MICRO-CLIMATIC DETERMINATION OF VEGETATION PATTERNS ALONG TOPOGRAPHICAL, ALTITUDINAL, AND OCEANIC-CONTINENTAL GRADIENTS IN THE HIGH MOUNTAINS OF NORWAY

With 7 figures, 2 tables, 4 photos, and 3 supplements (VII, VIII, IX)

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Zusammenfassung: Mikroklimatische Steuerung von Vegetationsmustern entlang topographischer, höhenwärtiger und ozeanisch-kontinentaler Gradienten im norwegischen Hochgebirge.

Allgemeine Annahmen hinsichtlich der umweltbedingten Steuerung der norwegischen Hochgebirgsvegetation werden vor dem Hintergrund neuer Ergebnisse eines landschaftsökologischen Langzeitprojekts hinterfragt. Einige der geläufigen Erklärungsversuche erweisen sich als unzureichend und werden unter Berücksichtigung verschiedener geographischer Dimensionen überarbeitet: a) Die kleinräumige Reliefdifferenzierung wird innerhalb von zwei Kausalketten für die Steuerung der Vegetation verantwortlich gemacht. 1. Exponierter Standort – geringmächtige Schneebedeckung – starke vorherrschende Winde – erhöhte Verdunstung – Mangel an verfügbarer Bodenfeuchte – Dürrestress – kalte Winter aber lange Vegetationsperiode; und 2. Leelage – mächtige Schneebedeckung – Schutz vor Wind und niedrigen Temperaturen – ausreichende Wasserversorgung aber kurze Vegetationsperiode. Quantifizierungen von Bodenfeuchte und Mikroklima belegen, dass Wassermangel selbst unter extremsten Bedingungen zu keiner Zeit auftritt. Stattdessen zeigen sich komplexe raum-zeitliche Temperaturgradienten als übergeordnete Einflussgrößen. b) Der Höhenstufenwandel wird im Allgemeinen durch die höhenwärtige Abnahme der Temperaturen bei gleichzeitiger Zunahme der Niederschläge erklärt. Dabei werden höhere Lagen grundsätzlich mit extremeren Lebensbedingungen assoziiert. Ganzjährige mikroklimatische Untersuchungen zeigen, dass höhere Niederschläge in größerer Meereshöhe mit einer früheren und mächtigeren Schneedecke gekoppelt sind und die niedrigsten Temperaturen zur Zeit winterlicher Inversionswetterlagen in den tieferen Lagen am stärksten wirken; hier ist die Schneedecke am geringsten und die Gefahr der Frostschädigung in Oberflächennähe am bedeutendsten. c) Der ozeanisch-kontinentale Wandel wird mit einer charakteristischen übergeordneten Vegetationsdifferenzierung verknüpft. Der Westen der Skanden erhält bei gemäßigten Temperaturen höchste Niederschlagssummen, die mit deutlich feuchteren Verhältnissen gegenüber dem trocken-warmen Osten charakteristisch ozeanisch-kontinentale Vegetationsunterschiede bedingen sollen. Es zeigt sich, dass einzelne Pflanzenarten eine statistische Bindung an die Klimaregionen aufweisen, jedoch unter vergleichbaren Standortbedingungen gleiche Vegetationstypen ausgeprägt sind. Trotz großer Feuchteunterschiede sind Flechtenvegetationstypen entlang des West-Ost-Gradienten mit ähnlicher Artenzusammensetzung verknüpft. Die Ähnlichkeit der Umweltbedingungen wird als Grund für fehlende Vegetationsunterschiede herausgestellt.

Summary: General assumptions regarding on environmental determination of the Norwegian mountain vegetation are scrutinized as to new results of a long-term landscape ecological project. Some explanations are insufficient regarding different spatial scales: a) the fine-scale topography is supposed to impact upon the vegetation within two causal chains. 1. exposed site – thin snow cover – strong prevailing winds – enforced evapotranspiration – lack of soil moisture – drought stress – cold winters but long vegetation period, and 2. lee slope – thick snow cover – shelter against winds and low temperatures – good supply of water but short vegetation period. Quantification of soil moisture and micro-climate shows that a lack in water availability is not found at any time. Instead, complex spatio-temporal temperature gradients affect the vegetation superiorly. b) Moreover, the altitudinal gradient across the alpine belts has been explained by temperature and precipitation means that are corresponding with specific changes in the vegetation. Higher elevations are principally combined with harder environmental conditions. Results of micro-climatic measurements provide evidence that higher precipitation results in earlier and thicker sheltering snow cover in higher elevations. Thus, the lowest temperatures are found in lower elevations as to inversions, where snow cover is thinnest and frost damage has the greatest effect. Vegetation determination functions by prevailing near surface temperatures. c) Finally, continental-oceanic gradients are expected to contrast in superior vegetation patterns. High precipitation in western Norway differs from the lowest found in the eastern parts, indicating continental mountains being dry and warm during summer. Consequently, mountain vegetation is differentiated into oceanic and continental types. On the one hand, plant species distribution along that broad-scale gradient is statistically evident. On the other, equal topographical conditions show the same vegetation types in east and west; lichen-dominated associations show similar species compositions. Similarities in environmental features are stressed as superior determinants for equality of vegetation.

1 Introduction

This paper is based upon experiences during a long-term research project established in 1991 (Köhler et al. 1994; Löffler 1998; Löffler u. Wundram 2001). The aim is to synthesise quantified results on specific locations along different ecological gradients. It is framed by many other case studies on Fennoscandian alpine vegetation; recent supplements of literature are given by Dahl (1998), Wielgolaski (1998), and Moen (1999). Among those, many papers result from the *International Biological Programme* (Rosswall a. Heal 1975; Wielgolaski 1975; Bliss et al. 1981). Some additional supplements, partly from unpublished references, are gives by Fremstad (1997). Comparative research has been done on the functioning of ecosystems in northern Norway and the Alps (Mosimann 1985). The investigations led to profound knowledge of alpine environments quite early (Fries 1913, 1917; Nordhagen 1928, 1943; Kalliola 1939; Knaben 1950; Dahl 1956; Gjærevoll 1956). Hence, scientific challenges in the mountain geography of northern Europe are still to intensify research on fine-scale temperature and snow cover determinants, and superior broad-scale oceanic-continental gradients (Fægri 1972).

Many results of Fennoscandian mountain vegetation surveys from the past are found in concordance with geographical theory given by Lautensach (1952). Current assumptions regarding vegetation determination by a) topography, b) altitude, and c) region are undisputed. Consequently, the Norwegian alpine vegetation types are explained by a combination of different factors: topography – snow cover – soil moisture – substrates including nutrient status – ground frost activity – and regional and local climate (Fremstad 1997). Relevant hypotheses and derived research questions are:

a) Fine-scale vegetation patterns are explained by superior topographical gradients that most decisively affect the snow cover (Walker et al. 2001). Within this frame topographical gradients are correlated with higher soil moisture according to snow melt figures (Dahl 1956). Relief also determines insolation, and resulting warming combined with strong winds increase the evapotranspiration, and turns to drought stress (Isard a. Belding 1989). Relatively elevated sites, where the soil dries and warms quickly, additionally lose water as to position and slope gradient (Molenaar 1987). According to Gjærevoll (1990) the vegetation of snow-free areas consists of species adapted to low temperatures and strong winds, where they have to survive the winter severely exposed to drought. Thus, dominant species are xerophilous, forming various chionophobous communities and having longer growing seasons. Chionophilous plant communities are not exposed to particular low temperatures but are well supplied of moisture. At the upper margin of a snow drift the soil dries out rapidly, whereas lower slopes are irrigated. Exposed heaths are characterised by xeromorphic vascular plants and a number of lichens. Where snow lasts longest *Salix herbacea* becomes increasingly dominant. As a consequence, a characteristic gradient is explained by "dry ridges – moist slopes – wet depressions" (Billings 1973), although dry conditions or even droughts have not been measured (May 1976). As Tranquillini (1964, 1979) noted, summer drought is seldom subject to European alpine plants; some evergreen species suffer from ground frost-induced drought stress during winter. Obviously, it makes an important difference to explain vegetation patterns by a lack of soil moisture availability, air humidity, or frost-induced drought. Within this frame, substrate conditions and soil properties have also been found to determine the vegetation patterns by drainage, nutrient availability, and correlated conditions (Burns 1980; Stanton et al. 1994). If so, spatial patterns of those different ecological determinants should be found in reasonable accordance with the vegetation. Some links in the causal chains interpreting vegetation along topographical gradients are found to be non-transparent (Köhler et al. 1994).

b) The adiabatic air mass distribution affects different altitudes as precipitation increases and temperatures decrease with height, superimposing topographic and seasonal deviations (Barry 1992). Thus, effects on mountain plants and vegetation are found in accordance with mean values of temperatures and humidity (Fægri 1972; Myklestad 1993; Huggett 1995). Following Gjærevoll (1990), woody species drop out with increasing altitude and the vegetation gradually assumes a snow bed character due to reduction in the growing season. Arguments that address the vegetation period are often found in addition to overlaying mean meteorological data, especially concentrating on the summer temperatures (Dahl 1987). These are considered to be determined by altitudinal gradients, along which species are physiologically adapted (Dahl 1998). But since conditions and vegetation patterns in the higher elevations are not well known in Norway (Fremstad 1997), the importance of those factors as vegetation determinants might also be scrutinised. How are micro-climatic conditions influenced along the altitudinal range? What are the determinants of the environment that in turn influence the vegetation? Finally, which are the most superimposing parameters responsible for the emerging altitudinal vegetation gradient?

c) A high frequency of zonal circulation types influences northern Europe, accompanied by a west-east gradient from advective to convective precipitation genesis (WEISCHET 1995). The influence of the Scandes as barriers within this Atlantic western drift results in a clearly defined oceanic-continental gradient along a short distance. In central Norway the most continental climate is found 150 km east off the coast, resulting in spatial differentiations of all climate factors (WALLÉN 1970). This gradient covering areas with 300–2,000 mm of precipitation is supposed to have a superior influence on the mountain vegetation (DAHL et al. 1986). Five climate sections are divided (JÄGER 1968; MOEN 1999): "O3 highly oceanic section", "O2 markedly oceanic section", "O1 slightly oceanic section", "OC indifferent section", "C1 slightly continental section". These sections are used to distinguish between regional distribution patterns of vegetation types (FREMSTAD 1997). It is assumed that the vegetation differs fundamentally across the regions (LAAKSONEN 1976; TUHKANEN 1986; MOE 1995; MOEN a. ODLAND 1993; MOEN 1999). Ecological explanations should not be based on single plant species, their physiological adaptation, or their floristic history. The above discussions a) and b)

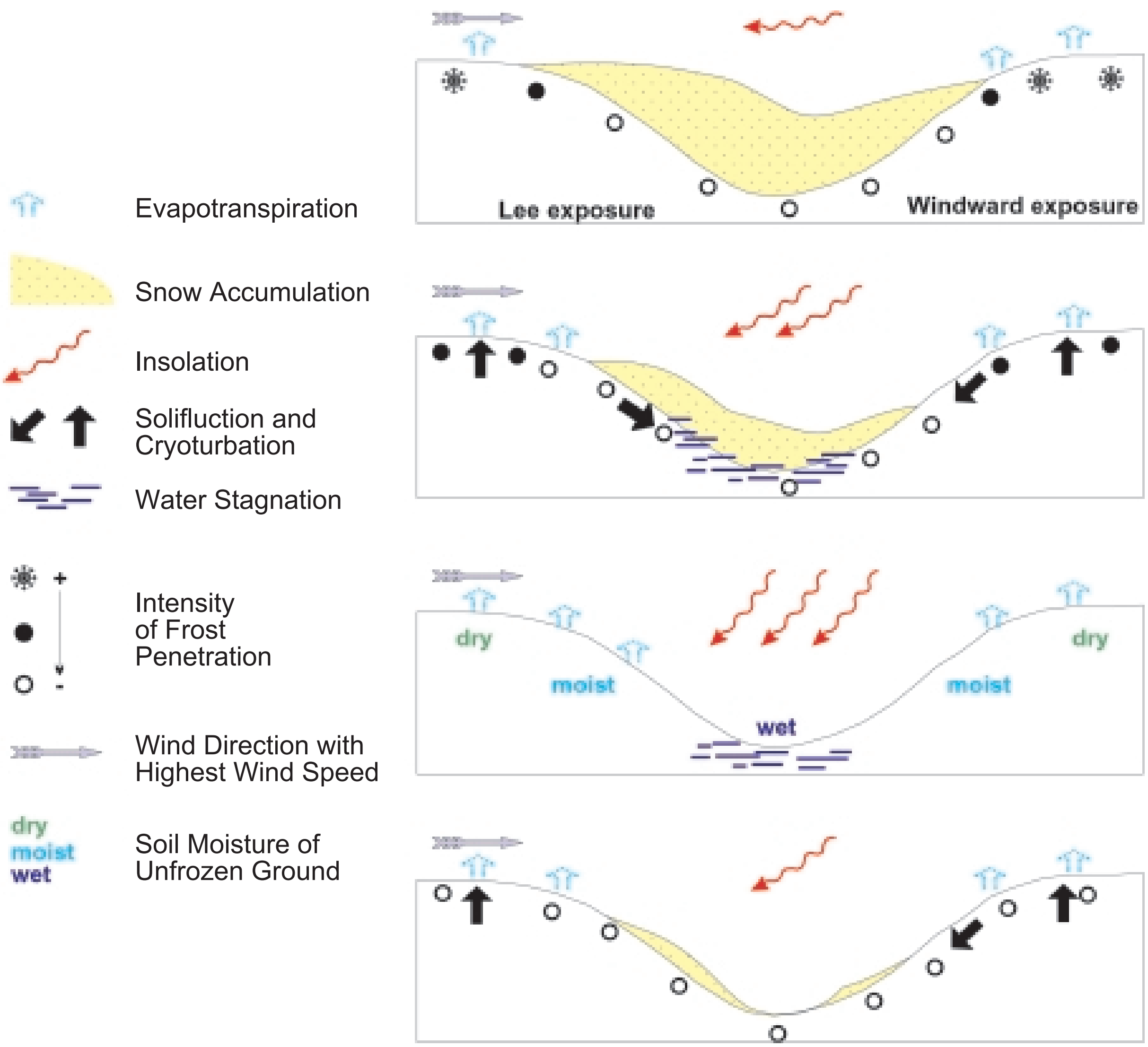

Fig. 1: Mountain vegetation determination along fine-scale topographical gradients – common hypotheses (after: BILLINGS 1973; KÖHLER et al. 1994)

Geläufige Hypothesen zur Steuerung der Hochgebirgsvegetation entlang von kleinräumigen topographischen Gradienten show that fine-scale gradients and altitudinal changes have to be covered by overlaying regional determinants. So, what makes the regional differences in the mountain vegetation? How can those possible broad-scale vegetation patterns be explained by environmental determination?

Figure 1 sums up common hypotheses on fine-scale determination of mountain vegetation. Assumed hypotheses of spatial patterns of the alpine vegetation along altitudinal and oceanic-continental gradients are given with figure 2. The figure shows a scheme of summer and winter temperatures, as well as humidity gradients with altitude and region. The east-west orientated mountains are comprised of different altitudinal belts (hatching) and a generally assumed vegetation change from the continental (transparent) to the oceanic region (grey). The three-dimensional system is structured by straight lines that span vector plains; these illustrate the spatial semi-quantitative change of the three environmental variables.

2 Study areas

The investigations were carried out in central Norway. A broad-scale transect has been used along the climatic gradient, resulting in latitudinal and altitudinal observations. Four investigation areas were chosen as representative catchments and delimited in the low and middle alpine belts. The eastern investigation area ranges from the tree line at about 1,000–1,050 m to the highest peak (Blåhø, 1,618 m). The transition zone between the low and the middle alpine belts is found at around 1,350 m. The alpine environment within the western investigation area reaches from the tree line at about 840–880 m to the highest peak (Dalsnibba, 1,476 m a.s.l.). The low-middle alpine transition zone ranges from 1,100–1,200 m a.s.l. (Fig. 3).

The continental-most (C1) region Vågå/Oppland (ca. 61°53´N; 9°15´E) is characterised by lowest annual precipitation of 300–500 mm (in the valleys) showing highest aridity found in Norway (Kleiven

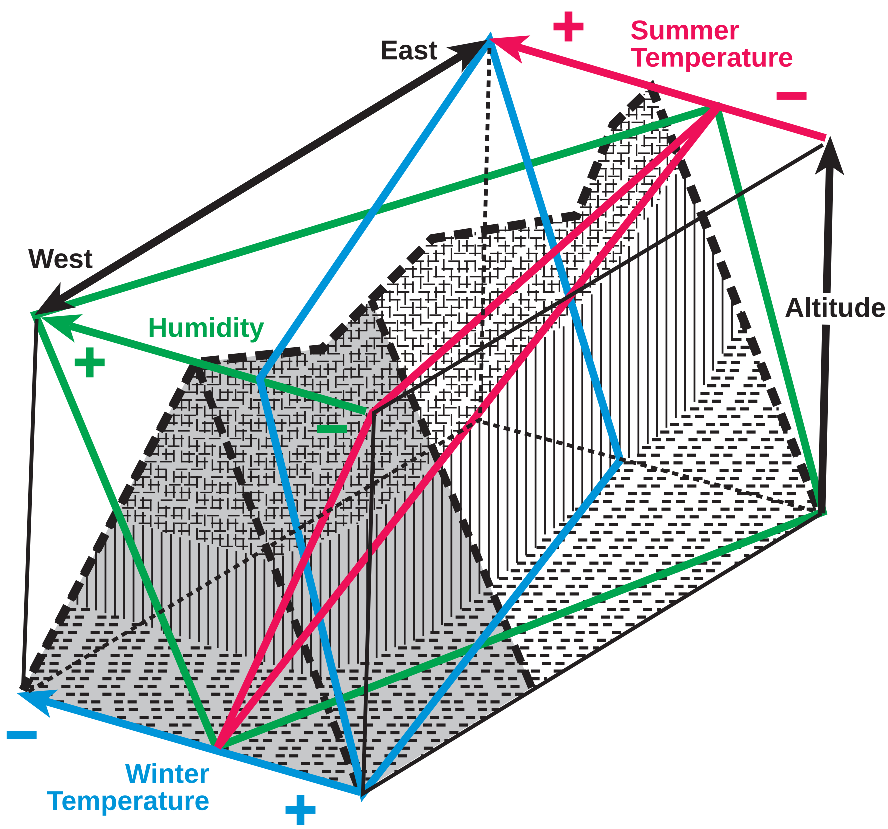

Fig. 2: Mountain vegetation determination along broad-scale altitudinal and oceanic-continental gradients – common hypotheses (Orig.)

Geläufige Hypothesen der Steuerung der Hochgebirgsvegetation entlang von großräumigen Höhenstufen- und Ozeanitäts-Kontinentalitäts-Gradienten

1959). The slightly to markedly oceanic (O1–O2) region Stranda/Møre og Romsdal (62° 03´ N; 7° 15´ E) of the inner fjords is characterized by humid conditions under annual precipitation of 1,500–2,000 mm (in the valleys) (AUNE 1993).

Vegetation belts (DAHL 1986), periglacial zonation (GARLEFF 1970), and soil distribution (LÖFFLER 1998) are found as follows. Above the tree-line the alpine environment comprises of a continuous cover of dwarf shrubs. This low alpine landscape shows chionophilous vegetation at slopes. Chionophobous lichen heaths are found in exposed topography. Depressions are characterised by mires. Podzols are common at well-drained sites, replaced by brown soils under cooler conditions, commonly in northern exposure. Poorly drained sites are characterized by stagnation, where humus and bog soils are developed, gleyic by mineral substrates. Profiles show signs of solifluction and cryoturbation. Periglacial micro-features are common, such as solifluction lobes, earth hummocks, and mudpits. The middle alpine environment comprises of discontinuous vegetation dominated by graminaceous. Brown soils are

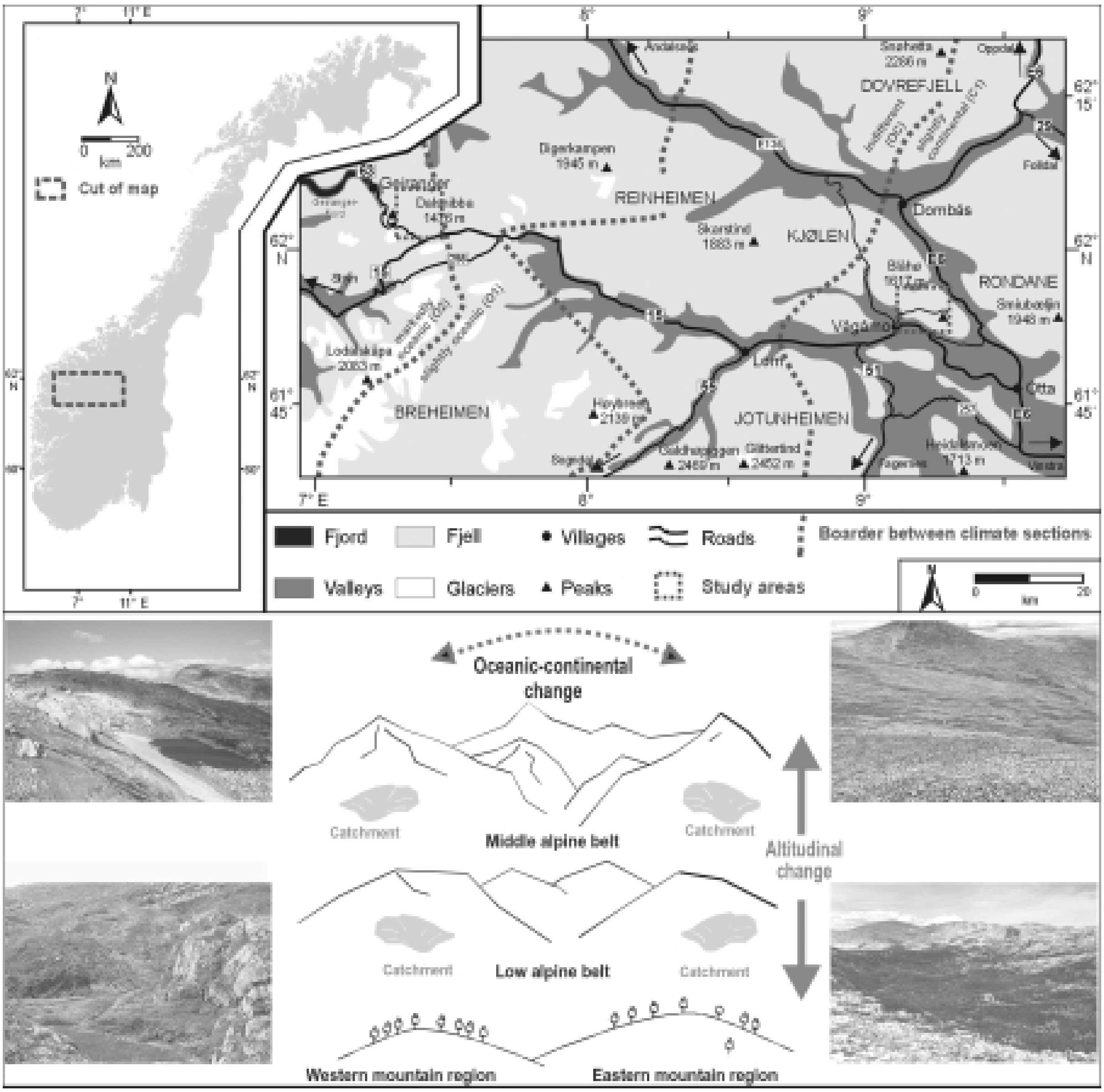

Fig. 3: Investigation areas and research design in central Norway (after: LÖFFLER et al. 2001; LÖFFLER 2002)
Untersuchungsgebiete und Forschungsdesign in Mittelnorwegen

found at well drained sites; podzols are missing; poorly drained sites are gleyic. The dominance of the skeleton fraction widely shapes the environment. Profiles and surfaces are influenced by fine fluvial sedimentation, debris accumulation, structured solifluction, and micro-sorting; macro-sortings are fossils.

Petrography of the Vågå area is characterised by glacially shaped phyllitic parent rocks of moderate weathering capacity but silicate-acid chemistry (Strand 1951). The substrates are composed of glacial till down to 100 cm depth. Higher elevations are dominated by coarse block-rich periglacial debris. Ridges are predominantly built from weathering substrates. Active periglacial block fields are found. Depressions of lower altitudes are covered by organic substrates mostly as peat; depressions of higher elevation show thin organic accumulations enriched by fine sheet-wash sediments. Mineral substrates are permeable, organic layers often tend to stagnation. Permafrost is sporadic at 30–50 cm depth from 1,050 m a.s.l. upwards and probably discontinuous (> 150 cm depth) above 1,300 m a.s.l. upwards (King 1984). The Stranda area is characterised by glacial shaped gneiss parent rocks of moderate weathering capacity of silicate-acid chemistry (Sigmond et al. 1984). The substrates are glacial till down to 50 cm depth. Higher elevations are dominated by coarse rich debris. Ridges are pure bedrock besides weathering substrates. Active block fields are combined with late snow beds. Organic substrates are widespread and cover depression, slopes, and ridges at lower altitudes up to 1,150 m a.s.l. Depressions in higher elevation show very thin organic layers. Stagnation is common where bedrock is convex shaped. Permafrost is not present.

3 Methods and materials

3.1 Mappings

Structural investigations comprise of mappings practised in fine-scale topography with high spatial resolution, along topographical and altitudinal gradients, and at single sites. Some thousands of sites were analysed between 1991 and 2002, characterising the relief, elevation, drainage, soil moisture, and depth to water table. Relevés were transposed to the vegetation using a verified scale for plant species abundance based upon Braun-Blanquet (1964) (Fig. 4). The nomenclature follows Lid and Lid (1994) for species, Nordhagen (1936) and Dahl (1987) for plant communities, and Fremstad (1997) for vegetation types. Moreover,

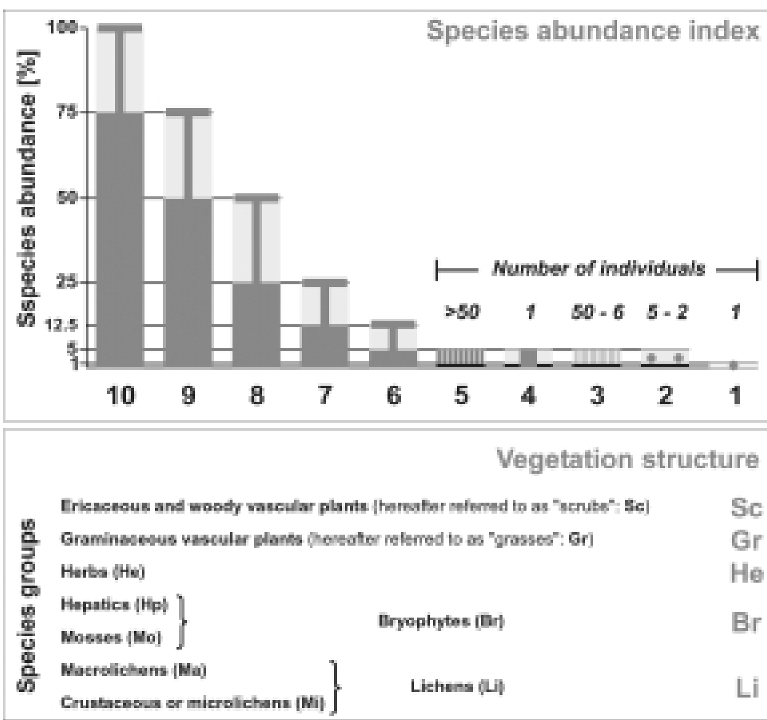

Fig. 4: Scheme of sampling plant species abundance and vegetation structure (Orig.)

Schema zur Erfassung von Deckungsgraden der Pflanzenarten und Vegetationsstrukturen

Andromeda polifolia	And_pol
Arctostaphylos alpinus	Arc_alp
Arctostaphylos uva-ursi	Arc_uva
Betula nana	Bet_nan
Calluna vulgaris	Cal_vul
Cassiope hypnoides	Cas_hyp
Empetrum nigrum ssp. hermaphroditum	Emp_her
Juniperus communis ssp. alpinum	Jun_com
Loiseleurea procumbens	Loi_pro
Phyllodoce caerulea	Phy_cae
Rubus chamaemorus	Rub_cha
Salix div. spec.	Sal_div
Salix glauca	Sal_gla
Salix herbacea	Sal_her
Salix phylicifolia	Sal_phy
Sorbus aucuparia	Sor_auc
Vaccinium myrtillus	Vac_myr
Vaccinium oxycoccus ssp. microcarpum	Vac_oxy
Vaccinium uliginosum	Vac_uli
Vaccinium vitis-idea	Vac_vit
Anthoxanthum odoratum	Ant_odo
Calamagrostis purpurea	Clm_pur
Carex atrata	Car_atr
Carex bigelowii	Car_big
Carex canescens	Car_can
Carex cespitosa	Car_ces
Carex dioica	Car_dio
Carex lachenalii	Car_lac
Carex paupercula	Car_pau
Carex rostrata	Car_ros
Deschampsia caespitosa	Des_cae
Deschampsia flexuosa	Des_fle
Eriophorum angustifolium ssp. angustifolium	Eri_ang
Eriophorum vaginatum	Eri_vag
Festuca div. spec.	Fes_div
Festuca ovina	Fes_ovi
Festuca vivipara	Fes_viv
Juncus filiformis	Jun_fil
Juncus trifidus	Jun_tri
Luzula arcuata ssp. confusa	Luz_con
Luzula div. spec.	Luz_div
Luzula spicata	Luz_spi
Nardus stricta	Nar_str
Poa div. spec.	Poa_div
Poa vivipara	Poa_viv
Trichophorum cespitosum ssp. cespitosum	Tri_ces
Antennaria dioica	Ant_dio
Bistorta vivipara	Bis_viv
Campanula rotundifolia	Cam_rot
Cardamine bellidiflora	Car_bel
Cerastium cerastoides	Cer_cer
Cornus suecica	Cor_sue
Cryptogramma crispa	Cry_cri
Diphasium alpinum	Dip_alp
Equisetum silvaticum	Equ_sil
Geranium silvaticum	Ger_sil
Gnaphalium supinum	Gna_sup
Gymnocarpium robertianum	Gyc_rob
Hieracium alpinum	Hie_alp
Huperzia selago	Hup_sel
Melampyrum pratense	Mel_pra
Minuartia biflora	Min_bif
Pedicularis lapponica	Ped_lap
Pinguicula vulgaris	Pin_vul
Ranunculus glacialis	Ran_gla
Rumex acetosa ssp. acetosa	Rum_ace
Rumex acetosella ssp. acetosella	Rum_acl
Saxifraga stellaris	Sax_ste
Sedum rosea	Sed_ros
Sibbaldia procumbens	Sib_pro
Solidago virgaurea	Sol_vir
Trientalis europaea	Tri_eur
Viola biflora	Vio_bif

Anthelia juratzkana	Ant_jur
Barbilophozia div. spec.	Bar_div
Cephalozia div. spec.	Cep_div
Fossombronia div. spec.	Fos_div
Gymnocolea inflata	Gym_inf
Lophozia div spec.	Lop_div
Marsupella emarginata	Mar
Moerckia blyttii	Moe_bly
Mylia anomala	Myl_ano
Ptilidium ciliare	Pti_cil
Andreae div. spec.	Adr_div
Aulacomnium palustre	Aul_pal
Brachythecium reflexum	Bra_ref
Calliergon cordifolium	Cli_cor
Calliergon stramineum	Cli_str
Conostomum tetragonum	Con_tet
Depranocladus div. spec.	Dep_div
Depranocladus fluitans	Dep_flu
Dicranella palustris	Dcr_pal
Dicranum div. spec.	Dic_div
Hylocomium splendens	Hyl_sp
Kiaeria starkei	Kia_sta
Oligotrichum herzynicum	Oli_her
Philonotis fontana	Phi_fon
Pleurozium schreberi	Ple_sch
Pohlia drummondii	Poh_dru
Pohlia nutans	Poh_nut
Polytrichum div. spec.	Pol_div
Polytrichum piliferum	Pol_pil
Rhacomitrium lanuginosum	Rha_lan
Sphagnum div. spec.	Sph_div
Alectoria nigricans	Ale_nig
Alectoria ochroleuca	Ale_chr
Bryocaulon divergens	Bry_dvg
Cetraria cucullata	Cet_cuc
Cetraria delisei	Cet_del
Cetraria ericetorum	Cet_eri
Cetraria islandica	Cet_isl
Cetraria nivalis	Cet_niv
Cetraria pinastri	Cet_pin
Cladina arbuscula	Cld_arb
Cladina rangiferina	Cld_ran
Cladina stellaris	Cld_ste
Cladina sulphurina	Cld_sul
Cladina uncialis	Cld_unc
Cladonia bellidiflora	Cla_bel
Cladonia chlorophaea	Cla_chl
Cladonia coccifera	Cla_coc
Cladonia div. spec.	Cla_div
Cladonia ecmocyna	Cla_ecm
Cladonia fimbriata	Cla_fim
Cladonia furcata	Cla_fur
Cladonia gracilis	Cla_gra
Cladonia pyxidata	Cla_pyx
Nephroma arcticum	Nep_arc
Ochrolechia androgyna	Och_and
Ochrolechia div. spec.	Och_div
Ochrolechia frigida	Och_fri
Peltigera aphtosa	Pel_aph
Peltigera malacea	Pel_mal
Pertusaria dactylina	Per_dac
Psoroma hypnorum	Pso_hyp
Solorina crocea	Soa_cro
Sphaerophorus globosus	Sro_glo
Stereocaulon div. spec.	Ste_div
Thamnolia vermiculata	Tha_ver
Ephebe lanata	Eph_lan
Hypogymnia physodes	Hyp_phy
Parmelia centrifuga	Par_cen
Parmelia saxatilis	Par_sax
Rhizocarpon div. spec.	Rhi_div
Umbilicaria arctica	Umb_arc

Fig. 5: List and code of plant species in supplements VII, VIII and IX (Orig.)
Liste und verwendete Abkürzungen der Pflanzenarten in den Beilagen VII, VIII und IX

parent material and substrates, percentage of surface coarse fragments, and soil profiles as to horizon combination and thickness were described. Their pH-values were measured in H_2O and $CaCl_2$ in volumetric sample-liquid proportion of 1: 2.5 in the field. Soil texture, root system, and soil temperature were recorded. Methodology and classification are performed after LÖFFLER (1998). Within this concept a differentiated mapping hierarchy is used to distinguish several scales of examinations. Three dimensions are used: sites, catchments, and entire landscapes within an altitudinal belt. Techniques and tools of landscape analysis are applied and structured after AG BODEN (1982–1996) and BASTIAN and SCHREIBER (1994).

Concepts were developed to extrapolate local measurements from the catchments into larger areas using digital elevation models and remote sensing data such as aerial black and white photos of 1:15.000 scale, and Landsat-TM scenes (LÖFFLER u. WUNDRAM 2001). Current modelling and regionalization approaches from central Europe served as a basis (DIEKKRÜGER a. RICHTER 1997; DUTTMANN 1999; STEINHARDT a. VOLK 2002).

3.2 Measurements and external data

The ecosystems approach is based upon extensive programmes of structure analyses, mappings, and measurements on different ecological parameters within the *landscape ecological complex analysis* (MOSIMANN 1985). The methodological concept is designed for different scales (LÖFFLER 2002). Water and energy fluxes are measured by ecological stations, data loggers, and hand-held equipment. The cyclicity of seasonal dynamics leads to a full year programme. In each catchment one ecological base station, several major and minor stations, and spatial sets of water level stations were installed. Data material for fine-scale analysis is derived from 24 data loggers for different positions along topographical gradients measuring hourly means throughout the year. Each logger is combined with three Pt–100 sensors for air temperature at 15 cm above ground protected from direct radiation (hereafter referred to as air temperature T+15), near surface temperature at 1 cm depth (hereafter referred to as surface temperature T–1), and ground temperature at 15 cm below the surface (hereafter referred to as soil temperature T–15). Additional measurements of temperatures and air humidity with hand-held sensors, soil moisture with TDR-equipment (uncalibrated), Piché-evaporation, condensation with digital weighing, and percolation with small lysimeters are practised throughout the vegetation period.

Broad-scale analysis is based upon measurements from meteorological equipment installed in the mountains: two stations were established at Jetta and Vågåmo in 1994, two further at Blåfjell-Dalsnibba and Geiranger in 2000. Hourly intervals registering air and soil temperature, precipitation, solar radiation, air humidity, soil moisture, wind speed and direction were adopted. At well-drained sites percolation meters were used for water balancing. Poorly drained sites comprise of a network of water level stations. During the winter season snow accumulation was mapped and quantified by snow pack measurements; snow melt dynamics is observed using colour tracers.

Additional data were received from the NORWEGIAN METEOROLOGICAL INSTITUTE (1991–2002) comprising of long-term measurements at official stations. The eastern investigation area is represented by Kjøremsgrende No. 16740 (1976) (Lesja, Oppland) at 626 m, the western area by Tafjord No. 60500 (1930) (Møre og Romsdal) at 15 m.

3.3 Data processing

3.3.1 Analysis of fine-scale spatial gradients

Resulting material is organized digitally in a data base, combined with a geographical information system. Mapped spatial data layers such as vegetation, relief, etc. are used to define structural ecotope types by overlay routines. Complex ecotope type geometries function as the spatial basis for data extrapolation (LÖFFLER u. WUNDRAM 2001). Regularities statistically deduced from functional data are quantified for all catchments. Qualitative and quantitative interrelations between the compartments are synthesised. Systematic spatial analysis is based upon spatial proportions of the distribution of structural parameters and process attributes. Typological, ordinal-scaled, and numerical spatial attributes are used to identify the degree of spatial correlations between different factors. Finally, canonical correspondence analysis (CCA, see below) is adopted to the multidimensional systems for multivariate statistics using vegetation types with spatial proportions in the main matrix and total data sets of each catchment in the second one (Suppl. VII).

3.3.2 Analysis of broad-scale gradients

Altitudinal gradients are analysed using two data sets each of one region, representing the low and middle alpine belt. Topographical gradients are analysed using transect methods for the vegetation and process measurements of environmental determinants. Vegetation patterns are correlated with samples using detrended correspondence analysis (DCA, see below). Superior ecological parameters are secondly used for CCA of plant species composition and aggregated process attributes such as minimum soil moisture, maximum surface temperature, snow cover thickness, and length of vegetation period. Micro-climatic and ecological data are combined with general altitudinal gradients. Vertical adiabatic interpolation by calculating an adiabatic lapse rate for the extrapolation of data from valley stations is problematic, but used to show differences between calculated and measured air temperatures are analysed. Deviations from generally expected superior meso-climate are shown for near ground conditions using generalised micro-climatic data (Suppl. VIII).

Exemplary sites are chosen to analyse broad-scale oceanic-continental changes. Similar topography and substrate conditions found at the ridges are chosen to analyse differences of vegetation features as to superior climatic gradients (Suppl. IX). Plant species composition is correlated with environmental conditions based upon measurements during 2001. This year shows a standard deviation of < 0.2 K of normal annual temperatures and < 3% of normal annual precipitation at the official stations. Precipitation measurements from the mountain stations only give hints for liquid precipitation events and proportions but cannot be used for total quantification.

3.3.3 Multivariate statistics and ordination

Multivariate statistics is combined with ordination of plant species compositions using abundance at the plot, spatial size of vegetation units, nominal data for structural environmental parameters, and different quantified environmental factors. DCA is used to ordinate species and samples simultaneously. It yields an eigenanalysis ordination based upon reciprocal averaging. This method results in an interpretation of species distribution patterns correlating with the sample site (Hill a. Gauch 1980). Topographical niches of vegetation types and plant species were defined by direct gradient analysis of all sample site data using CCA. This method aims at interpreting species distribution patterns by relating them to environmental gradients. The ecological gradients are weighted according to their importance in explaining species dispersion using canonical coefficients. In CCA ordination diagrams different important types of information are graphed: position of species, position of sample sites, position of nominal environmental factors, and length and direction of quantitative determinant vectors. The position of the sample site represents a vegetation type and a species respectively, but approximates its relations to the involved ecological gradients (Ter Braak 1986, 1994; Jongman et al. 1995). A list of plant species and their codes used in diagrams is given by figure 5.

4 Results

4.1 Topographical gradients

As an example of the continental low alpine catchment the environmental situation along spatial gradients of topography is illustrated (Suppl. VII). Proportions of prevailing winds indicate south-eastern streams responsible for precipitation. The most decisive factor determining the distribution of snow is the highest wind speed during winter. This has distinct northern components resulting in pronounced snow drift patterns of southern exposed lee-slopes and northern exposed windward snow beds. Snow is blown off the ridges and narrow depressions are completely filled up with snow, while the wide depressions show a thin snow cover. Vegetation patterns are highly complex results from those figures. Snow cover thickness and length of the vegetation period are found in correlation with vegetation types. Snow-free summers are short and last for 100–180 days.

Different structural compartments determine the water balance. Besides relief, ground substrate influences water fluxes and soil moisture. Vegetation patterns are also found as results from liquid water distribution besides snow cover.

The vegetation map illustrates ridges covered by three different lichen heath types along a snow cover gradient: *Alectoria ochroleuca* occurs under extreme conditions without snow cover during winter. *Cetraria nivalis* competes under a thin snow cover, while *Cladina stellaris* appears where snow extends up to 30 cm. Sites covered by thicker snow packs are characterised by *Betula nana, Vaccinium myrtillus,* or *Calluna vulgaris,* where snow melts out early but gives shelter against frosts. Late snow beds with maximum snow pack at southern foot-slopes are characterised by *Nardus stricta*. Depressions show mosaics of different mire vegetation types along moisture gradients. *Sphagnum – Carex* and *Sphagnum – Eriophorum* types are found in wet mires, where near surface water is found throughout the year, while the latter shows slightly lower water levels at about 0 to 5 cm below the surface. The *Sphagnum – Rubus chamaemorus* type is characterised by a varying water level between 0 and 15 cm below the surface.

Spatial correlation analysis of vegetation distribution with soil, pH, and humus shows that the most abundant vegetation types are not strictly correlated with those factors. Exceptions are found in mires where vegetation, soil, and humus closely correspond with each other. Most constant pH profiles show slightly oligotrophic conditions increasing with depth throughout the entire catchment. Mineromorphic soils do not show any correlation either with the pH or with vegetation and humus. Stagnation soils are present under lichen and *Calluna*-dominated vegetation. Podzols are found within a wide range of ecological conditions, being dominant in southern exposures. Moss-dominated surfaces, pure organic humus, and fermented humus are most frequent over an extremely wide range of site conditions.

Spatio-temporal soil moisture variability directly corresponds with frost penetration, snow cover, and snow melt. The distribution of different moisture profiles shows fine-scale differentiations according to the relief. Ridges and convex slopes are "driest" throughout the year, characterised by moist profiles. This phenomenon describes the most decisive hydrological constellation of the low alpine landscape. Concave positions tend to wet conditions and function as temporary surface runoff and stagnation ecotopes. Wet conditions are found during snow melt. Tracer experiments show that melt-water passes through the entire catchment without penetrating the ground. However, water equivalents of the snow pack at a site do not correspond with higher soil moisture. Moisture variability is illustrated by four maps. The correlation analysis between vegetation and moisture dynamics is based upon minimum and maximum moisture under different vegetation types. Lichen, heather, and shrub vegetation appear under moist conditions where the upper layer is not wet. Wet conditions in deeper ground obviously do not influence the vegetation distribution. By way of contrast, continuous wet conditions determine a distinct change in the vegetation. Near surface water saturation and flooding is found to be most decisive for plant species turnover.

Temperature maps demonstrate the spatial dynamics throughout a high pressure weather situation. Surface and soil temperatures are influenced by moisture. Before sunrise, air temperatures show warmer ridges and upper slopes, and cool depressions due to cold air flows originate from strong radiative cooling during nights. At noon, air temperatures at southern-exposed slopes are warmest, at northern-exposed coldest. Soil temperatures also depend on moisture and thermal properties of substrates. Depressions are cold as to high heat capacity; wet substrates do not show any temperature changes. Air temperatures of south-facing slopes are correlated with greatest temperature amplitudes, those of north-facing slopes and depressions with the lowest. Soil temperatures in areas with low heat capacity show the greatest variations. Influences of the energy balance on the vegetation are analysed using a hierarchical classification of temperature dynamics attributes. Daily and seasonal air, surface, and soil temperatures are aggregated integrating various functional features. Duration of daily means, duration of frosts, annual amplitude, and duration of daily maximums are classified for different temperature layers. The micro-climatic map shows resulting units with major features of temperature dynamics. Pronounced daily air and surface temperatures are found during summer periods. Higher soil moisture content leads to less expressed differences, while the slope aspect is the most determining factor for daily variations. Daily soil temperature dynamics during summers is decently distinct on ridges and southern exposed slopes, but hardly found in northern exposure and depressions. Annual variations of the air temperature depend on thickness and duration of snow cover and are extremely pronounced between summer and winter seasons. The importance of micro-climatic influences on vegetation is stressed by three variables of T+15: frost index (FIndex), heat index (HIndex), and temperature sums. According to Kira (1949) frost and heat indices, respectively are the sum of monthly mean temperatures < and > 5° C, respectively (pre-calculating each value minus 5° C). The highest frost index correlates with distribution of lichen vegetation, accompanied with second highest heat index. Open depressions show the second highest frost index as to thin snow cover, and the lowest heat index as to high moisture. Shrub and heath vegetation is strictly correlated with the highest heat index and second lowest frost index; *Betula nana* type is also found with the lowest heat and frost indices. *Nardus stricta* type shows the lowest indices as to long lasting and thick snow cover, and wet vegetation period. Additionally, temperature sums of daily means > 0° and > 5° C, respectively are used for correlation analysis. These two values are simultaneously graphed as to spatial correspondence, differentiating five classes. In contrast to results regarding heat index, vegetation statistics show that lichen-dominated vegetation receives the highest amounts of heat by daily means, reduced in other vegetation types; *Vaccinium myrtillus* and *Salix glauca* receive lowest temperature sums. Longer vegetation periods obviously result in sums of daily temperatures higher than those induced by higher temperatures during shorter periods.

The ordination diagram of CCA 1 sums up the results: soil moisture, snow cover, and micro-climatic dynamics (ClimDyn) superiorly determine the vegetation along spatial topographical gradients. Statistically, none of the single parameters explains these vegetation patterns. The highest correlations found on soil moisture explain very few samples. Snow cover determines the second highest accompanied with a lot of samples explained, negatively correlated with the length of the vegetation period. Micro-climatic dynamics additionally explains a lot of samples also framed by separate heat and frost index clusters along the ClimDyn vector.

4.2 Altitudinal gradients

Altitudinal gradients are demonstrated as an example of the continental region. The underlying assumption is based upon the adiabatic coefficient of 0.6 K per 100 metres. Table 1 shows results from calculations using this model to simulate mountain temperatures. Measured values are given for stations in the mountains. The general adiabatic calculation is valid for mean annual, spring maximum, and autumn and winter minima, and for spring and autumn minima of the low alpine air temperature. It results in very low calculated values for middle alpine annual means, summer maximums, and summer minima. Most decisive under-calculations of more than 10 K are achieved for middle alpine winter minima. Winter frosts are strongest in the low alpine belt. The conditions for plants are given by near surface temperatures, that are reasonable for a thin snow cover, so that low and middle alpine conditions during winter are quite similar, although frosts penetrating the ground are found to be slightly more intense in the middle alpine belt.

Topographical gradients are analysed in the two altitudinal belts (Suppl. VIII). Vegetation transects illustrate fine-scale differentiations of plant compositions. Differences between low and middle alpine vegetation are demonstrated by species abundance. Superior altitudinal change is shown by woody plants retreating with altitude. Ordination of DCA 1 interpreting plant species composition as to samples yields five clusters: 1) strictly low alpine ridge species, 2) low and middle alpine ridge and upper slope species, 3) strictly low alpine wet mire species, 4) low alpine snow bed species, and 5) middle alpine snow bed species. The clusters show the distribution optimum of species as to their abundance.

The amount of snow increases with altitude, resulting in a thicker snow cover that additionally lasts longer. Furthermore, water balance features comprise a set of calculated total amounts of water input from rain and snow melt, percolation, and potential evaporation during the vegetation period, and soil moisture dynamics in two layers. Thermoisopleth diagrams for T+15, T–1, and T–15 explain resulting micro-climatic conditions near ground. Duration of daily means, duration of the frosts, annual amplitude, and duration of daily maxima are further attributes. The legend systematically scales temperatures according to their environmental influence. Air, surface, and soil thermoisopleths show daily and annual changes of seven different ranges of temperatures with similar ecological values for a particular site. Those temperature ranges subdividing the outer circle of the diagram into seven circle segments are grouped according to literature data, own investigations, and theoretical considerations on 13 landscape ecological process attributes (LÖFFLER 2002).

Multivariate statistics are adopted using all sites, abundance of all plant species, altitude, and a set of different micro-climatic and hydrological parameters (CCA 2). The analysis gives evidence that none of the different factors superiorly determines the vegetation along the altitudinal gradient. Soil moisture is important as to its maximum in upper layers (XMoist1) and minima in deeper ground (MiMoist2). Three clusters of plant species are found along these vectors, most of

	Valley AirT	Calcul. LowAlp AirT	Low Alp T+100	Calcul. MidAlp AirT	Mid Alp T+100	Low Alp T+15	Mid Alp T+15	Low Alp T-1	Mid Alp T-1	Low Alp T-15	Mid Alp T-15	Low Alp T-30	Mid Alp T-30
Annual Mean	1.7	1.1	-1.2	-3,2	-1.9	-0.6	0.1	0.5	0.5	0.4	0.6	0.4	0.6
Summer Max	18.2	15.4	16.7	13.3	15.5	18.0	15.8	16.6	14.3	17.2	12.6	14.4	9.9
Winter Min	-26.8	-29.6	-29.2	-31.7	-19.9	-19.3	-18.7	-12.9	-16.9	-11.9	-15.8	-11.6	-14.4
Spring Max	10.8	8.0	7.6	5.9	4.9	7.0	3.6	6.8	2.2	6.7	0.7	5.1	0.1
Spring Min	-5.0	-7.8	-11.1	-9.9	-11.0	-5.7	-2.9	-4.8	-2.4	-5.3	-2.1	-5.2	-1.7
Summer Min	4.7	4.2	2.3	2.1	0.1	2.8	0.5	3.7	1.6	4.7	0.7	4.7	0.1
Autumn Min	-6.9	-9.7	-10.0	-11.8	-11.6	-9.7	-11.8	-8.0	-8.5	-7.1	-7.9	-5.7	-6.6

Table 1: Calculation of mountain temperatures compared to measured values. Valley air temperature (AirT) at 626 m a.s.l. and calculated temperatures for the low and middle alpine belt (Calcul. LowAlp, MidAlp) at 1,100 and 1,450 m a.s.l., respectively

Berechnung der Gebirgstemperaturen im Vergleich zu gemessenen Werten. Lufttemperatur der Talstation auf 626 m üdM sowie errechnete Werte für die untere und mittlere alpine Stufe auf 1.100 bzw. 1.450 m üdM them in the low alpine belt. The strongest correlations between vegetation and micro-climate are found by the number of days with freeze-thaw processes at the surface (–1<S<1) increasing with altitude. Direction and length of "–1<S<1" and "Altibelt" vectors indicate the determination of vegetation by surface frost action in the different belts. On the contrary, maximum surface temperatures (SMax) are found in correlation with a specific group of plant species most frequently in early low alpine snow beds, among those *Vaccinium myrtillus*, *Calluna vulgaris*, *Phyllodoce caerulea*, and other dwarf shrubs. These two combined vectors comprising of "–1<S<1" and "SMax" show that the altitudinal change of the vegetation is closely correlated with surface temperatures.

4.3 Oceanic-continental gradients

The meteorological oceanic-continental gradient is sketched by general data (Tab. 2). Annual mean temperatures in the low alpine west are higher than those of the east, middle alpine values being similar. Annual maxima are similar in western and eastern low alpine belts, higher in the eastern middle alpine belt. Annual minima are lowest in western and eastern low alpine, differences being larger in continental Norway. Summer and autumn minima are similar in the same belts of both regions; the latter slightly lower in eastern middle alpine. Spring maxima are much higher in both altitudinal belts of the west; spring minima are lower in the east, especially in the low alpine belt. It is shown that temperature dynamics is not strictly explained by principle rules of regional meteorological changes.

Vegetation determination analysis along the oceanic-continental gradient is based upon samples from exposed ridges and upper slopes. These show direct influences of the superior climate. Others are influenced by topographic gradients as shown above. All samples, abundance of species at all sites, soil moisture measurements, and micro-climatic recordings are analysed. The photos 1 a – d give an overview of differences between the investigation areas exemplified by the ridges; the pictures also show installed meteorological equipment. Results on vegetation determination along the oceanic-continental gradient are illustrated (Suppl. IX), summing up temporal dynamics of water and temperature fluxes by raw data from hourly intervals and evaporation data from daily intervals with interpolated curvature of August 2001. During summers, continental mountains are characterised by high amounts of solar radiation due to prevailing low degrees of cloudiness. Temperature dynamics is pronounced, showing dependences on solar radiation, and superior influences of prevailing weather situations. Ridges are well drained and soils are characterised by relatively low heat capacity. Diurnal temperature dynamics is low, leading to steep temperature gradients from the surface into depth. Although single events cause huge amounts of precipitation, the overall precipitation sum is relatively low and percolation processes are reduced. High evaporation occurs under warm, dry, and windy conditions in the low alpine belt, sometimes even exceeding precipitation rates at same times. This dry situation contrasts with a volumetric soil moisture of 20 to 30%. Middle alpine conditions are characterised by gradually higher precipitation and lower temperatures, but a sparse vegetation cover results in relatively high sur-

	WestValley AirT		WestLA AirT		WestMA AirT	EastValley AirT	EastLA AirT	EastMA AirT
Annual Mean	(3.0)	6.8	(0.7)	1.9	-1.4	1.7	-1.2	-1.9
Annual Max	**(15.7)**	**19.5**	**(16.0)**	**17.2**	**12.9**	**18.2**	**16.7**	**15.5**
Annual Min	**(-17.3)**	**-13.5**	**(-24.6)**	**-23.4**	**-22.9**	**-26.8**	**-29.2**	**-19.9**
Spring Max	(10.2)	14.0	(9.7)	10.9	8.5	10.8	7.6	4.9
Spring Min	(-3.4)	0.4	(-3.6)	-2.4	-9.7	-5.0	-11.1	-11.0
Summer Min	(5.5)	9.3	(2.4)	3.6	-0.1	4.7	2.3	0.1
Autumn Min	(-6.5)	-2.7	(-9.1)	-7.9	-8.2	-6.9	-10.1	-11.6

Table 2: Temperature of western and eastern altitudinal belts. Data from western valley and low alpine stations interpolated by adiabatic coefficient (0.6 K/100 m) for comparison of same altitude of eastern stations; calculated values used given in brackets. Air temperatures (AirT) from western and eastern valley stations (WestValley, EastValley) and from low and middle alpine stations (WestLA, WestMA, EastLA, WestMA)

Temperaturen der westlichen und östlichen Höhenstufen. Daten der westlichen Tal- und der unteren alpinen Station sind für den Vergleich mit dem östlichen Gebiet mit dem adiabatischen Koeffizienten von 0.6 K/100 m interpoliert; errechnete Werte sind in Klammern angegeben. Dargestellt sind Lufttemperaturen der westlichen und östlichen Tal- und Gebirgsstationen face temperatures compared with low alpine conditions; this leads to slightly uneven soil moisture curvature, but lower amounts of evaporation. The result is a constantly high soil moisture. Ridge vegetation does not suffer from a lack of soil moisture. Oceanic mountains are characterised by lower radiation and higher precipitation. Thus, low and middle alpine ridges are characterised by balanced temperature dynamics with lower maximums and higher moisture. Constant rainfalls and shorter periods without precipitation explain soil saturation despite similar evaporation. Oceanic mountains generally show wet conditions. 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 according to 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 ridges are dominated by higher water inputs and higher potential evaporation due to sparse and patchy vegetation resulting in high surface temperatures. Evaporation is reduced due to low air temperatures. Western ridges are covered by a dense lichen heath despite high soil moisture and high air humidity. Thus, vegetation distribution cannot be explained by hydrological patterns, apart from a surplus of water. Instead, snow cover conditions determine the spatial arrangement of plants. Lichen heaths at western alpine ridges also superiorly correspond with thin snow cover during winter.

Vertical profiles illustrate temperature dynamics at the four ridges by a set of integrated parameters: winter minimum, winter, spring, summer and autumn average, summer minimum and maximum. Curvatures of winter minima show a wide range but eastern conditions being coldest. Middle alpine soils are hardest affected by extremely low temperatures, although the

Photos 1 a–d: Ridges with ecological base stations. Western a) middle, b) low alpine, and eastern c) middle, d) low alpine belt. Middle alpine lichen vegetation characterised by *graminaceous (Luzula confusa, Carex bigelowii, Juncus trifidus)*, low alpine lichen heaths characterised by dwarf shrubs *(Loiseleuria procumbens, Arctostaphylos uva-ursi, A. alpina)*

Kuppenstandorte mit ökologischen Basisstationen. a) Mittlere und b) untere alpine Stufe im Westen sowie c) mittlere und d) untere alpine Stufe im Osten. Die Flechtenvegetation ist in der mittleren alpinen Stufe von Grasartigen, in den unteren alpinen Stufe von Zwergsträuchern charakterisiert coldest air temperatures are found in the low alpine belt (see above). A similar gradient is found in the western region, where low air temperatures do not affect the ground. Summer maxima are highest in the low alpine belt and do not show any differences between eastern and western mountains. Winter averages are similar in the low alpine east, and middle alpine east and west, but much higher in the low alpine west. The summer average distinguishes between low and middle alpine conditions; it is equal at oceanic and continental ridges. The same rule is indicated by autumn averages and summer soil minima; but summer air minima might be used to distinguish between east and west.

Plant species distribution is analysed as to samples using DCA 2. Four clusters illustrate most frequent plant species at different sites. Species abundance of eight samples exemplify the analysis. All ridges have similar species compositions, some species being restricted to single areas. *Cetraria nivalis* is the only species occurring at all ridges with high abundance. Low alpine

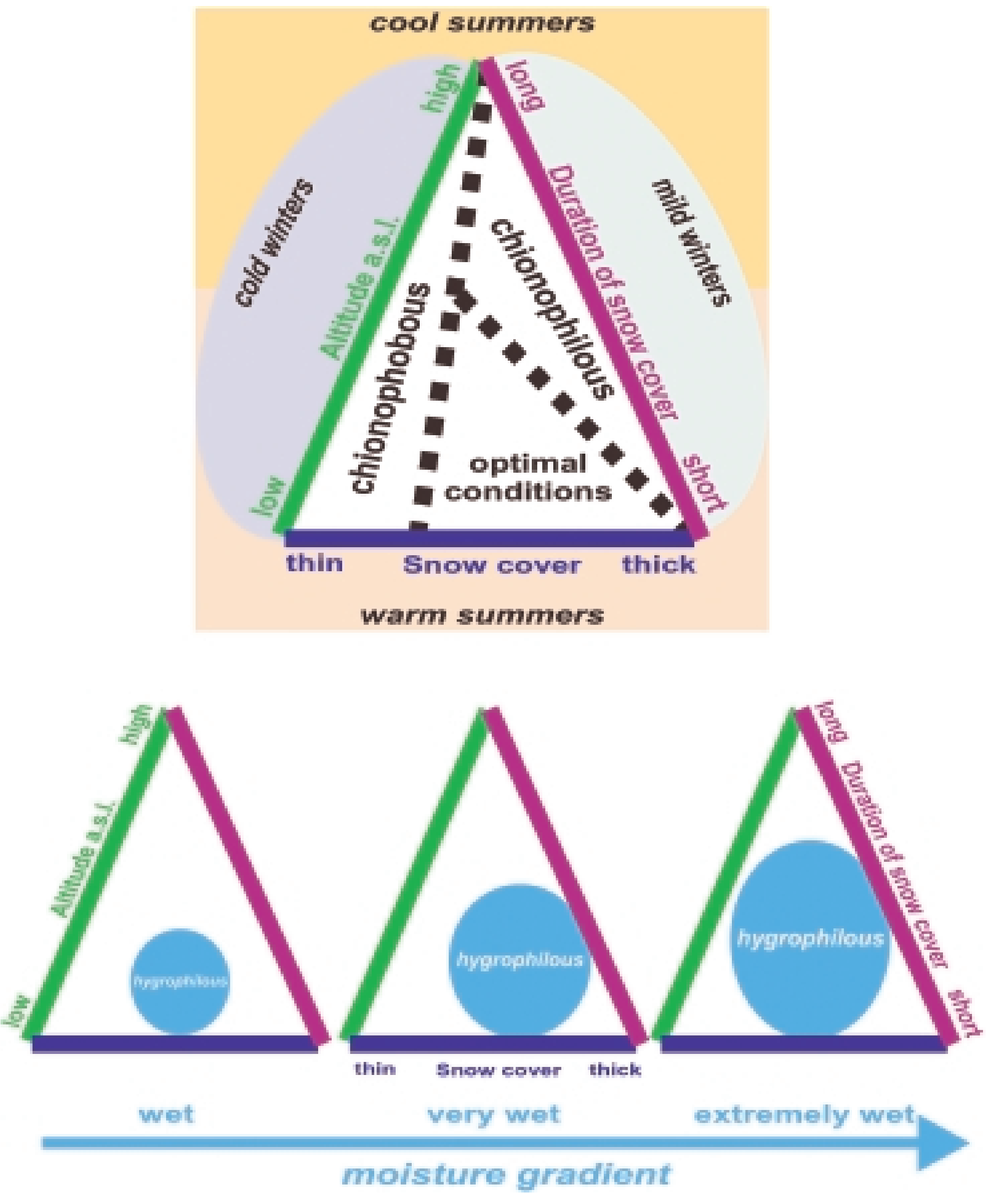

Fig. 6: Scheme of snow cover and soil moisture influences on vegetation in the altitudinal belts (based upon Fægri 1972, modified and supplemented)

Schema der Steuerung der Vegetation entlang von Schneedecken- und Bodenfeuchtegradienten in den Höhenstufen western ridges are characterised by *Rhacomitrium lanuginosum*, while *Arctostaphylos uva-ursi* is only found at the continental low alpine ridges. Graminaceous plants are frequent in the middle alpine belt, *Luzula confusa* characterising the eastern, *Carex bigelowii* the western ridges. CCA 3 and 4 are used for vegetation interpretation along the oceanic-continental gradient illustrating statistically most evident correlations, although none of the vectors explains the total variance. Air temperatures T+100 used in CCA 3 do not give reason to explain why the conditions in the western mountains contrast with the eastern areas. Given vectors explain correlations found with single areas; a division into western and eastern climate is not feasible. Other attributes tested show same results. Clusters of western and eastern ridges are produced between single altitudinal belts, e.g. western low alpine vegetation with different soil temperature attributes of T–30 (CCA 4), and eastern middle alpine ridges with T+100 spring temperatures etc. Summing up the negative results, it has to be assumed that there is hardly any difference between the oceanic and continental micro-climatic vegetation determination at ridges. Similar vegetation types obviously occur with slightly different plant species compositions and abundances in both regions.

Ordination of all variables using all plots from ridges and exposed upper slopes in CCA 5 illustrates the complexity of mountain vegetation determination along different gradients. A pronounced gradient is found and explained by altitude, corresponding with a large number of plant species most frequently found in the different belts. Especially middle alpine species show a distinct cluster, while low alpine species are rare. Only one species is found in continental low alpine and a group of few species commonly found in oceanic low alpine areas. Many species are centred, showing their distribution at all ridges. The "region" vector slightly contrasts with "exposure", explaining why *Vaccinium myrtillus* occurring on the oceanic southern exposed upper slopes, where it competes under a thicker snow cover and slightly warmer summers at the limit of its distribution. A last group is characteristic of the oceanic middle alpine belt. All in all, the results show similar environmental conditions along broad-scale oceanic-continental gradients.

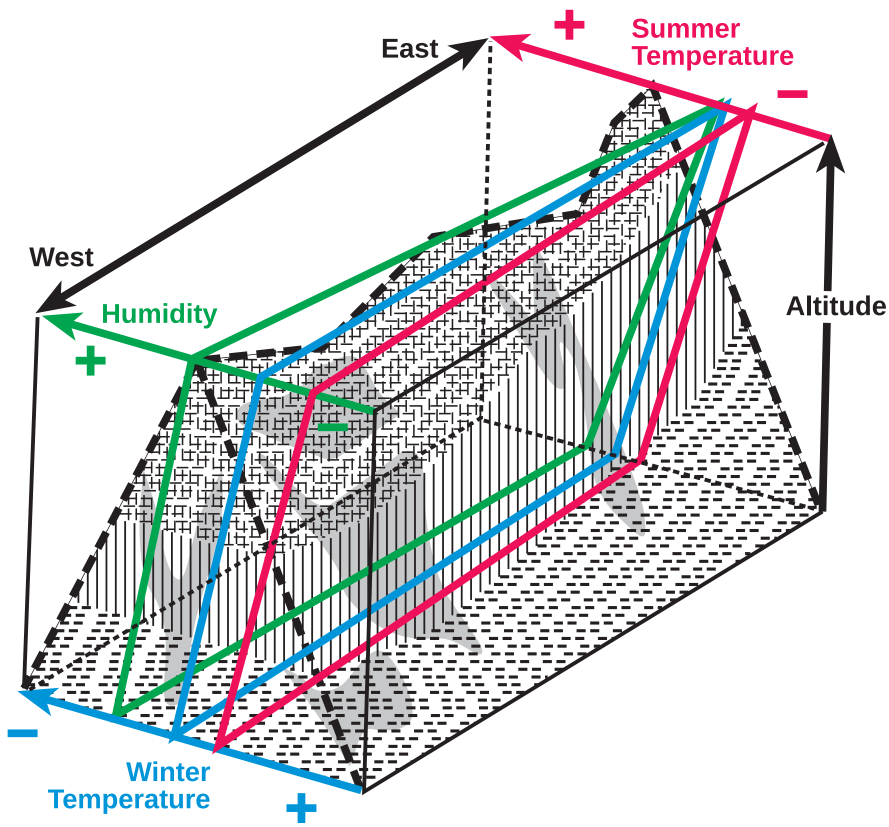

Fig. 7: Antitheses on broad-scale mountain vegetation determination (Orig.)
Antithesen zur großräumigen Steuerung der Gebirgsvegetation

5 Conclusions and discussion

Topographical, altitudinal, and oceanic-continental gradients are regarded as spatio-temporal phenomena. Analyses on different spatial scales show that the determining factor on mountain vegetation is topography influencing landscape functioning paramount to other structural factors. The results of this study reveal that the driest ridge sites show high soil moisture profiles throughout the year. Temperature and moisture gradients determine vegetation patterns and plant species composition by means of cooling and wetness during summer. Fine-scale environmental gradients are explained by dynamics of snow cover explicitly including formation, thickness, duration, and melting. Additionally, spatio-temporal temperature and soil moisture gradients have been proved.

Figure 6 sums up the results. During winter, extreme cold and harsh conditions occur and ecosystem functioning is superiorly determined by snow cover thickness and duration of snow cover. Snow cover distribution corresponds with topography and the strongest prevailing winds during winter, while thick snow cover negatively determines frozen ground. Surface and soil temperatures are also positively determined by snow cover. Survival of plants is determined by snow during periods of lowest temperatures; vegetation distribution follows a gradient along spatial snow pack distribution. Optimal conditions are seldom found in the mountains. The most important distinction is that of chionophobous vegetation surviving cold winters for the sake of a longer vegetation period. On the contrary, chionophilous vegetation is more frequently found with altitude, where the snow cover is thicker, the vegetation period shorter and the summers cooler. Principles of these results are in accordance with the literature (Vestergren 1902; Gjærevoll 1956; Billings a. Bliss 1959; Holtmeier a. Broll 1992; Körner 1999; Jones et al. 2001). Moisture gradients are contrasting: dry conditions do not occur in the mountains at any time, but near surface wet conditions are most decisive determining species turnover and distinct vegetation changes. Wet conditions are considered to be optimal for vegetation most frequently found in low alpine areas. With increasing moisture chionophilous vegetation also in the middle alpine belt is influenced superiorly, but chionophobous vegetation is not affected. Under extremely wet conditions hygrophilous determination might occur at the exposed sites (Fig. 6).

The climatic oceanic-continental gradient of vegetation determination is critical. A strongly pronounced gradient in vegetation patterns is geomorphologically determined (steep slopes, sharp ridges, narrow valleys). But vegetation types are determined equally in the east and west. The broad-scale conditions are different, the local environments are not. Figure 7 shows an update explanation model contrasting with figure 2. The given antithesis is superimposed and roughly sketched. Curvature is drawn quite narrowly and explains similar environmental conditions along oceanic-continental gradients, while the altitudinal gradients are pronounced in both regions, showing a decrease of summer temperatures near ground, of humidity as to soil moisture availability, and of hardest frosts. These conditions illustrate the micro-environmental condition and do not touch the general meteorological characteristics used by Moen (1999) and others.

Hardest ecological conditions determine vegetation distribution; the most important determinants are the following limiting factors:

– exposure to frost damage, “too much water”, and frost index combined with danger of inversion frosts;

– length of growing season, and heat index combined with “too much snow”.

Nearly all listed ridge, early and late snow bed vegetation types used by Fremstad (1997) are grouped in O2-C1 climates. Some types are seldom or not present in C1 (two sub-types are not found in O3-O2). Three of five important climate regions correlate with about 65 vegetation types (counted excluding distinct calcicolous types): O3, where mountains are spatially rare and many types are absent; C1 the extreme continental region, where some types are absent, and O2-OC nearly making up the entire Scandes. The results given in this paper correspond with this classification, but scrutinise the differentiation of oceanic and continental mountain vegetation of Norway.

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References

AG BODEN (Arbeitsgruppe Bodenkunde d. geolog. Landesämter u. d. Bundesanst. f. Geowiss. u. Rohstoffe in der Bundesrepublik Deutschland) (Hg.) (1982–1996): Bodenkundliche Kartieranleitung. Stuttgart.

AUNE, B. (1993): National atlas of Norway: climate. Hønefoss.

BARRY, R. G. (1992): Mountain weather and climate. London.

BASTIAN, O. u. SCHREIBER, K.-F. (Hg.) (1994): Analyse und ökologische Bewertung der Landschaft. Stuttgart.

BILLINGS, W. D. (1973): Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. In: Bio. Science 23, 697–704.

BILLINGS, W. D. a. BLISS, L. C. (1959): An alpine snowbank environment and its effects on vegetation, plant development, and productivity. In: Ecology 40, 388–397.

BLISS, L.; HEAL, O. W. a. MOORE, J. J. (eds.) (1981): Tundra ecosystems: a comparative analysis. IBP 25, Cambridge.

BRAUN-BLANQUET, J. (1964): Pflanzensoziologie. Wien.

BURNS, S. F. (1980): Alpine soil distribution and development, Indian Peaks, Colorado Front Range. PhD thesis. University of Colorado, Boulder.

DAHL, E. (1956): Rondane. Mountain vegetation in south Norway and its relation to the environment. Skr. Norske vidensk.-akad. mat.-naturvid. kl. 3, 1–374, Oslo.

– (1986): Zonation in arctic and alpine tundra and fellfield ecobiomes. In: POLUNIN, N. (ed.): Ecosystem theory and application. Chichester, 35–62.

– (1987): Alpine-subalpine plant communities of south Scandinavia. In: Phytocoenologia 15, 455–484.

– (1998): The phytogeography of northern Europe (British Isles, Fennoscandia and adjacent areas). Cambridge.

DAHL, E.; ELVEN, R.; MOEN, A. a. SKOGEN A. (1986): Vegetations regioner i Norge 1:1.500.000. Nasjonalatlas for Norge. Hønefoss.

DIEKKRÜGER, B. a. RICHTER, O. (1997): Regionalization in hydrology. Landschaftsökologie und Umweltforschung 25, Braunschweig.

DUTTMANN, R. (1999): Partikuläre Stoffverlagerungen in Landschaften. Ansätze zur flächenhaften Vorhersage von Transportpfaden und Stoffumlagerungen auf verschiedenen Maßstabsebenen unter besonderer Berücksichtigung räumlich-zeitlicher Änderungen der Bodenfeuchte. Geosynthesis 10, Hannover.

FÆGRI, K. (1972): Geo-ökologische Probleme der Gebirge Skandinaviens. In: Troll, C. (Hg.): Geoecology of the high-mountain regions of Eurasia: proceedings of the Symposium of the Intern. Geogr. Union Comm. on High-Altitude Geoecology, Nov. 20–22, 1969 at Mainz. Erdwissenschaftliche Forschung 4, Wiesbaden 98–106.

FREMSTAD, E. (1997): Vegetationstyper i Norge. Norsk institutt for naturforskning. Temahefte 12, Trondheim.

FRIES, T. C. E. (1913): Botanische Untersuchungen im nördlichsten Schweden. Vetenskapliga och praktiska undersøkningar i Lappland. Flora och Fauna 2, Uppsala.

– (1917): Über die regionale Gliederung der alpinen Vegetation der fennoskanidschen Hochgebirge. Vetenskapliga och praktiska undersøkningar i Lappland. Flora och Fauna 4, Uppsala.

GARLEFF, K. (1970): Verbreitung und Vergesellschaftung rezenter Periglazialerscheinungen in Skandinavien. Gött. Geogr. Abh. 51, Göttingen.

GJÆREVOLL, O. (1956): The plant communities of the Scandinavian alpine snowbeds. Det Kgl. Norske videnskabers selskraps skrifter 1, 1, Trondheim.

– (1990): Alpine plants. In: BERG, R. Y.; FÆGRI, K. a. GJÆREVOLL, O. (eds.): Maps of distribution of Norwegian vascular plants, Vol. II, Trondheim.

HILL, M. O. a. GAUCH, H. G. (1980): Detrended correspondence analysis: an improved ordination technique. In: Vegetatio 42, 47–58.

HOLTMEIER, F.-K. a. BROLL, G. (1992): The influence of tree islands and microtopography on pedological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. In: Arctic and Alpine Research 24, 216–228.

HUGGETT, R. J. (1995): Geoecology. An evolutionary approach. London.

ISARD, S. A. a. BELDING, M. J. (1989): Evapotranspiration from the alpine tundra of Colorado, USA. In: Arctic and Alpine Research 21, 71–82.

JÄGER, E. (1968): Die pflanzengeographische Ozeanitätsgliederung der Holarktis und die Ozeanitätsbindung der Pflanzenareale. In: Feddes Rep. 79, 157–355.

JONES, H. G.; POMEROY, J. W.; WALKER, D. A. a. HOHAM, R. W. (eds.) (2001): Snow ecology. An interdisciplinary examination of snow-covered ecosystems. Cambridge.

JONGMAN, R. H. G.; TER BRAAK, C. J. F. a. VAN TONGEREN, O. F. R. (eds.) (1995): Data analysis in community and landscape ecology. Cambridge.

KALLIOLA, R. (1939): Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. In: Ann. Bot. Soc. Zoo.-Bot. Fenn 13. Vanamo.

KING, L. (1984): Permafrost in Skandinavien. Ergebnisse aus Lappland, Jotunheimen und Dovre/Rondane. Heidelberger Geogr. Arb. 76, Heidelberg.

KIRA, T. (1949): The forest zones of Japan. Tokyo. (Japanese; cited by WALTER, H. a. BRECKLE, S.-W. [1991]: Spezielle Ökologie der gemäßigten und arktischen Zone außerhalb Euro-Nordasiens. Ökologie der Erde 4. Stuttgart).

KLEIVEN, M. (1959): Studies on xerophile vegetation in northern Gudbrandsdalen, Norway. In: Nytt Magasin for Botanikk 8, 1–60.

KNABEN, G. (1950): Botanical investigations in the middle districts of western Norway. Univ. i Bergen, Årbok 1950. Naturv. rekke 8, Bergen.

KÖHLER, B.; LÖFFLER, J. u. WUNDRAM, D. (1994): Probleme der kleinräumigen Geoökovarianz im mittelnorwegischen Gebirge. In: Norsk Geografisk Tidsskrift 48, 99–111.

KÖRNER, C. (1999): Alpine plant life. Functional plant ecology of high mountain ecosystems. Berlin.

LAAKSONEN, K. (1976): The dependence of mean air temperature upon latitude and altitude in Fennoscandia (1921–1950). In: Ann. Acad. Sci. Fenn. A III, 119, 1–18.

LAUTENSACH, H. (1952): Der geographische Formenwandel. Studien zur Landschaftsdynamik. Coll. Geogr. 3, Bonn.

LID, J. a. LID, D. T. (1994): Norsk flora. Oslo.

LÖFFLER, J. (1998): Geoökologische Untersuchungen zur Struktur mittelnorwegischer Hochgebirgsökosysteme. Oldenburger Geoökologische Studien 1, Oldenburg.

– (2002): Altitudinal changes of ecosystem dynamics in the central Norwegian high mountains. In: Die Erde 133, 155–186.

LÖFFLER. J. u. WUNDRAM, D. (2001): Räumliche und zeitliche Differenzierung des Temperaturhaushalts von Hochgebirgsökosystemen. In: Norden 14, 85–102.

LÖFFLER, J.; FINCH, O.-D.; NAUJOK, J. u. PAPE, R. (2001): Möglichkeiten der Integration zoologischer Aspekte in die landschaftsökologische Untersuchung von Hochgebirgen. Methodendiskussion am Beispiel ökologischer Prozesssysteme und Biozönosen. In: Naturschutz und Landschaftsplanung 33, 351–357.

MAY, D. E. (1976): The response of alpine tundra vegetation in Colorado to environmental modification. PhD thesis, University of Colorado, Boulder.

MOE, B. (1995): Studien on the alpine flora along an east-west gradient in central Norway. In: Nord. J. Bot. 15, 77–89.

MOEN, A. (1999): National atlas of Norway: vegetation. Hønefoss.

MOEN, A. a. ODLAND, A. (1993): Vegetationssektioner i Norge. University of Trondheim vitensk. mus. In: Rapp. Bot. Ser. 2, 37– 53.

MOLENAAR, G. J. d. (1987): An ecohydrological approach to floral and vegetational patterns in arctic landscape ecology. In: Arctic and Alpine Research 19, 414–424.

MOSIMANN, T. (1985): Untersuchungen zur Funktion subarktischer und alpiner Geoökosysteme (Finnmark [Norwegen] und Schweizer Alpen). Basler Beiträge zur Physiogeographie / Physiogeographica 7, Basel.

MYKLESTAD, Å. (1993): The distribution of Salix species in Fennoscandia a numerical analysis. In: Ecography 16, 329–344.

NORDHAGEN, R. (1928): Die Vegetation und Flora des Sylenegebietes. Eine pflanzensoziologische Monographie. Skr. Norske vidensk.-akad. mat.-naturvid. kl. 1927 1, Oslo.

– (1936): Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. In: Bergens Museums Årbok, Naturv. rekke 7, Bergen.

– (1943): Sikilsdalen og Norges Fjellbeiter, en plantessosiologisk monografi. Bergens Museums Skrifter 22, Bergen.

NORWEGIAN METEOROLOGICAL INSTITUTE (1991–2002): Yearly rapports – daily values. Climate data of 60300 Geiranger, 605000 Tafjord (Møre og Romsdal), 14550 Prestulen, 14580 Vågåmo – N.Grindstugu, 16740 Kjøremsgrende (Oppland). Oslo.

ROSSWALL, T. a. HEAL, O. W. (eds.) (1975): Structure and function of tundra ecosystems. In: Ecological Bulletin 20, 1–450.

SIGMOND, E.; GUSTAVSON, M. a. ROBERTS, D. (1984): Berggrunnskart over Norge – M. 1: 1.000.000. Trondheim.

STANTON, M. L.; REJMANEK, M. a. GALEN, C. (1994): Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, USA. In: Arctic and Alpine Research 26, 364–374.

STEINHARDT, U. a. VOLK, M. (2002): The investigation of water and matter balance on the meso-landscape scale: A hierarchical approach for landscape research. In: Landscape Ecology 17, 1–12.

STRAND, T. (1951): The Sel and Vågå map areas. Norges Geologiske Undersøkelse 178, Trondheim.

TER BRAAK, C. J. F. (1986): Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. In: Ecology 67, 1167–1179.

– (1994): Canonical community ordination. Part I: basic theory and linear methods. In: Ecoscience 1, 127–140.

TRANQUILINI, W. (1964): The physiology of plants at high altitude. In: Annu. Rev. Plant Physiol. 15, 345–362.

– (1979): Physiological ecology of the alpine timberline. Berlin.

TUHKANEN, S. (1986): Delimitation of climatic-phytogeographical regions a the high-latitude area. In: Nordia 20, 105–112.

VESTERGREN, T. (1902): Om den olikformiga snöbetäkningens inflytande på vegetationen i Sarekfjällen. In: Botanisker Notiser, 241–268.

WALKER, D. A.; BILLINGS, W. D. a. MOLENAAR, J. G. d. (2001): Snow – vegetation interactions in tundra environments. In: JONES, H. G.; POMEROY, J. W.; WALKER, D. A. a. HOHAM, R. W. (Eds.): Snow ecology. An interdisciplinary examination of snow-covered ecosystems. Cambridge, 266–324.

WALLÉN, C. C. (ed.) (1970): Climates of northern and western Europe. World survey of climatology 5. Amsterdam.

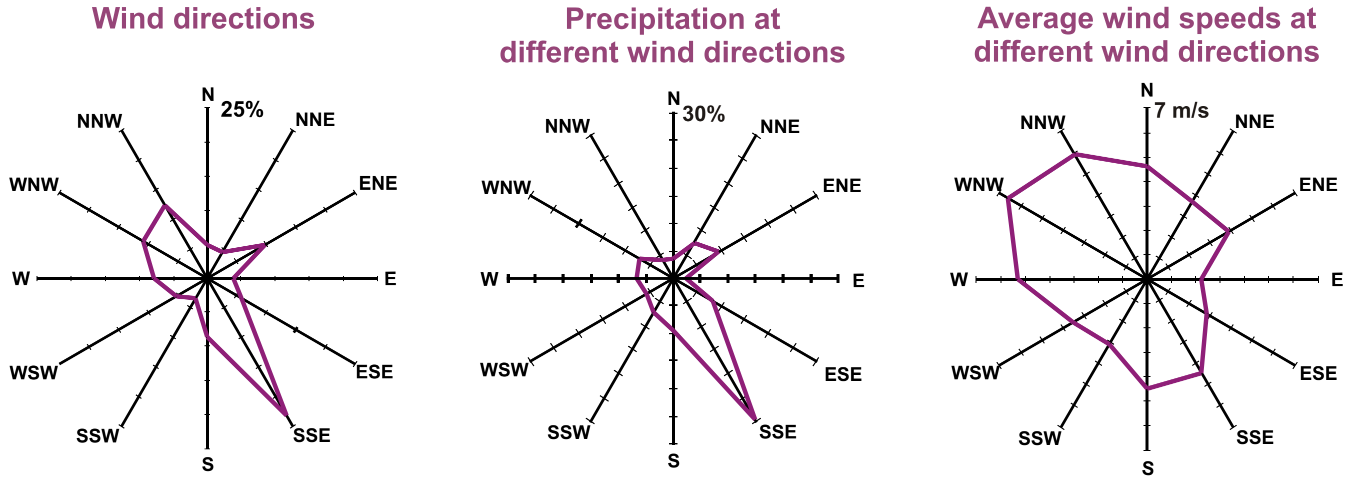
WEISCHET, W. (1995): Einführung in die allgemeine Klimatologie. Physikalische und meteorologische Grundlagen. Stuttgart.

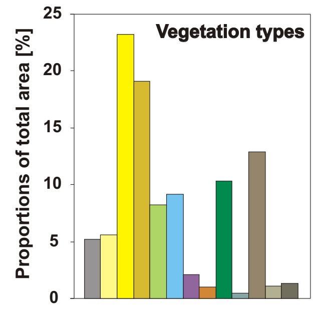
WIELGOLASKI, F. E. (ed.) (1975): Plants and microorganisms. Fennoscandian tundra ecosystems 1. Ecological Studies 16.

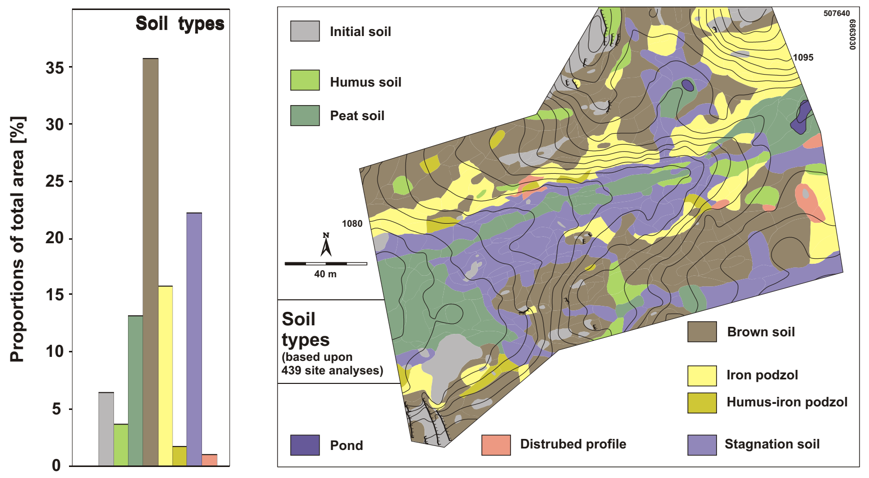
– (ed.) (1998): Polar and alpine tundra. Ecosystems of the World 3. Amsterdam.

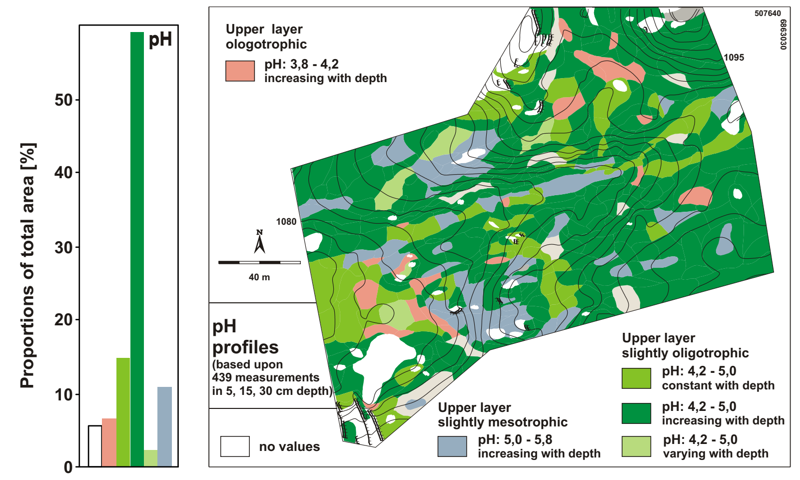
Supplement VII to ERDKUNDE 57,3 Article Löffler

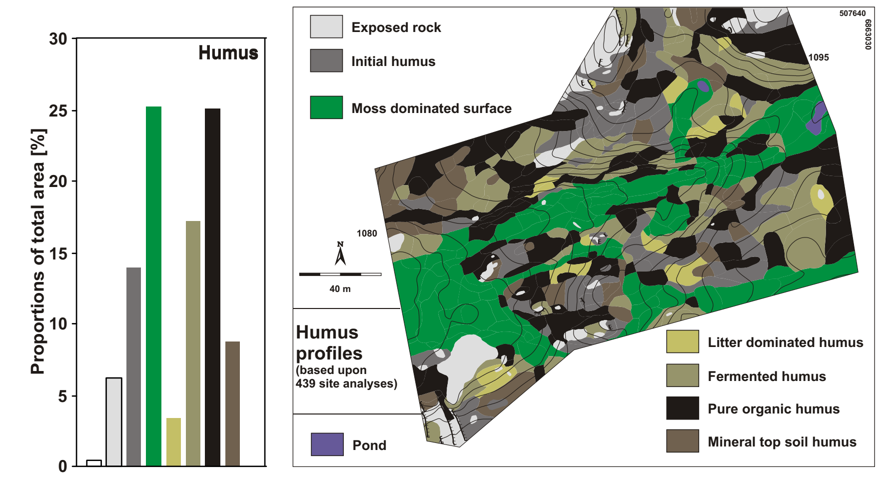
Vegetation determination along topographical gradients - low alpine belt, eastern Norway *Steuerung der Vegetation entlang topographischer Gradienten - untere alpine Stufe, Ostnorwegen*

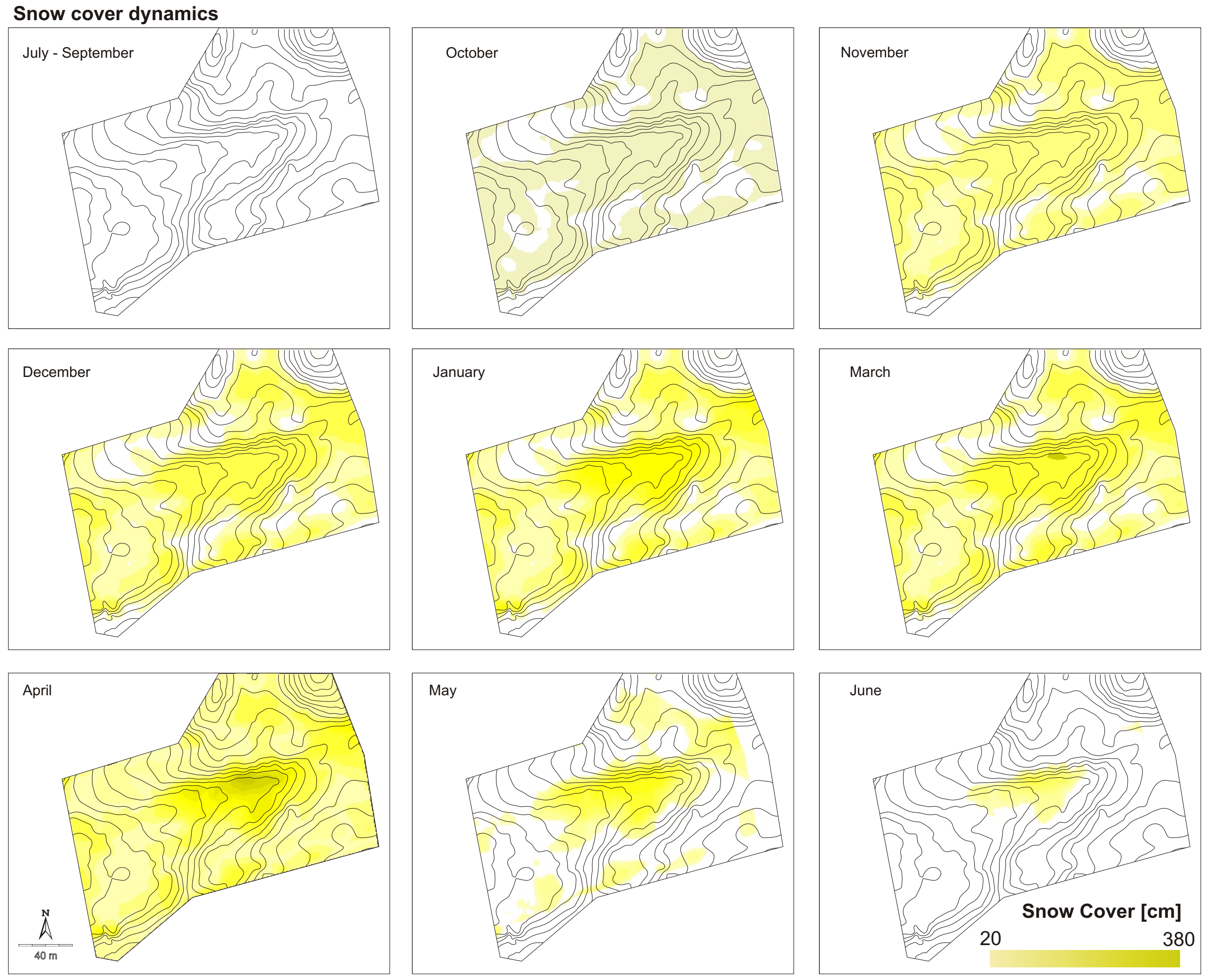


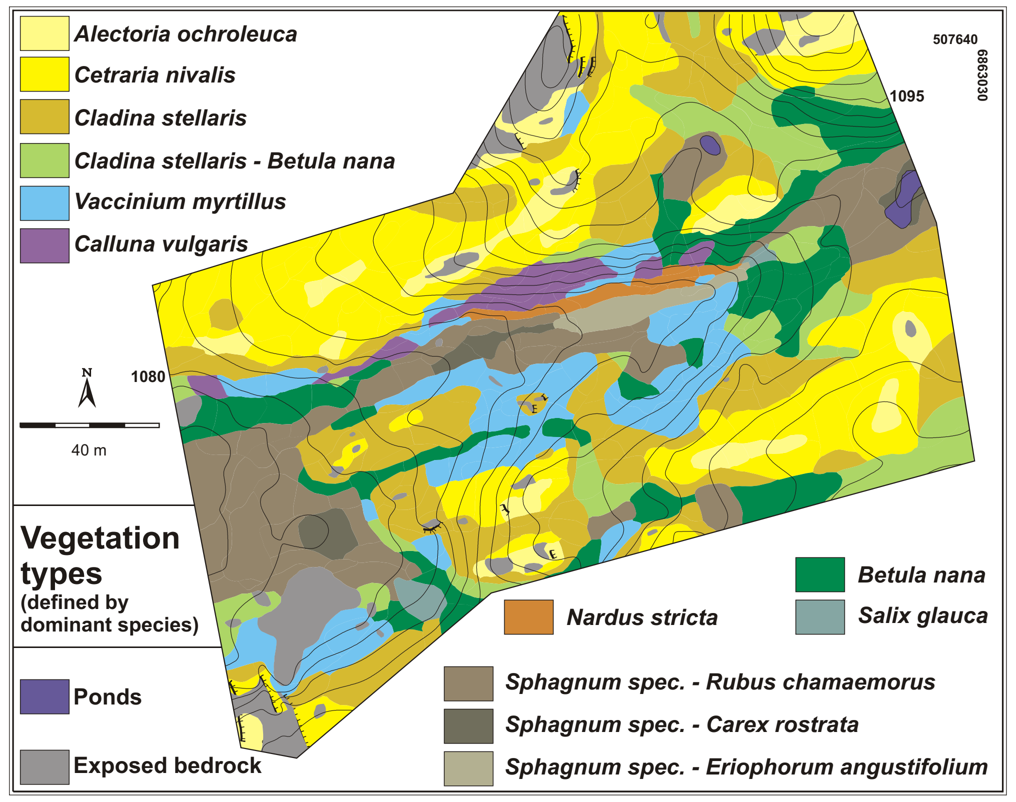


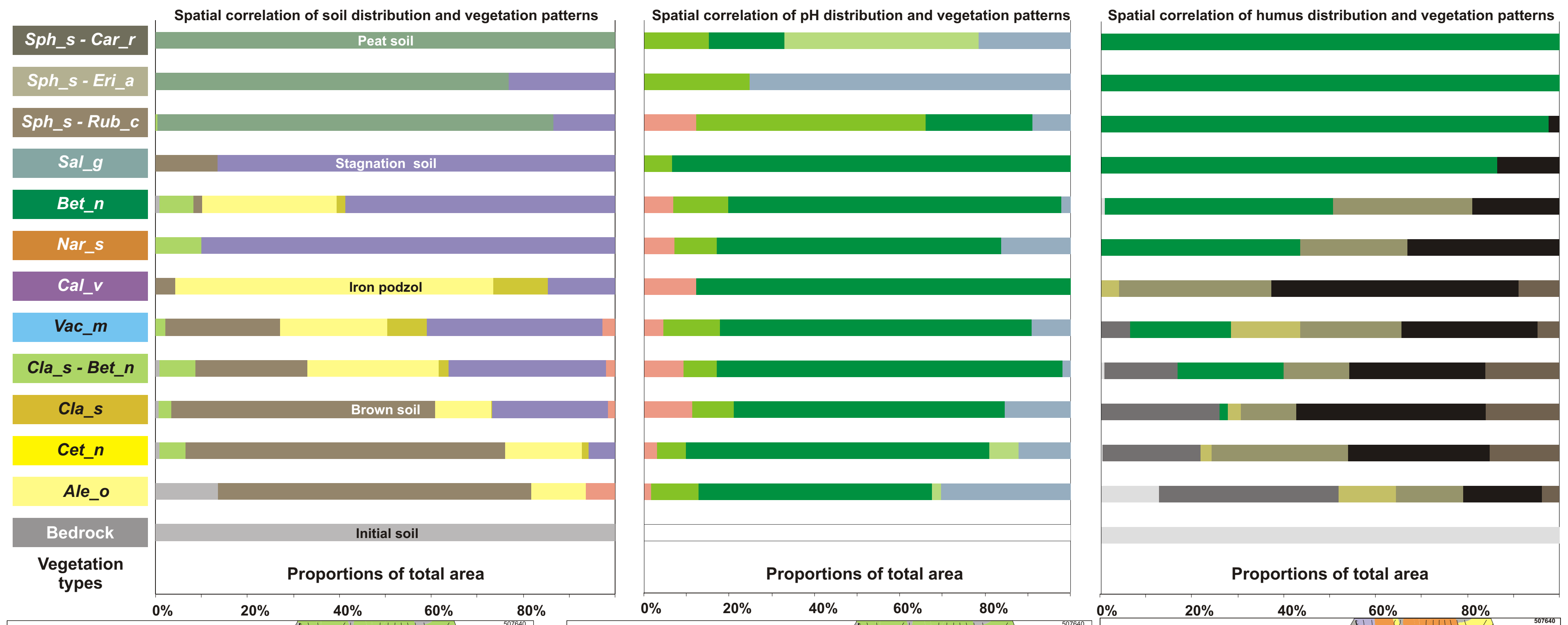






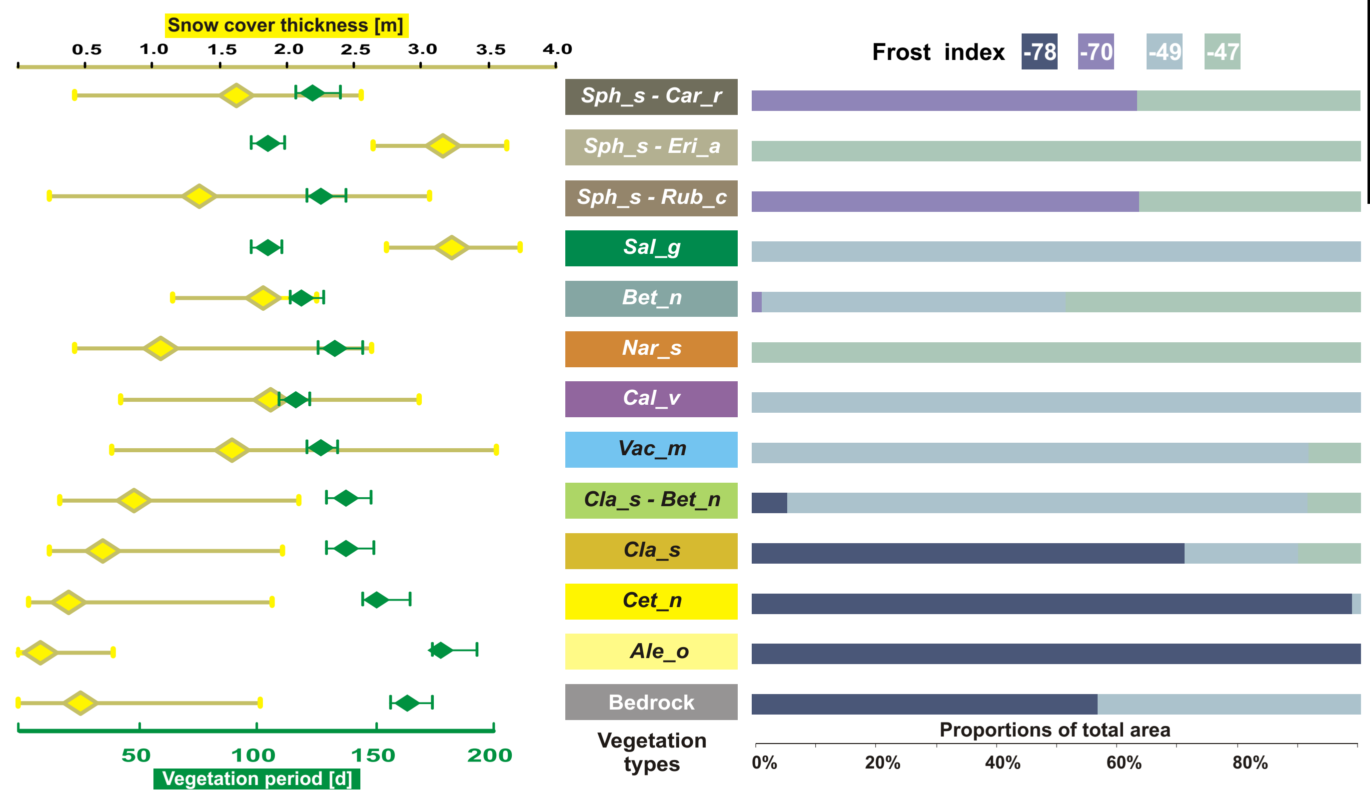


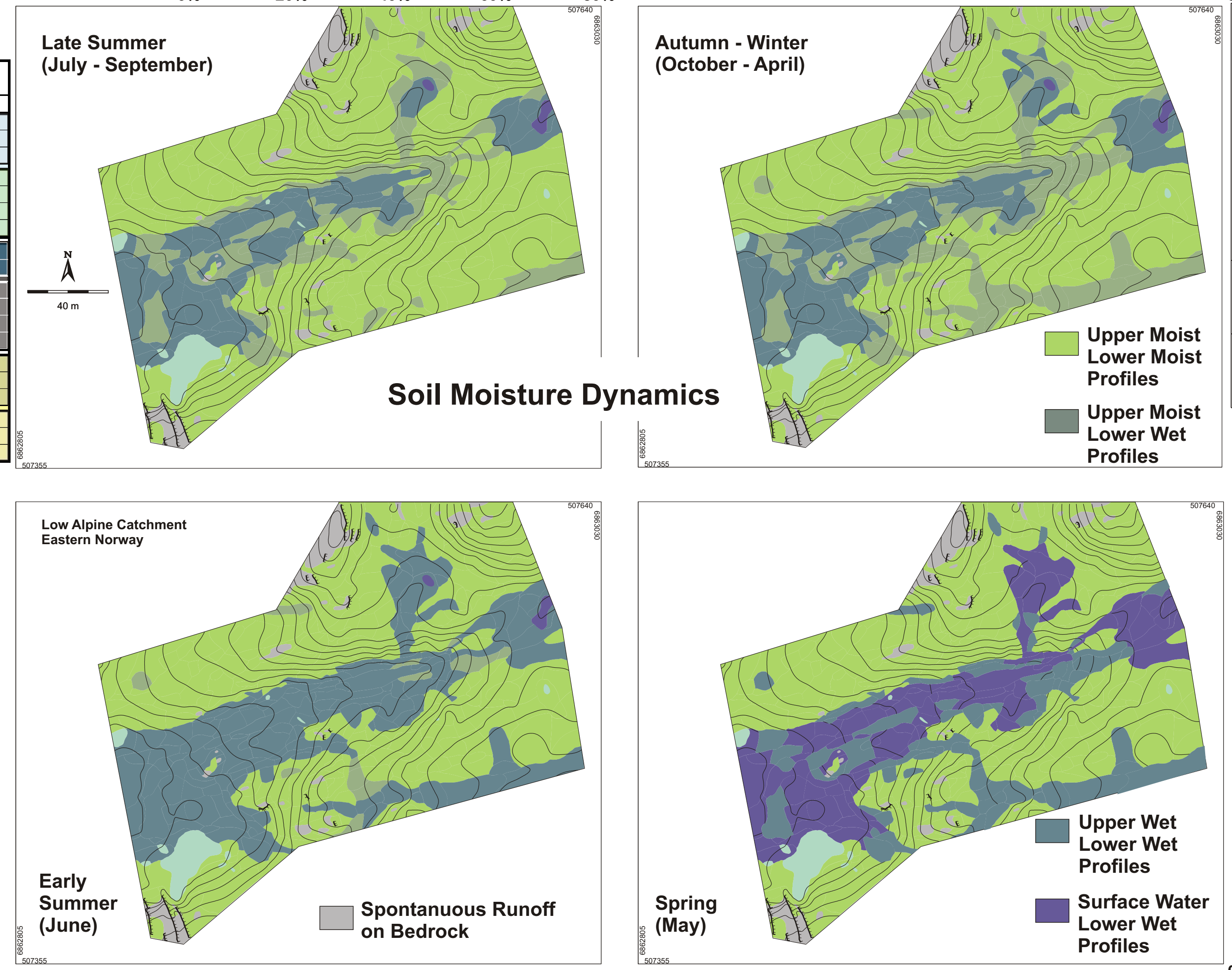


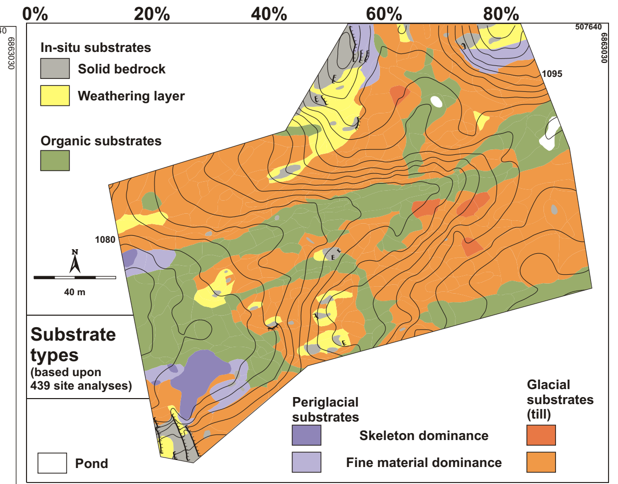


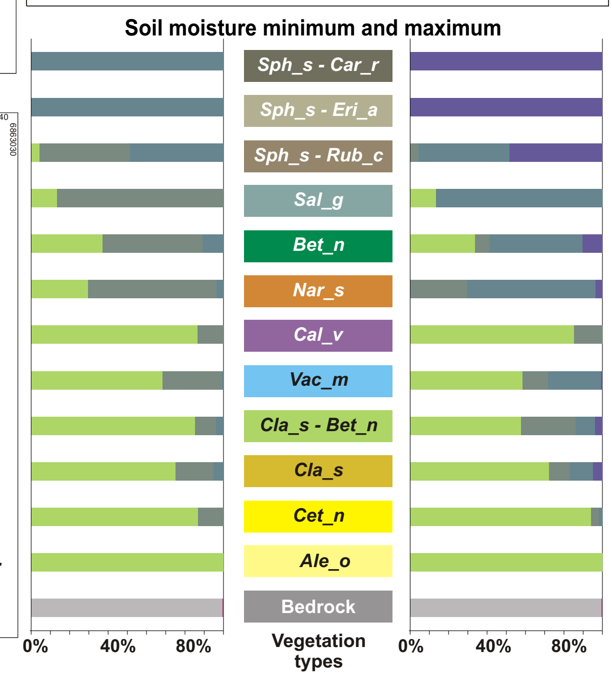
Classification of temperature dynamics

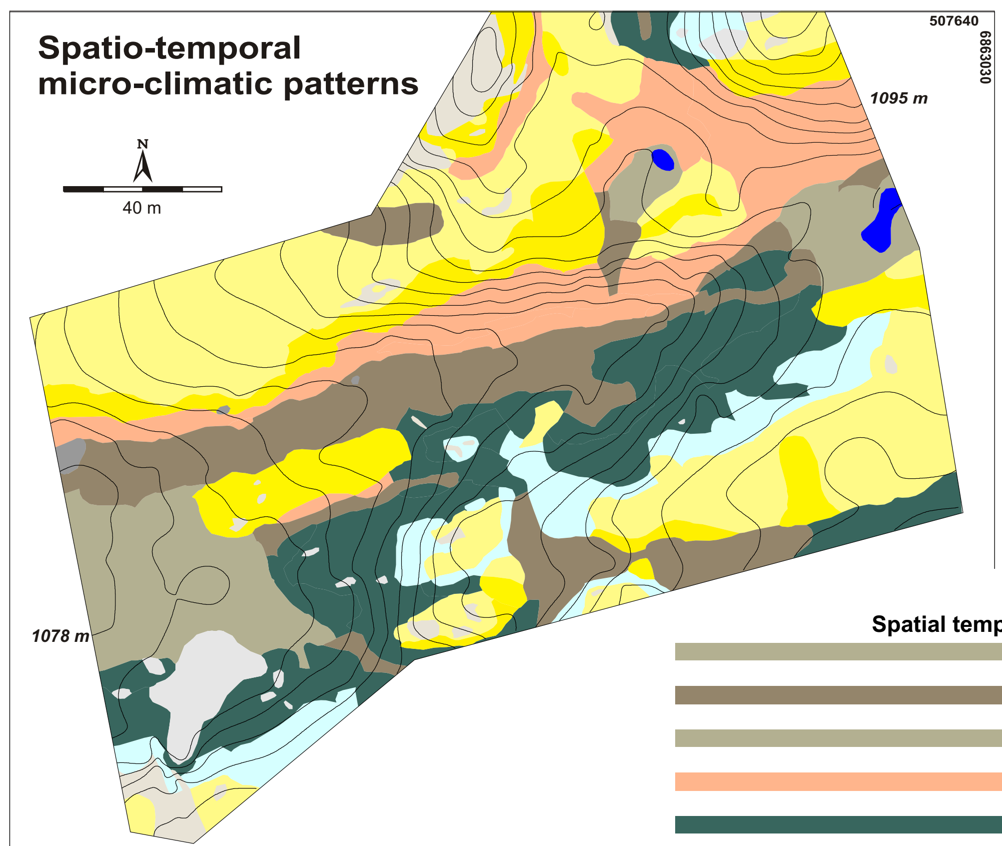
	Temperature type	Code	Duration of daily means [months] > 10°C	Duration of daily means [months] > 5°C	Duration of frost [months]	Annual amplitude [K]	Duration of daily maximum [months] > 25°C	Duration of daily maximum [months] > 13°C	Duration of daily maximum [months] < -1°C	Duration of daily maximum [months] < -13°C
air	extreme-cold	ex-cold	never	<3	>6	>45	never	<1	>6	<1
air	persistant cold	per-cold	never	<3	>6	<40	never	<1	>6	never
air	moderate-cold	mod-cold	never	<3	<6	<40	never	>1	<6	never
air	extreme-cool (eutherm)	ex-cool-eu	>1	>3	<6	>45	<1	<3	<6	<1
air	extreme-cool	ex-cool	>1	>3	<6	>45	never	<3	<6	<1
air	moderate-cool	mod-cool	>1	>3	never	<40	never	<3	<3	never
air	eutherm-cool	eu-cool	>1	>3	<6	>40	<1	>3	<6	never
surface	persistant-cold	per-cold	never	<3	>6	<30	never	<1	>6	never
surface	moderate-cold	mod-cold	never	<3	<6	<30	never	<1	<6	never
surface	extreme-cool	ex-cool	>1	>3	<6	>40	<1	<3	<6	never
surface	extreme-cool (moderate)	ex-cool-mod	>1	>3	<6	>30	never	<3	>3	never
surface	extreme-cool (eutherm)	ex-cool-eu	>1	>3	never	>45	>1	>3	never	never
surface	moderate-cool	mod-cool	>1	>3	<1	>25	never	>1	never	never
soil	extreme-cold	ex-cold	never	<3	>6	>20	never	never	>6	never
soil	persistant cold	per-cold	never	<1	>6	<20	never	never	>6	never
soil	moderate-cold	mod-cold	never	<3	<6	<20	never	never	>3	never
soil	extreme-cool	ex-cool	>1	>3	<6	>30	never	<1	<6	never
soil	moderate-cool	mod-cool	never	>3	never	<15	never	never	never	never
soil	moderate-cool (extreme)	mod-cool-ex	never	>3	<3	<20	never	never	>1	never



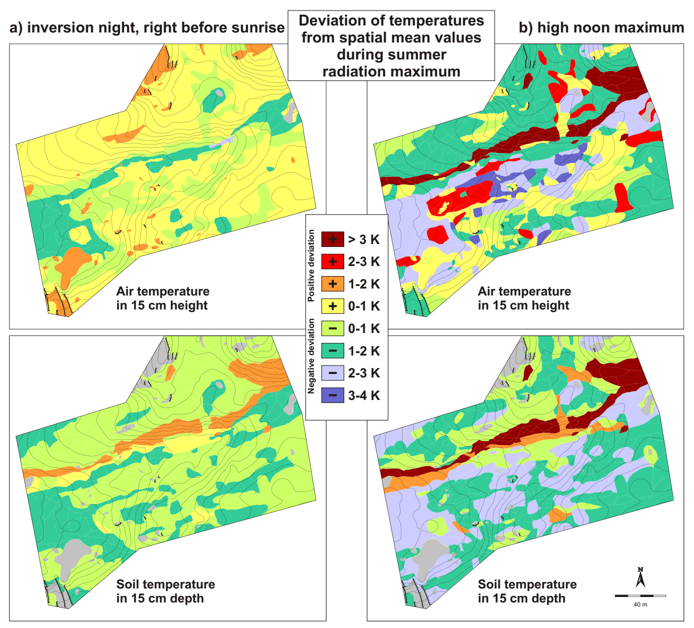


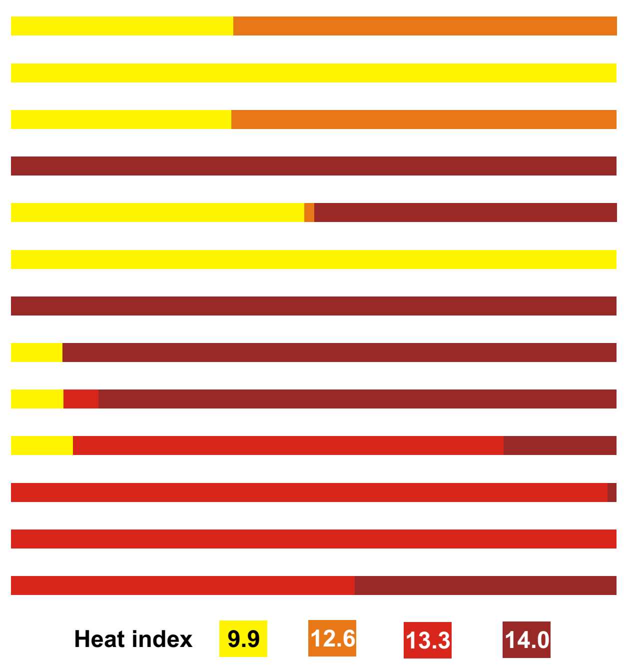


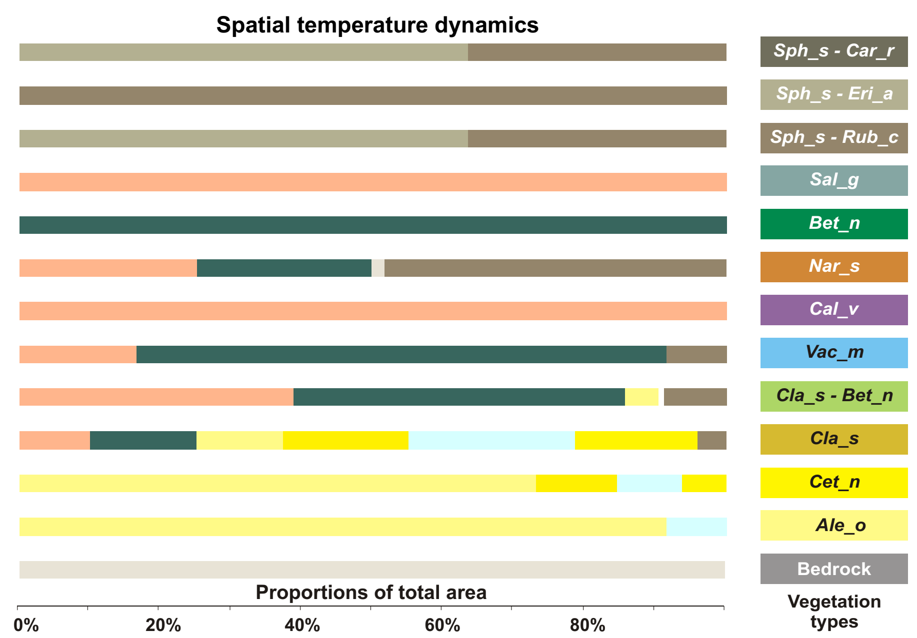


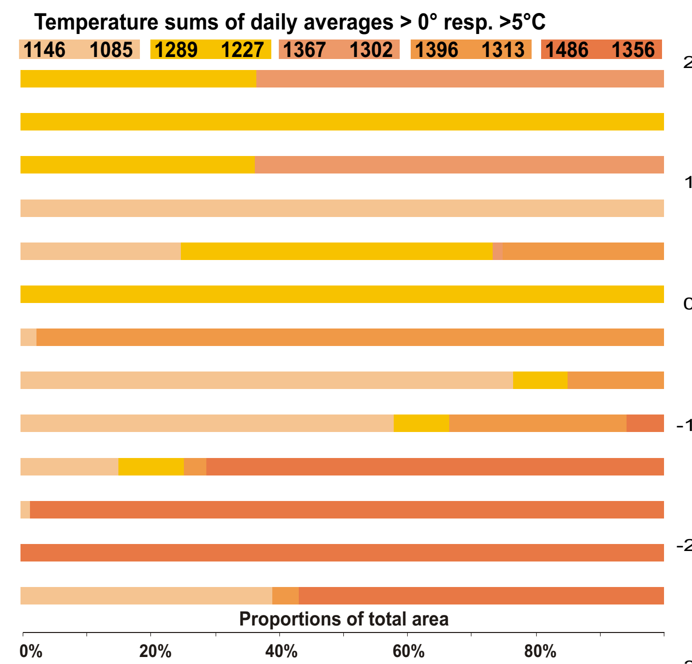


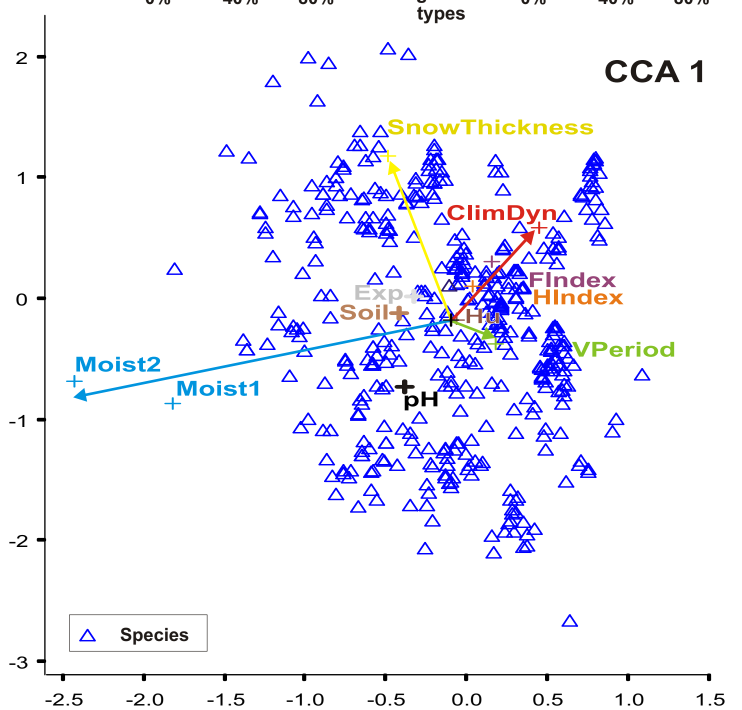
soil	surface	air	ecotopes with
-	-	ex-cool-eu	temperature profiles of ridges
ex-cool	ex-cool	ex-cool-eu	temperature profiles of ridges
mod-cool-ex	ex-cool	ex-cool-eu	temperature profiles of ridges
-	-	eu-cool	temperature profiles of northern exposures
mod-cool	ex-cool-mod	ex-cool-eu	temperature profiles of northern exposures
mod-cool	mod-cool	eu-cool	temperature profiles of northern exposures
mod-cool	mod-cool	mod-cool	temperature profiles of depressions
mod-cool-ex	ex-cool-mod	ex-cool	temperature profiles of depressions
mod-cool	ex-cool-eu	eu-cool	temperature profiles of southern exposures
mod-cool	ex-cool	ex-cool-eu	temperature profiles of southern exposures
-	-	eu-cool	temperature profiles of southern exposures



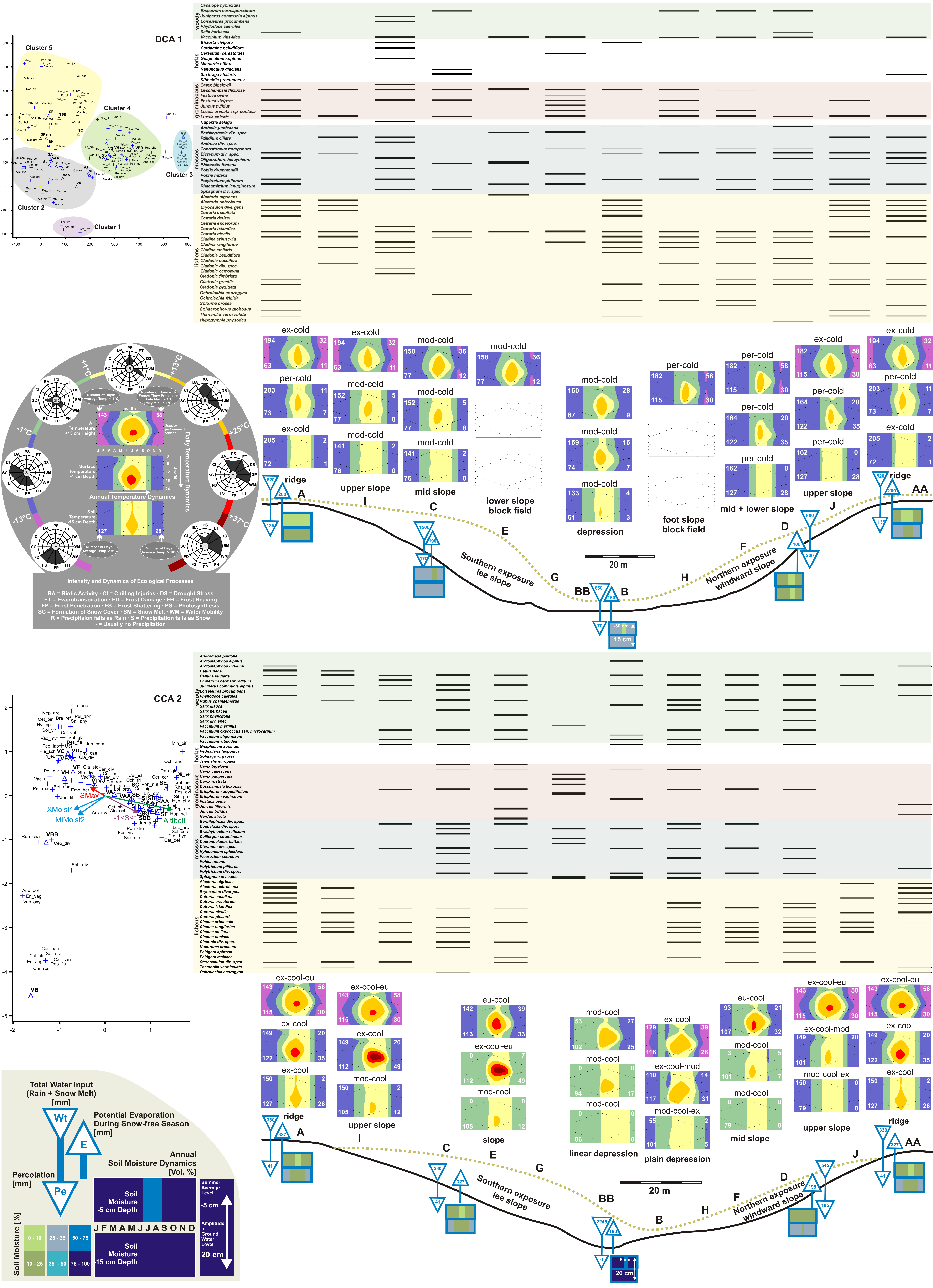








Vegetation determination along altitudinal gradients *Steuerung der Vegetation entlang von Höhengradienten*



Vegetation determination along oceanic-continental gradients *Steuerung der Vegetation entlang von Ozeanitäts-Kontinentalitäts-Gradienten*

		W LA R1	W LA R2	W MA R1	W MA R2	E LA R1	E LA R2	E MA R2	E MA R1
woody	*Arc_alp*		6			3	3		
	Arc_uva					7	5		
	Bet_nan	7				6			
	Emp_her	7	7			4	7		
	Loi_pro		3	3		4	3		
	Phy_cae								1
	Sal_her			6	8			5	
	Vac_uli	8	8						
	Vac_vit			5	7	4	3		
	Ran_gla							3	
greminacous	*Car_big*	6		5	6				6
	Fes_ovi						2		5
	Jun-tri			7			2		5
	Luz_con				6			5	6
	Poa_viv				1				
	Hup_sel								2
mosses	*Bar_div*							5	
	Lop_div			5					
	Pti_cil		5		5				
	Con_tet			2				6	6
	Dic_div			5	6			5	5
	Poh_nut			2					5
	Pol_div				7				
	Pol_pil			2	7		5	5	6
	Rha_lan	7	6						
lichens	*Ale_nig*			2	8	5	3	3	5
	Alc_chr			5	6	9	7	5	5
	Bry_div			2	5	5	6	5	6
	Cet_cuc				5	5	2	5	5
	Cet_niv				7			6	
	Cet_eri					5	2		
	Cet_isl	8	2	7					5
	Cet_niv	6	5	9	9	6	8	7	6
	Cla_arb	8	8	6		3	2		
	Cla_chl			2					
	Cla_coc							3	
	Cla_fim							2	2
	Cla_gra							3	2
	Cla_ran	7	7	5		5		2	
	Cla_ste				3	3			
	Cla_sul		9			6			
	Cla_unc	6	5	2					
	Och_and						2		
	Och_fri			2					2
	Sol_cro							2	
	Sph_glo			2	2				2
	Ste_div					3			
	Tha_ver		2	2	5	3	3	3	2