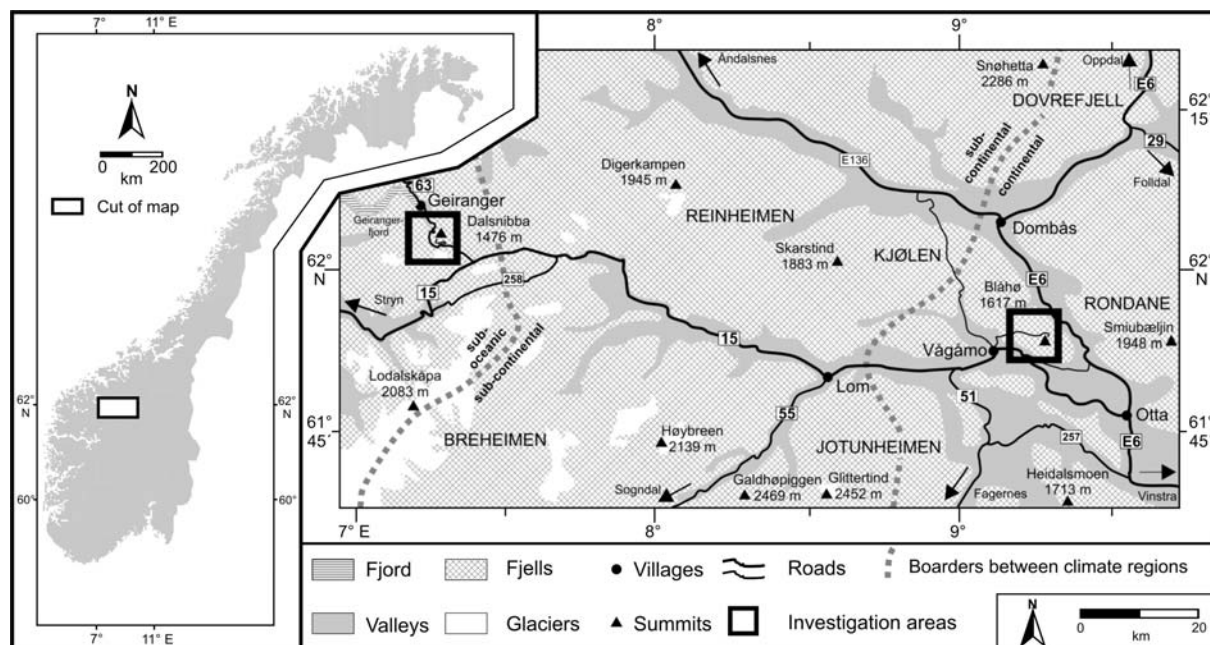


FIGURE 1. Location of the regions of investigation in central Norway (Löffler et al., 2001).

- Analysis of interdependencies between abiotic process systems and spatio-temporal dynamics of populations of certain animal groups (Löffler et al., 2001);
- Characterization of zoocoenoses with respect to different aspects of biodiversity, i.e., species numbers and compositions, ecological guilds as well as interactions and dynamics (Naujok and Finch, 2004);
- Quantification of abiotic process determinants and their influence on the zoocoenoses; and
- Analysis of environmental determination principles of biocoenoses along fine-scaled topographical, meso-scaled altitudinal, and broad-scaled oceanic-continental gradients (Löffler, 2003).

Investigation Regions and Study Areas

This approach is applied to the central Norwegian high mountain region (Fig. 1). Climatic conditions show a clearly defined oceanic-continental gradient between the western coast and the eastern slope of the Scandes mountain chain. The western mountain region is influenced by strongly oceanic conditions, while at an air distance of 100 km to the east the mostly continental-climate of Norway is found. In both regions the alpine altitudinal zonation is differentiated into a low alpine belt dominated by low shrub and heather communities, a middle alpine belt dominated by grassy vegetation, and a high alpine belt where only vegetation patches occur between block fields and debris (Dahl, 1986). The region in Norway with the most well developed continental mountains (Vågå/Oppland; 61°53'N, 9°15'E) is characterized by low annual precipitation (about 300–400 mm a⁻¹ in the valleys), resulting in the highest aridity found in Norway. The alpine environment within this eastern area of investigation reaches from treeline at about 1000–1050 m a.s.l. to the highest peak, Blåhø, at 1618 m a.s.l. The transition zone between the low alpine and the middle alpine belts is found at around 1350 m a.s.l. The oceanic mountain region Stranda/Møre og Romsdal (62°03'N, 7°15'E) is found in the inner fjords of western Norway and is characterized by humid conditions with annual precipitation of about 1500–2000 mm in the valleys. The alpine environment within this western investigation area reaches from treeline at about 840–880 m

a.s.l. to the highest peak, Dalsnibba, at 1476 m a.s.l. Four investigation areas are chosen as representative alpine catchments and delimited in each altitudinal belt (Fig. 2).

Methodology and Techniques

Within the framework of the *landscape ecological complex analysis* of Mosimann (1984a, 1984b), we used a modified methodological concept for high mountain landscape ecological research in Norway. In each catchment we installed one ecological base station, several major and minor ecological stations, and several water level stations. The spatial organization of measurements and the use of technical equipment at the different types of stations strictly follow a spatio-temporal approach. We observed the seasonal dynamics of the ecosystems by means of hourly measurements taken throughout the year by data loggers, using air and soil temperature, precipitation, solar radiation, air humidity, soil moisture, wind direction, and wind speed sensors. Additionally, we investigated spatial temperature, soil moisture, and wind speed differentiation using hand-held measurements at various locations during several characteristic climatic situations and seasons. At the well-drained sites, percolation meters were used for water and matter balancing. Poorly drained sites comprise a network of water level stations to quantify the spatial dynamics of stagnation processes. During the winter season snow accumulation was mapped and quantified by means of snowpack measurements as well as analyses on water equivalent. We observed snow-melt dynamics by means of color tracers.

The combination of water, energy, and matter attributes with further structural elements and faunistic characteristics results in a landscape ecological synthesis of sites by entering data material into a database that is standardized for GIS operations. Information from single sites was aggregated and classified by site in a sites catalogue. We used database routines to find spatial correlations between structural and process-oriented attributes. After digital data processing, the resulting qualitative and quantitative analyses of landscape functioning were combined with structural attributes of exposition, inclination, curvature, position in relief, substrate, geomorphodynamics, soil, humus, vegetation, and fauna (Hinzman et al., 1996). We



FIGURE 2. Catchments in the low and middle alpine belt of western and eastern Norway. Photos of the western catchments by R. Pape; those of the eastern catchments by J. Löffler.

analyzed vertical structure and functioning as an example of the catchments. This resulted in a fine-scaled extrapolation of processes. As a result, we were able to make lateral process correlations, reconstruct spatial fluxes, and analyze neighboring interactions of ecotopes.

In 100 ecotopes, 2–4 pitfall traps were exposed during the summer season of 2001. The exposure period lasted from the beginning of May until mid-October, and we used twice-weekly trapping intervals with formaldehyde (3%) as a trapping fluid, and a detergent. Based on Ellenberg et al. (1986) and our first experiences with the specific weather and soil conditions, we used a standardized trap type that combines roof and glass with a PE-ring on top of a tube (Naujok and Finch, 2004).

Pitfall trapping generally results in high individual and species densities of active arthropods and is principally an automatic method. It has been used successfully in high mountain landscapes where extreme conditions and draft vegetation are found (Hågvar et al., 1978; Ottesen, 1995). It can be used for permanent trapping during all weather situations and at night. In rocky and blocky terrain, pitfall traps are considered the only reliable method (Bell and Wheeler, 2001). Parallels between activity dynamics and changes in densities exist (Baars, 1979; Holland and Smith, 1999; Topping and Sunderland, 1992). Thus, species composition and seasonal changes of species activity of pitfall trap catches have to be analyzed carefully. As a consequence of the well known cons of this method, interpretation concentrates on intra-species analysis. This contributes to the fact that single species differ according to their activity and catchability (Sunderland et al., 1995).

Based on Uetz and Unzicker (1976), we adopted multivariate analyses (TWINSPAN, DCA, CCA, etc.) only to species of specific guilds with similar behavior using relative, semi-quantitative, or just qualitative data after transformation.

Faunistic investigations are strictly combined with spatial mappings and measurements of environmental structures and processes. We used ecotope types to analyse the impact of differences in topography, soil moisture, and soil temperature on the fauna; regression and multivariate statistic tools are used (Jongman et al., 1995). We also analyzed correlations between measurements and animal species distribution. For each species, a description of its niche is given (Ottesen, 1996) and its environmental determination is explained. Furthermore, we used arthropods for ecological site characterization.

Beyond the abundant arthropods of the central Norwegian mountains, we chose several groups for investigation. While different phytophagous arthropods (grasshoppers, leafhoppers) are determined by specific plant species, zoophagous arthropods correspond directly with the environmental conditions, and patterns of those animal distributions are the result of complex factor constellations. Consequently, zoophagous epigeic arthropods (Carabidae, Staphylinidae, Opiliones, and Araneae) could be used as indicator taxa. Additionally, phytophagous Caelifera and two beetle families (Chrysomelidae, Curculionidae) were included. These groups are abundant and show high activities at the ground surface. In contrast to, e.g., Collembola, the taxonomy and ecology are well known (Hågvar et al., 1978; Ottesen, 1995). Moreover, the existence of specific species

communities (Refseth, 1980) and stenotopic characteristic species are expected along horizontal and vertical gradients of the high mountain environment (Naujok and Finch, 2004; Schultz and Finch, 1997).

The extraordinary amount of resulting data was organized digitally in a database, and combined and structured within a GIS for spatial analysis. Mapped spatial data layers such as vegetation types, relief features, snow cover conditions, etc., were used to define structural ecotopes by overlay routines. The highly integrated ecotopes function as a spatial basis for data extrapolation (Löffler and Wundram, 2001). We quantified and generalized ecological regularities deduced from all functional data for all catchments with regard to their scale in ecosystem processes. This permits highly complex synthesis of qualitative and quantitative interrelations between the ecosystem compartments. In addition, the understanding of high mountain landscape functioning is made a part of landscape ecological modeling for quantified extrapolation routines and for process prognoses on different temporal scales.

Results

ECOLOGICAL GRADIENTS BETWEEN SINGLE SITES

Vertical water fluxes are illustrated by means of four representative examples from the low and middle alpine altitudinal belt in the western and eastern Norwegian high mountain region. We chose different sites for detailed measurements in order to demonstrate peculiar phenomena and general trends. Figure 3 shows the temporal dynamics of vertical water and temperature fluxes at four characteristic ridge positions in the low and mid-alpine belt of the oceanic and continental mountain regions, summarizing the most important results according to ecosystem function.

During the summer months, the continental eastern Norwegian mountains are characterized by a high amount of solar radiation due to a prevailing low degree of cloudiness. Temperature dynamics is well pronounced, on the one hand, showing dependence on the input of solar radiation and, on the other hand, the dominance of prevailing weather situations indicated by the barometric pressure. As the ridge positions are well-drained sites, the soil is characterized by relatively low heat capacity, resulting in a great daily temperature range. In comparison, their low diurnal temperature range results in a steep temperature gradient from the surface to depth. Precipitation events are commonly reduced to short convective showers. Although single showering events cause great precipitation, the overall precipitation sum is relatively low, and percolation processes are reduced except for intense rainfalls. Additionally, very high evaporation rates are present in a relatively warm, dry, and windy atmospheric layer in the low alpine belt, sometimes even exceeding precipitation rates at the same time. This supposed dry situation contrasts starkly with a nearly constant volumetric soil moisture content of 20% to 30% throughout the dry season, although the coarse rich silty sand is a substrate with a relatively low field capacity.

Middle alpine conditions are characterized by gradually higher precipitation rates and lower temperatures. A sparse vegetation cover results in relatively high surface temperatures compared with low alpine conditions during strong insolation. This constellation leads to slightly uneven soil moisture curves, but less evaporation rates, in the end. The result is a constantly high soil moisture content. As the ridge positions are the driest under all investigated sites, the ecosystems obviously do not suffer from lack of soil moisture availability during the summer period.

The oceanic western Norwegian mountain region is characterized by lower radiation input and higher precipitation sums than those found in continental Norway. Thus, low and middle alpine ridge positions can be characterized by balanced temperature dynamics, with lower

temperature maximums and higher soil moisture compared with the eastern mountain ridges. Constant rainfall and shorter periods without precipitation are the reasons for water saturation within the soils, despite similar evaporation rates due to higher wind speeds and equal structural parameters in all investigated sites. Therefore, the oceanic high mountain environment is generally wet throughout the summer.

The resulting altitudinal and latitudinal changes of ecosystem dynamics based upon the water and energy balance can be summed up as follows. Soil moisture is not a limiting factor in the high mountain landscapes when it comes to dry summer conditions; e.g., competition between plant species resulting in the ecological distribution of phytocoenoses therefore depends on access water.

In the eastern mountain region, low and middle alpine process constellations are different, but result in comparable conditions of constantly high soil moisture. Low alpine ridge ascendant water fluxes are reduced because of the lack of pull effects at the surface layer during warm and dry but short summer periods. This stresses the importance of a dense vegetation layer acting as isolation. Middle alpine ridge water balance is dominated by higher water inputs on the one hand and higher potential soil evaporation due to sparse and patchy vegetation on the other hand, resulting in a high surface temperature. Overall, evaporation rates are reduced due to low air temperatures. High evaporation rates can be explained by a combination of high air temperatures with resulting low relative air humidity and strong prevailing wind speeds; this is common during high-pressure weather situations with direct solar radiation input and convective air mass configurations. High evaporation rates during rainy periods are the result of overlying air stream configurations with dry air mass exchange in areas with local convective precipitation events; this phenomenon is common in the lower elevations of the alpine belts, while warm and dry air is produced in the neighboring areas. Cloud formation and higher precipitation rates are mostly found in the higher elevations during such periods.

Within the western mountain region ridge positions are covered by dense lichen heath in the low and middle alpine belt, despite high soil moisture and high air humidity. Similar to the eastern mountain region, vegetation distribution in the western high mountains therefore cannot be explained by hydrological patterns, apart from a surplus of water. Instead, snow cover conditions determine the spatial arrangement of plant association; this is known from continental mountain regions. Lichen heath in alpine ridge positions thus corresponds with a thin snow cover during winter.

To demonstrate local animal activity and to compare single sites in western and eastern Norway, the activity of spiders and harvestmen at ridge positions in all four investigation areas during the dry summer month of August 2001 is shown in Figure 4. Differences in arthropod activity are analyzed using equal vegetation structures mainly formed by dense lichen heaths at all four sites. For the middle alpine belt of the western investigation region, highly active opilionids are characteristic. Here, their activity is the highest of all four ridges. Wolf spiders (Lycosidae) show lowest activity on ridges in both middle alpine catchments, whereas they are one of the most active groups on ridges in the low alpine belt. The group with predominantly small body size, the money spiders (Linyphiidae), shows equal activity abundance at all four sites. They are the most active spider family. In contrast, ground spiders (Gnaphosidae) were caught only singularly.

ECOLOGICAL GRADIENTS ACROSS SPATIO-TEMPORAL PATTERNS

Different structural components of the ecosystems determine ecological gradients that in their turn follow characteristic spatio-temporal landscape patterns. Besides the topography, ground substrate with skeleton fractions influence water fluxes and soil moisture

Eastern Mountain Region

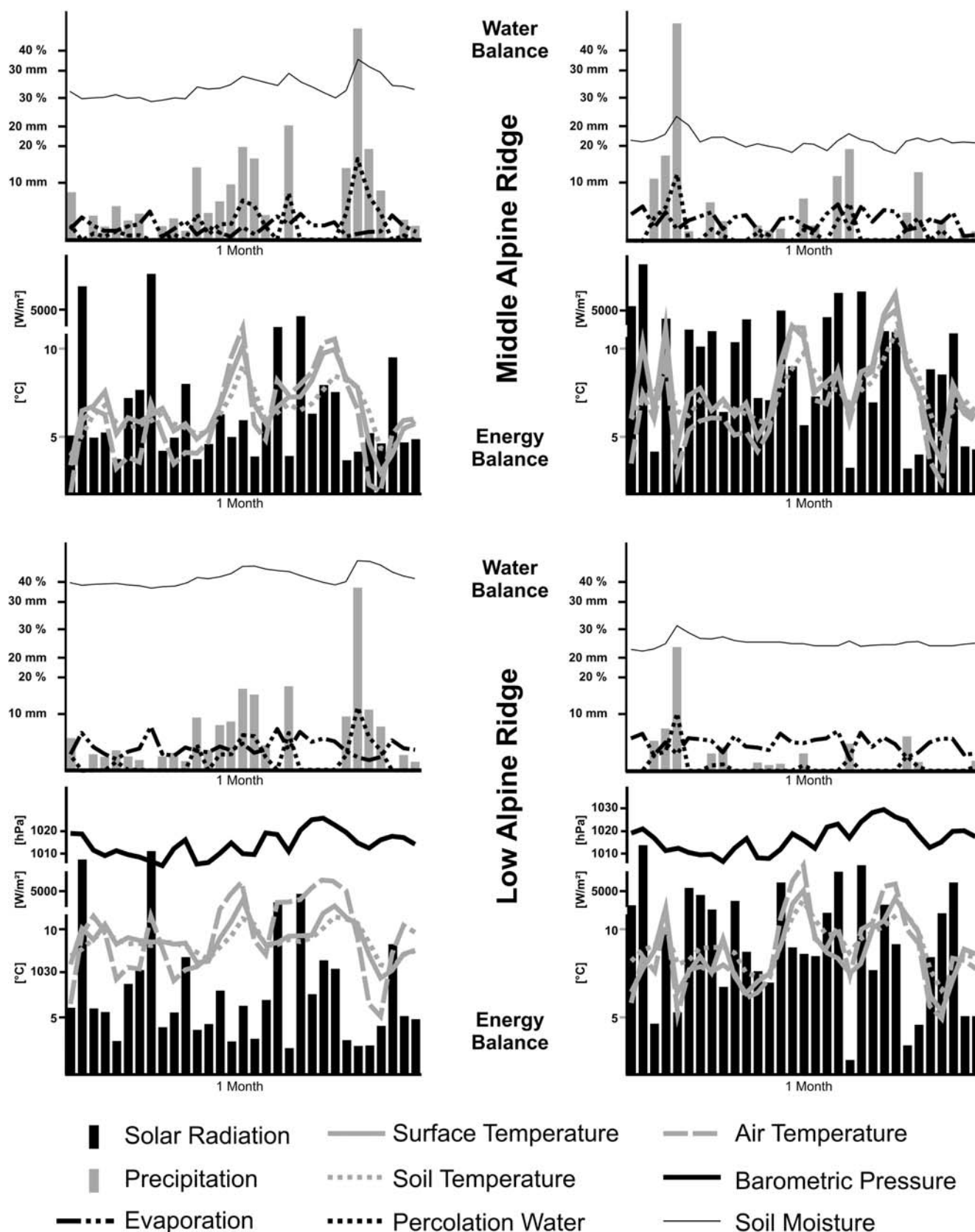


FIGURE 3. Vertical water and temperature fluxes in ridge positions of the low and middle alpine altitudinal belt in western and eastern Norway (raw data from hourly intervals, and evaporation line from daily intervals with interpolated curvature, August 2001). Graphs by R. Pape and O. Rößler.

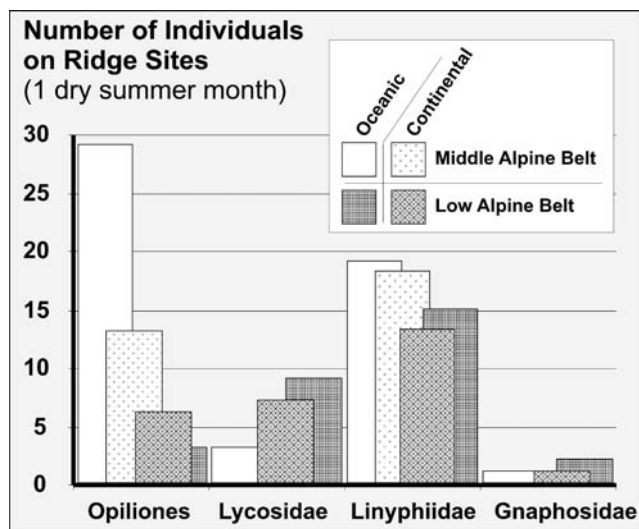


FIGURE 4. Activity of harvestmen and spiders in high mountain ridge positions of the low and middle alpine altitudinal belt in western and eastern Norway (during one dry summer month, August 2001).

variability. Vegetation patterns are highly complex. As an example of the low alpine catchment in the eastern Norwegian mountain region, interactions of landscape structures and hydrological dynamics have been analyzed. Figure 5 shows a map of the distribution of vegetation types in this catchment. Ridge positions are covered by lichen heath of which three different types can be differentiated along a snow cover gradient of 0 to 30 cm thickness. Those sites that are covered by a thicker snowpack are characterized by scrubs or heather; the snow melts off early in summer but gives shelter against late frosts. Late snow beds with maximum snowpack in southern foot-slope position are characterized by *Nardus stricta*, which can survive those extreme conditions with wet but warm and short vegetation periods. Depressions show a mosaic of different mire vegetation types along a moisture gradient.

Snow cover dynamics in continental eastern Norway is the most decisive factor regarding spatio-temporal gradients of ecosystem functioning. As the amount of precipitation is higher with increasing

altitude and snow is not completely blown off the ridges, snowpack during winter is thicker and covers the entire catchment in the middle alpine belt. Here late snow beds last longer than in the low alpine belt. The low alpine catchment in turn is characterized by thick snow accumulations in depressions but snow-free ridges throughout the winter. Snow lasts longest on foot-slopes, but melts off earlier than middle alpine snow beds. Snow-free summers are short and last for 13–15 weeks in the low alpine belt and 11–12 weeks in the middle alpine belt. Figure 6 illustrates the spatio-temporal distribution of snow cover in a low alpine catchment of the continental mountains. According to prevailing wind directions from north to northwest, with highest wind speeds during the winter season, the east-west-oriented valleys receive lee-side snow accumulation at southern-exposed slopes, where snow cover melts off late in June, lasting latest at the foot-slopes. Northern-exposed slopes are characterized by windward snow wreaths that melt off about three weeks earlier than the latest southern-exposed snow beds in the low alpine belt. Ridge positions are +/- snow free during winter, whereas upper slope positions show little snow cover but early snow melt. Depending on the topography in their surroundings, depressions are either the center of maximum snowpack, or due to their wind exposure +/- snow free during winter.

Figure 7 illustrates the spatio-temporal variability of soil moisture conditions, directly corresponding with processes such as frost penetration, snow cover, and snow melt in the same low alpine catchment of the continental eastern Norwegian mountains. The distribution of different soil moisture profiles shows a very large-scaled differentiation according to the pronounced relief conditions. Although ridges and convex slopes show driest conditions throughout the year, these ecotopes have to be characterized by moist soil profiles (see above). This phenomenon can be described as the most decisive hydrological process constellation of the low alpine mountain landscape. As also demonstrated in the figure, concave relief positions tend to wet conditions and function as temporary surface runoff and stagnation ecotopes. Wet conditions are dominantly found during and after snow melt. But as first tracer experiments show, most of the melting water directly rushes downward upon the frozen surface, and therefore passes through the entire mountain catchment before penetrating the ground. Thus, on the one hand, the water equivalent of the snowpack does not result in a higher amount of available water at most of the ecotopes for further ecosystem functioning. On the other hand, late melting of frozen grounds combined with disposability of liquid water in the soils

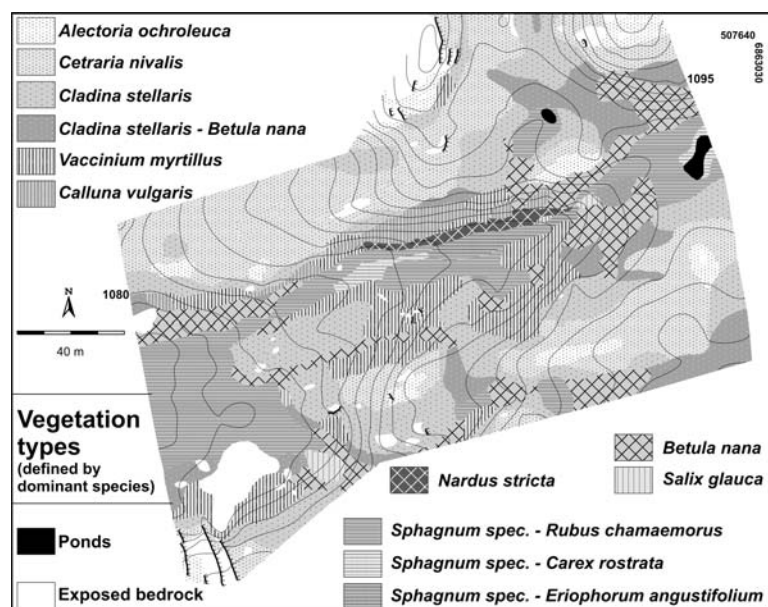


FIGURE 5. Spatial differentiation of vegetation types in the low alpine catchment in continental eastern Norway (Löffler, 1998).

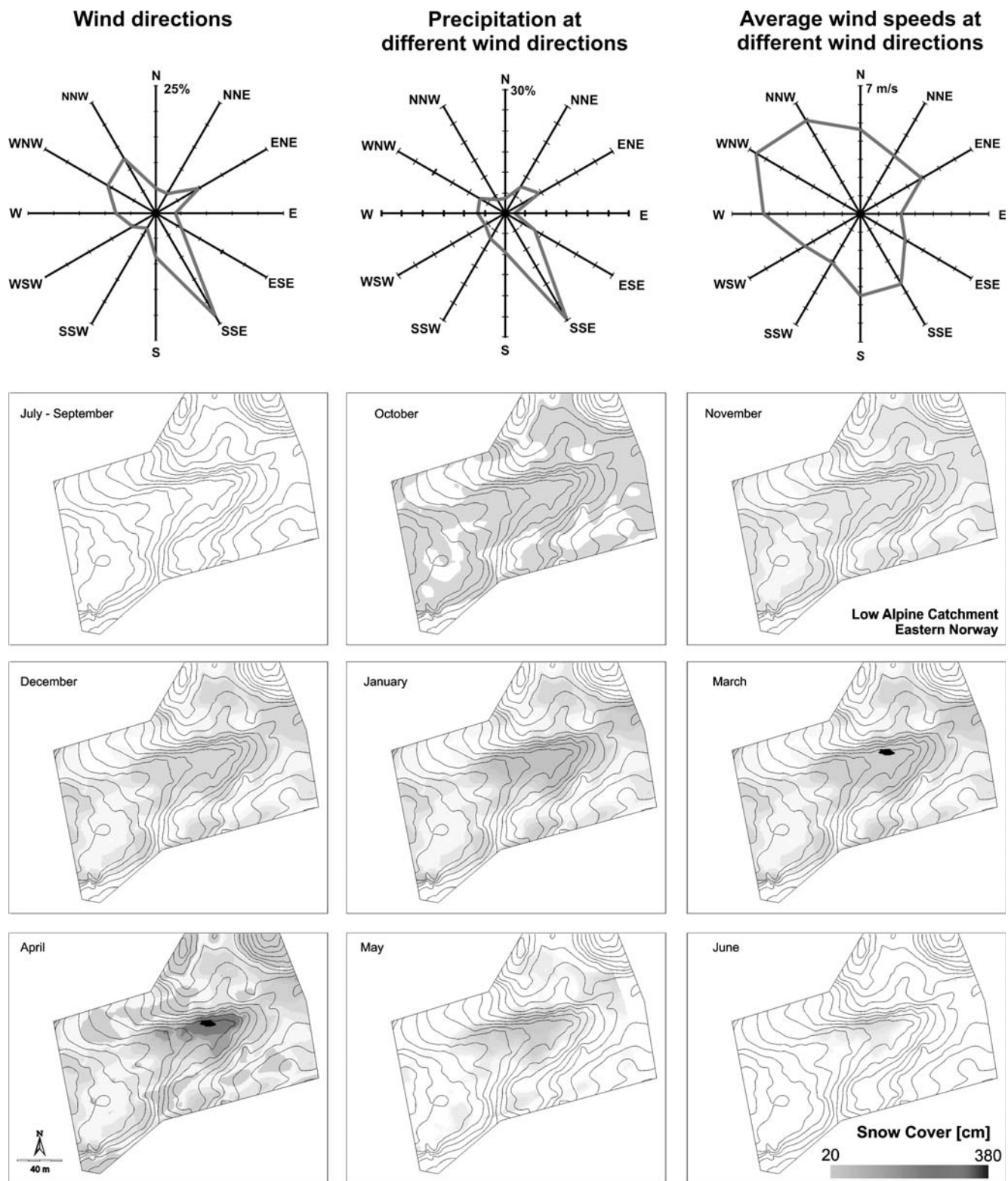


FIGURE 6. Spatial dynamics of snow cover conditions. Formation of snow cover is influenced by prevailing winds, but most important are highest wind speeds during winter. Relief conditions and snow cover layers are examined by leveling ~1000 points and by large-scaled mapping routines during different characteristic periods of the year. Spatial data modeling is based on long-term field experiments and is generalized as to the data's dominant character for the region since 1991. Snow nivellements and maps by D. Wundram and J. Löffler.

during long-lasting winter periods has been proved to be responsible for water fluxes during the summer period. This specific process constellation can be regarded as a particular water balance characteristic of the continental high mountain regions of central Norway. Spontaneous

rainfall events of higher amounts are as well characteristic for continental convective precipitation peaks, but the results in water storage processes just last for hours to a few days. So, these events do not explain the permanently high water saturation in the depressions of

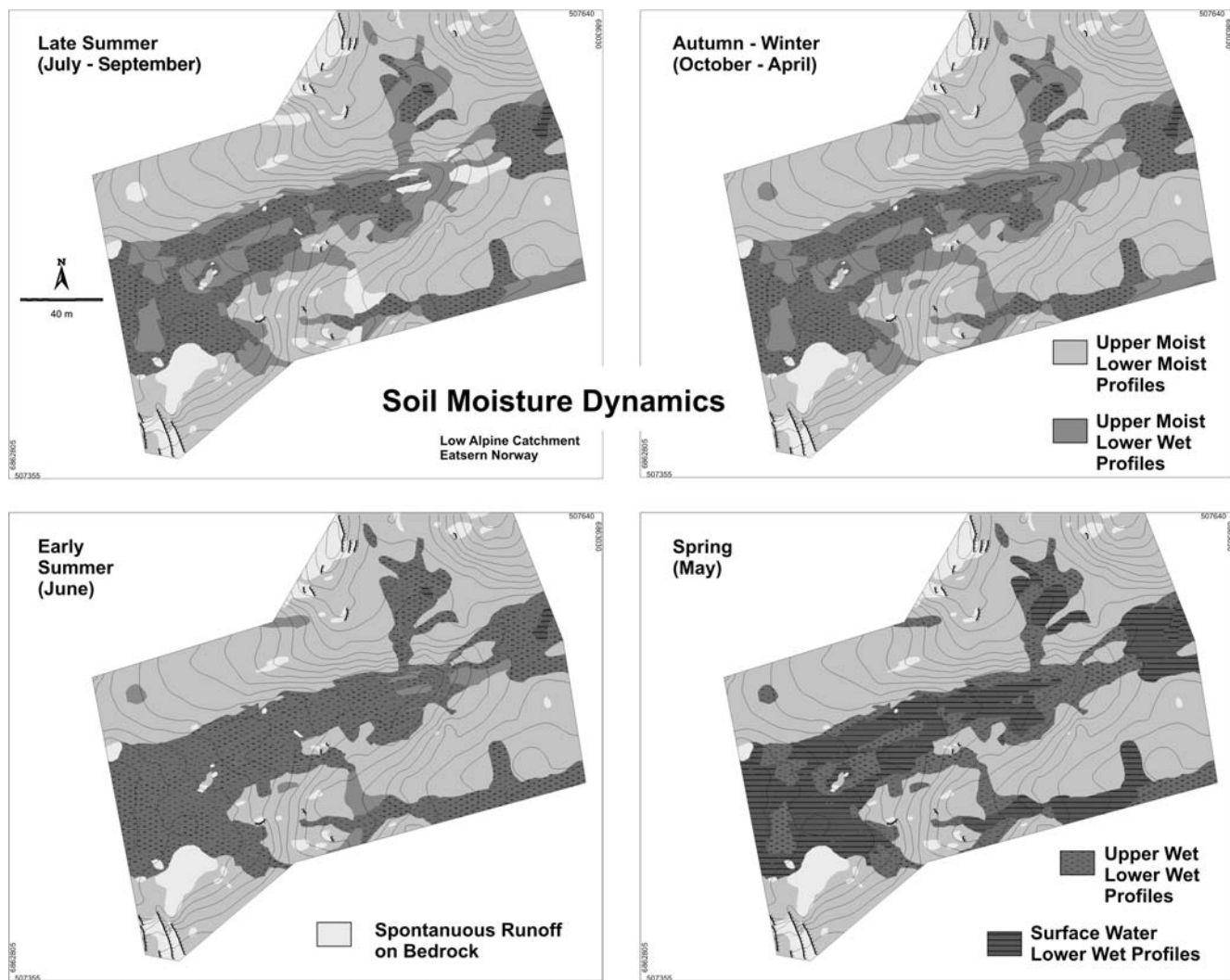


FIGURE 7. Spatial dynamics of soil moisture variability. The maps are based on spatial surface water measurements by water level stations and soil moisture mapping by hand-held TDR-measurements during different seasons (at ~400 points). Data are based on long-term field experiments and are generalized as to their dominant character for the region since 1991. The classification of soil moisture profiles is adapted from Löffler (1998). Short-term temporal changes in soil moisture conditions are examined by continuous TDR-logger measurements at single sites. For technical reasons, variations in frozen moisture conditions are not analyzed during winter except on sites with TDR-loggers, so that the last measurement taken before the winter is conserved until springtime. Measurements and maps by D. Wundram and J. Löffler.

the mountain catchments. Furthermore, a very high amount of percolation water does flow in between the root zone and the near ground passive layer. Root profiles show that most plants are adapted to near-surface conditions as solifluction processes predominantly occur in deeper mineral layers. This additionally means that a huge amount of soil water remains “unused” by the ecosystem, and therefore disposes of interflow and groundwater runoff inside the catchments.

From the investigations of epigeic arthropods that were captured using pitfall traps, animal-activity maps could be derived for different taxa. Despite methodological inconsistency, different species have a different area and intensity of activity around each trap.

Within the groups of indicator taxa that were chosen, results of the spatio-temporal activity dynamics for the carabid beetles are presented in Figure 8. In general, low numbers of species and individuals are characteristic of this beetle family in high mountain habitats in Scandinavia. During snow-free seasons the ridges, upper slopes, and north-facing middle slopes are distinct hot spots of carabid activity in the eastern low alpine catchment. These patterns are consistent during the whole snow-free season. This picture is very much influenced by

the dominant species *Amara alpina*, which prefers lichen heath habitats. Particularly in view of extreme temperature conditions during winter, it is remarkable that highest activity densities are achieved at those locations. *A. alpina* obviously is a species well adapted to cold. At the other plots, activity of carabids are lower or even absent, for example in the small mires or the boulder field. From DCA analyses *Amara alpina* can be regarded as a characteristic species of the lichen heaths, and *Patrobis assimilis* is a differential species, which is found in the moist scrub rich depressions of the catchment.

SYNTHESISING SPATIO-TEMPORAL LANDSCAPE ECOLOGICAL GRADIENTS

Synthesizing landscape functioning principles according to ecosystem reactions, the results from quantifying and modeling procedures are used to explain the different interrelations between the ecosystem compartments. For this purpose, a hierarchical, process-oriented classification of ecotopes is defined by specific landscape functioning attributes. Diurnal and seasonal air, surface, and soil

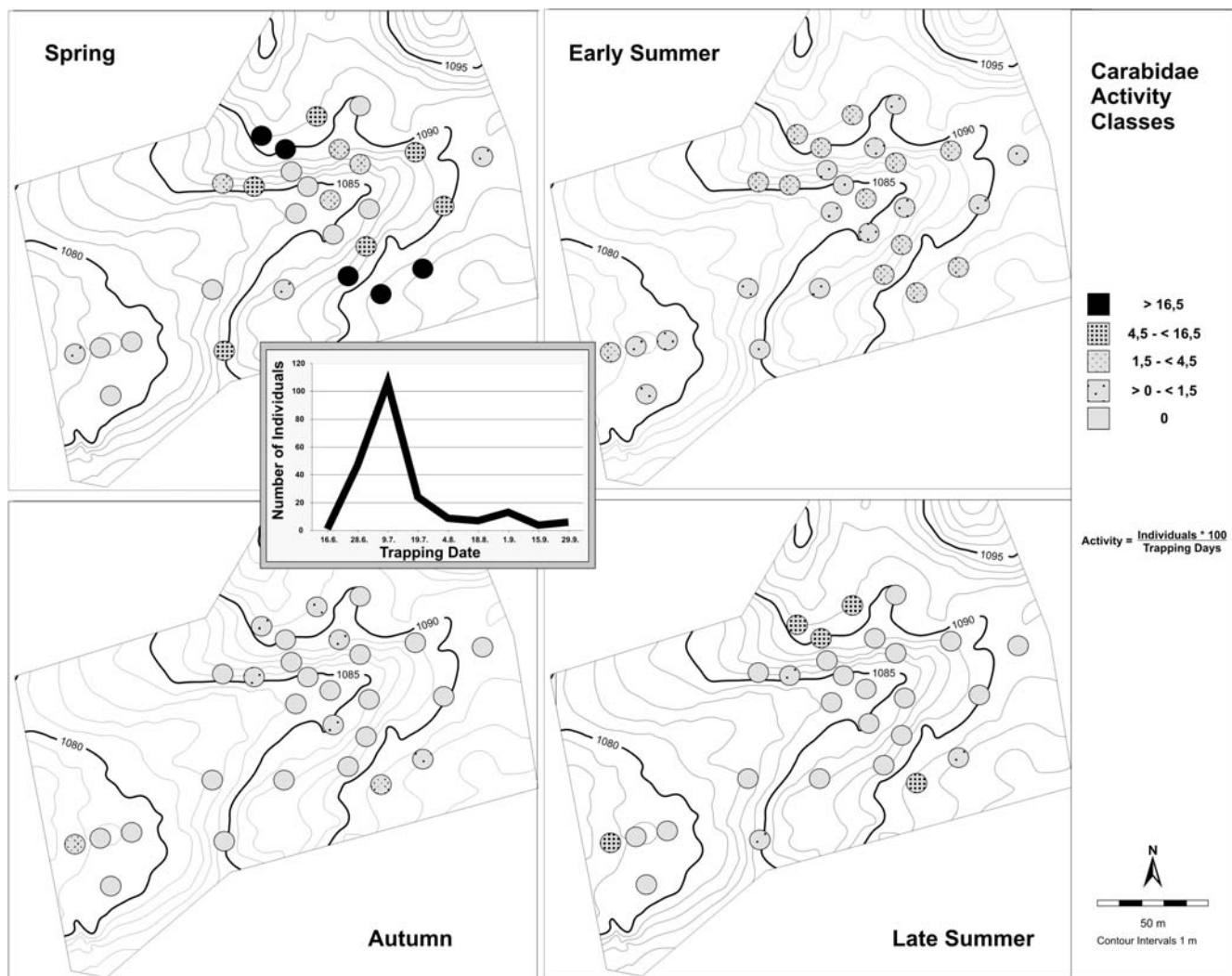


FIGURE 8. Spatio-temporal map of activity-density of ground beetles. The map is based on pitfall trap catches during the whole snow-free season of the year 2001, with 85 traps. Data and maps by J. Naujok.

temperature variations are used to aggregate dynamics of different functional features and are demonstrated by means of thermoisopleth diagrams for each type of structurally delimited ecotope. Differences along spatial and temporal temperature gradients are illustrated for the low alpine belt, showing a space- and time-scale characterization of ecosystem functioning.

Pronounced daily air and surface temperature dynamics during the summer in all ecotope types show different quantities within similar rules. Higher soil moisture content leads to less expressed differences, while the slope aspect is the most determining factor according to diurnal variations. Summer daily soil temperature dynamics are decently distinct on ridges and southern exposed slopes, but hardly found in northern exposures and depressions. Annual variations of the spatial air temperature distribution depend on snow cover thickness and duration of snow cover, but are extremely pronounced between summer and winter seasons. Ecotopes with thick snow cover are contrasted against those without snowpack as to the duration of transitional seasons. Spring and autumn air temperature dynamics combined with frost activity and freeze-thaw processes are temporarily distinct in ridge and upper slope positions as well as in wind exposed plain depression, while reduced to a few days in snow bed ecotopes. The seasonal variations of surface temperature dynamics are similar to that of the air, but buffered according to the isolation effects of the vegetation, and reinforced by soil moisture and snow cover conditions.

Annual variations of the soil temperatures are still slightly pronounced in well drained and less snowy ecotopes as well as wind exposed plain depressions; wet and snowy ecotopes do not show any seasonal dynamics for soil temperature.

Spider activity within the transect has been analyzed so far for four trapping positions and three trapping periods. Highest spider activity was measured in the depression. Here mainly small linyphiids contribute to the high values. Their abundance in this case obviously is favored by moist and mossy conditions. On the other hand, as expected because of unfavorable temperature conditions, activity was lowest on the north-facing slope. During the snow-free season at all four positions, a clear spring peak of activity was observed. During summer, activity was always very low, whereas in autumn activity increased again. The spring peak of activity may be explained by mating activity and activity in context with reproduction (e.g., searching for favorite conditions for the egg cocoon) of most spider species. A consequence of this activity early in the snow-free season is the lack of activity during summer; reproduction has taken place and most of the spiders are inactive (e.g., in egg stage, as juveniles in webs, most adults die after reproduction). In autumn, searching behavior for hibernation habitats may cause the second peak of activity (Fig. 9).

Another example is the fieldgrasshopper *Melanoplus frigidus* (Fig. 10). Its distribution pattern can be correlated with the high temperatures of the south-facing slope during summertime. These

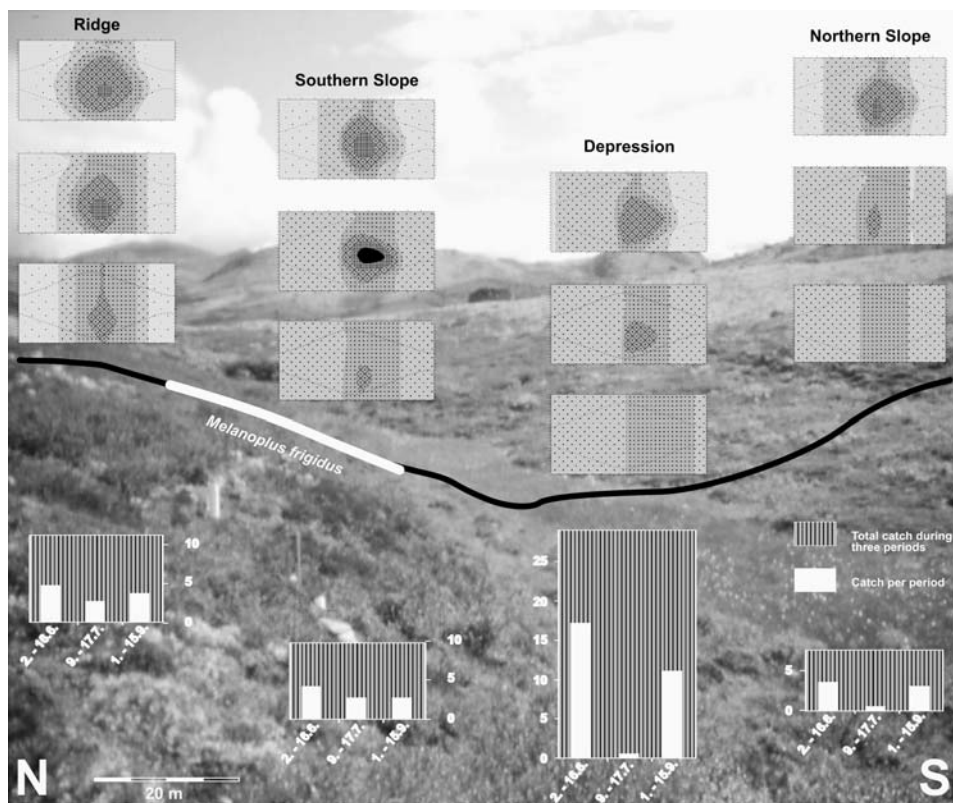


FIGURE 9. A schematic profile along a characteristic relief gradient illustrated by means of thermoisopleth triples, spider activity during three trapping periods, and occurrence of the fjeldgrasshopper *Melanoplus frigidus*. Legend is given in Figure 11.

temperatures are the highest measured within the whole transect through the catchment. These sites are characterized by a specific vegetation of, e.g., *Vaccinium myrtillus* and *Calluna vulgaris* shrubs (Fig. 9). The thick snow layer during winter and the occurrence of late snow beds at the foot of the south-facing slope isolate the soil, so that in these areas, where *M. frigidus* is assumed to lay its eggs, frozen soil occurs only very sporadically and only at the soil surface. *Nardus stricta* that survives these extreme conditions may serve as food resource for the fjeldgrasshopper.

Temperature data are classified into seven temperature intervals for spatial ecological interpretation. A legend for each ecotope describes those temperature intervals and their ecological significance by means of 13 different scaled landscape ecological parameters. Moreover, temper-

ature attributes show the duration of daily means, duration of frosts, the annual amplitude, and the duration of daily maximum (Fig. 11).

Conclusions and Discussion

Landscape ecological gradients are regarded as spatio-temporal phenomena. Analyses of different spatial scales show that the determining factor for high mountain ecosystem functioning is the topography, which influences landscape functioning more than any other structural factor. Broad-scale gradients within the oceanic-continental continuum of the Norwegian high mountains can be characterized by the blocking of the advective air stream configurations by the meridional shaped Scandes. Therefore, the western slope of the mountain chain is expected to be wet, while the eastern slope shows drier conditions within a convective pressure system during summer. New results reveal that the driest sites in ridge positions show high soil moisture profiles throughout the year (Löffler, 2003, 2005). Temperature and soil moisture gradients along the altitudinal and longitudinal gradients determine arthropod activity by means of cooling and wetness during summer. It has also been demonstrated that fine-scale landscape ecological gradients have to be explained by the dynamics of snow cover in small catchment areas explicitly including formation, thickness, duration, and snow melt. Additionally, the distribution of arthropods along spatio-temporal temperature and soil moisture gradients has been proved.

Ecosystems are primarily characterized by material cycle and energy fluxes. Boundaries between ecosystems are often not very clear. Thus, the spatial existence of an ecosystem is often defined arbitrarily. Ecosystems in turn are structured heterogeneously and build up a complex organization of different elements. Although not very obvious, gradients between single elements are found (internal heterogeneity), while at a spatial scale gradients between different ecosystems are visible (transitional heterogeneity) (Keddy, 1991; Turner, 1989; Wiens, 1995), the latter being the object of this article.



FIGURE 10. The fjeldgrasshopper *Melanoplus frigidus*. (Photo: O.-D. Finch)

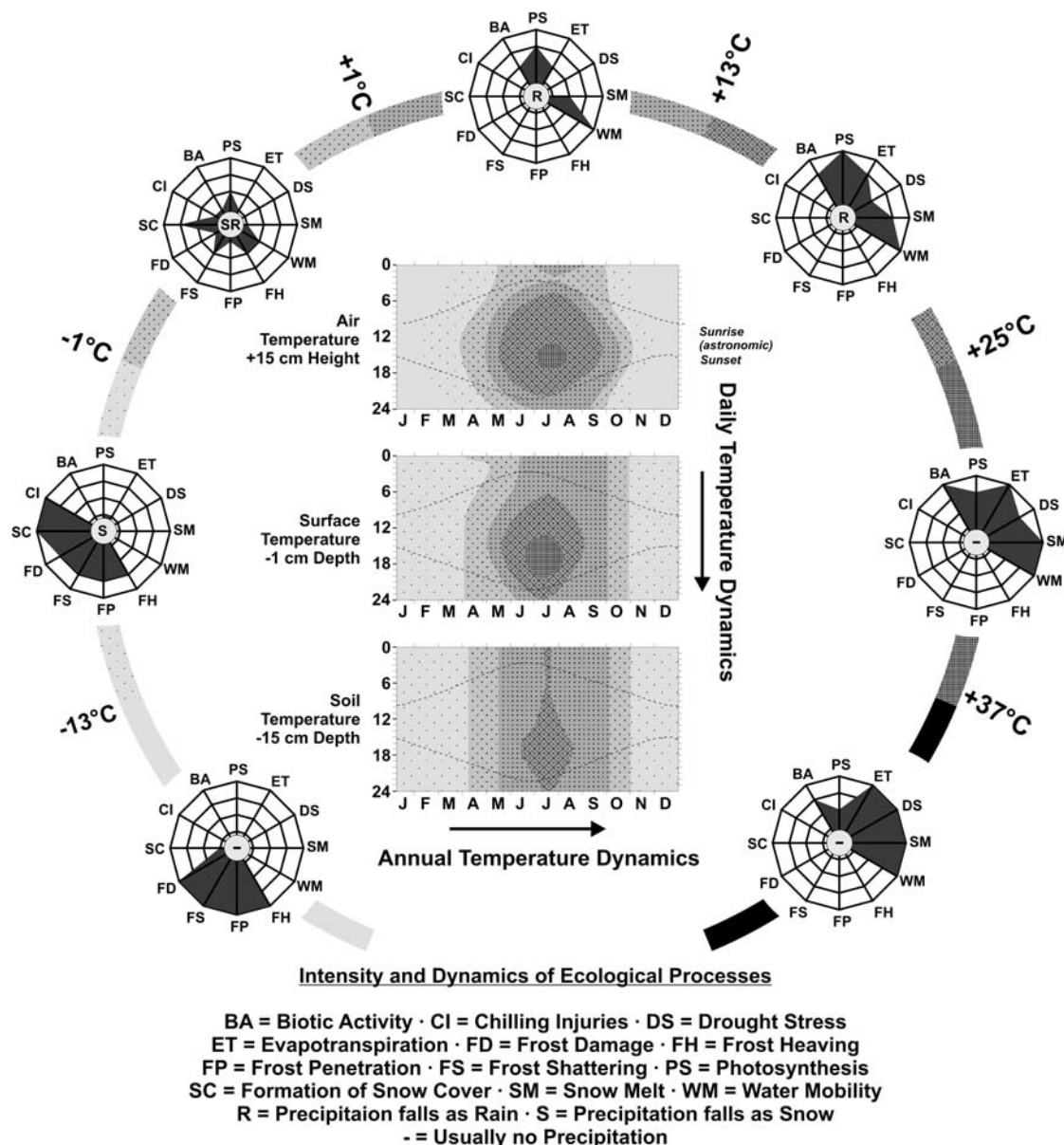


FIGURE 11. Legend for the landscape ecological profile in Figure 9 (Löffler and Wundram, 2001). The figure shows a complex scheme, systematically scaling temperatures according to their landscape ecological influence on ecosystem functioning. A triple of air, surface, and soil thermoisoopleth diagrams shows daily and annual changes of 7 different ranges of temperatures with similar ecological values for a particular site. The temperature ranges subdividing the outer circle of the diagram into 7 circle segments are grouped according to literature data, our own investigations, and theoretical considerations on 13 landscape ecological process attributes. Processes like photosynthesis, evapotranspiration, drought stress, etc., are in their turn scaled on the individual axes within the small net circles according to their ecological influence under those temperature conditions (from the inside to the outside: no, little, moderate, high, and extreme influence). For example, temperatures under -13°C are defined as no photosynthesis is done by any species; evapotranspiration is extremely reduced; processes like drought stress, snow melt, water mobility, etc., are absent but there is danger of severe frost damage to plants; there is frost weathering of minerals and bedrock; frost penetration is extreme; frost heaving takes place; and there is usually no precipitation. As shown by the example of the thermoisoopleth triple (low alpine ridge site), those conditions are only found within the air temperature at $+15\text{ cm}$ height during the whole day in December and January and during the nights in November and February.

When it comes to transitional heterogeneity of ecosystems, at every single point of the Earth's surface landscapes can be regarded as spatially homogenous with a vertical complex structure that determines vertical fluxes of energy and matter. With reference to Keddy (1991), gradients obviously organize environmental and biotic heterogeneity for generating and testing hypotheses. Relations among environmental conditions, distributions, abundance, and traits can easily be explored. Continuous gradients show conspicuous zonation patterns. Discontinuous gradients are constructed by the researcher, either by ordering patches per definition (direct gradient analysis), or by using

multivariate techniques (indirect gradient analysis). Different concepts of such continuous and discontinuous gradients, addressing the internal heterogeneity of ecosystems, have been worked upon (Kratochwil and Schwabe, 2001) (Fig. 12).

Based upon the concept of scales and dimensions, gradients are found between different landscape units. Entering from the micro-spatial dimension to the next larger one, boundaries between single ecosystems will appear as essential organization patterns of the next larger ecosystem. Thus, the most important and most thrilling question is: Which contemporary appearance of organization patterns is

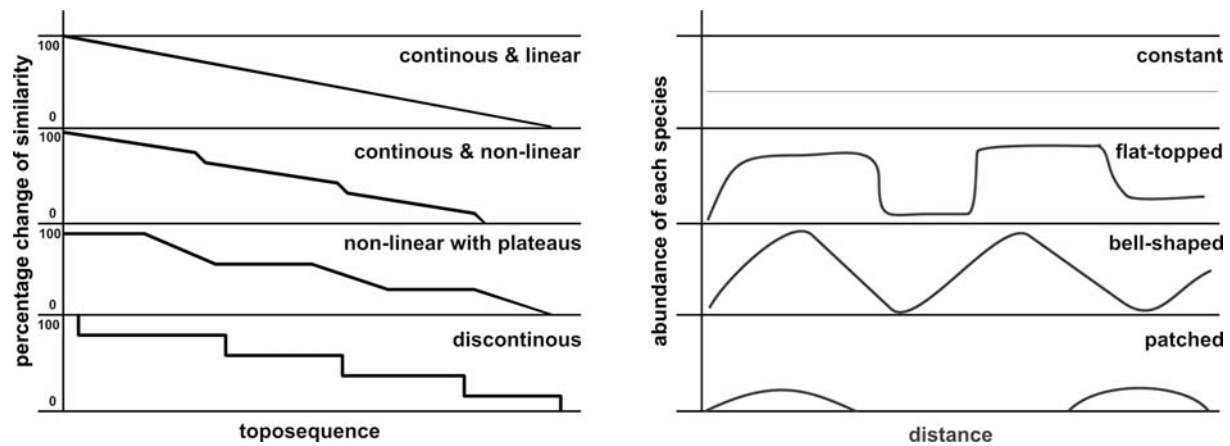


FIGURE 12. Different concepts of ecological gradients (after Scott, 1974, and Forman and Godron, 1986).

emerging on a higher spatial level of abstraction? In this frame the investigation of gradients contributes to different spatial scales respective of the theory of the geographical dimensions (Neef, 1963).

Figure 13 sums up the results of this paper. Ecosystem dynamics during the summer is determined by the topography that in turn directly defines surface heating. Low summer temperatures are most important for arthropods. Moreover, summer precipitation influences soil moisture dynamics, but late melting of frozen ground determines interflow and corresponding high soil moisture conditions during dry seasons, while snow melt is interior as runoff takes place above frozen ground. On the contrary, wetness positively influences the differentiation of animal species habitats. Summer surface warmth instead does not support specific activity of animals, while cool conditions are most determining. A lack of soil moisture does not occur at any site in the mountains and is therefore not limiting. During winter, extreme cold and harsh conditions occur and ecosystem functioning is mostly determined by snow cover thickness (isolation effects) and duration of snow cover (beginning, end, and length of the vegetation and animal activity period). Snow cover distribution corresponds with topography and strongest prevailing winds during winter, while thick snow cover negatively determines frozen ground. Surface and soil temperatures are positively determined by snow cover. The survival of plants and animals is determined by snow during periods of lowest temperatures,

so that the distribution of biocoenoses follows a gradient along spatial snowpack distribution.

Gradients in northern high mountain ecosystems are mostly determined by snow cover (Vestergren, 1902; Gjaerevoll, 1956; Dahl, 1956; Billings and Bliss, 1959; Barbour et al., 1991; Holtmeier and Broll, 1994; Stanton et al., 1994; Walker et al., 2001). The gradient of structural snow cover distribution is associated with the time in autumn when snow begins to cover the ground, the thickness of snow during winter, and the time of melting off in spring and summer. Results of a long-term analysis show that the local temperature balance has to be regarded as the superior factor for physical, chemical, and biotic process determination in the Norwegian high mountain ecosystems (Löffler and Wundram, 2001, 2003; Löffler, 2002).

The fundamental problem of landscape ecological gradient determination corresponds to the ecosystems as dynamic entities constantly responding to changes within themselves, their spatial arrangement, and the heterogeneity of ecosystem patterns (Forman and Godron, 1985). The integration of a process-oriented approach within this study has led to a multidimensional scheme of gradients across several spatio-temporal scales (Fig. 14). This last figure sums up the results using soil moisture, temperature, and animal activity between longitudinal, altitudinal, and topographical spatial changes of ecosystem dynamics. Moreover, temporal dynamics of animal activity,

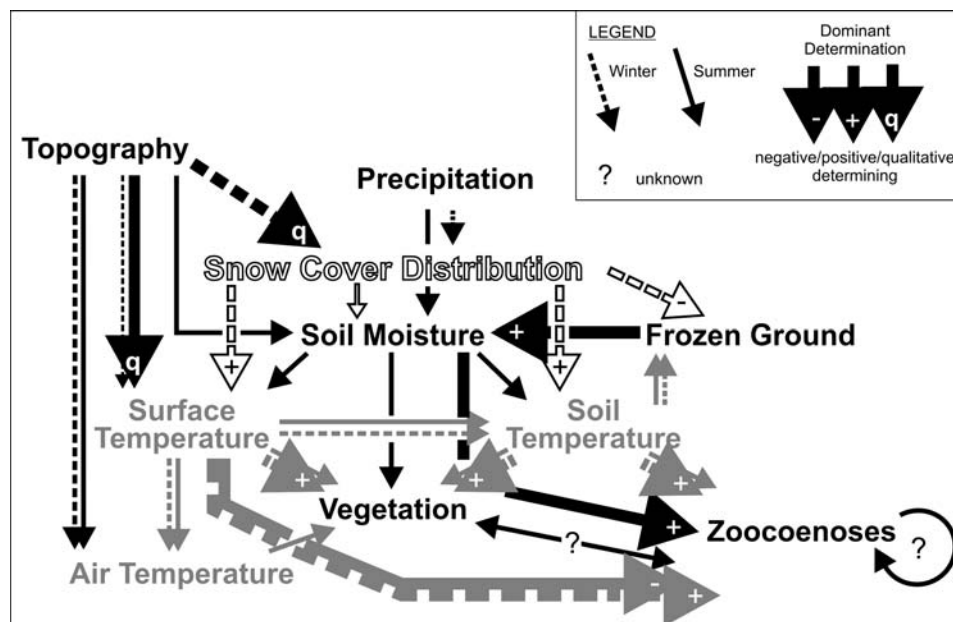
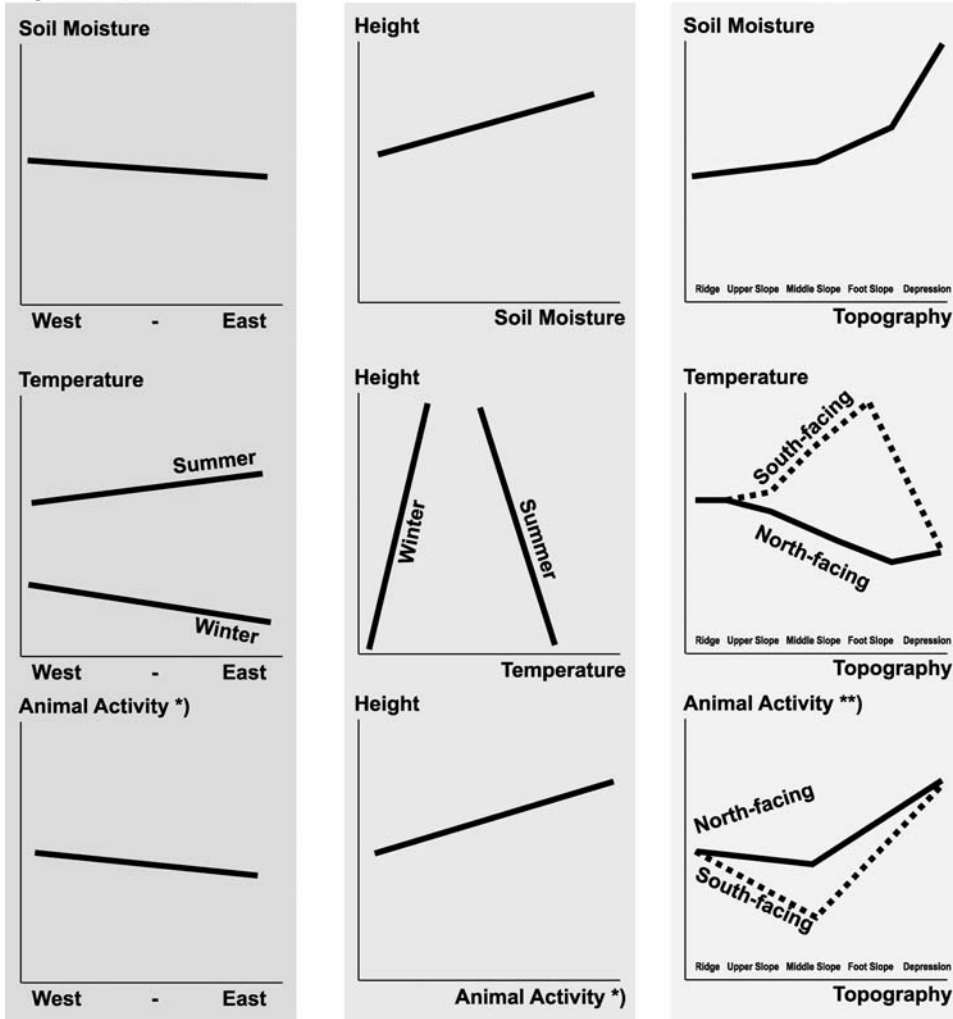


FIGURE 13. Complex model of ecosystem functioning in the high mountains of Norway showing major and minor determination of organism distribution and activity according to summer and winter environmental conditions.

Spatial Gradients



Temporal Gradients

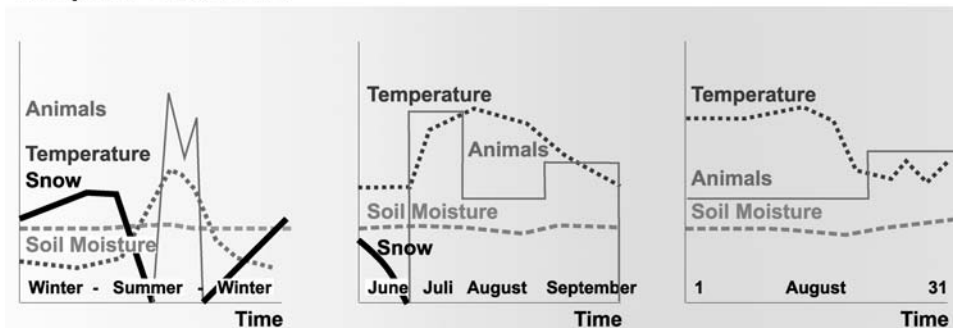


FIGURE 14. Multidimensional spatio-temporal gradients generalized from investigations of ecosystems on different scales. All trends are preliminary, exaggerated, and non-scaled (*—derived from catches of spiders and harvestmen during one dry summer month, **—based on carabid and spider activity during three periods of pitfall trapping of a vegetation period). Data on temperature, soil moisture and snow cover from long-term measurements.

temperature, snow cover, and soil moisture are compiled. Determining ecosystems by means of such a multidimensional procedure composed of multiple regressions allow modeling of complex gradients in high mountain landscapes. The extremely generalized trends shown in Figure 14 will be used as a hypothesis for further investigations. The future task is to prove and quantify the spatio-temporal gradients between the high mountain ecosystems of central Norway.

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