

Session 1

FS 05-I: Alpine Treeline Ecotones under Global Change I

Time:

Location: THEOLOGIE - Madonnensaal

Tuesday, 13/Sept/2022:

1:30pm - 3:00pm

Theologie - Madonnensaal, second floor

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Session Topics:

05_Alpine Treeline Ecotones under Global Change

[Exceptional Format: Please check program here.](#)

Session Abstract

Alpine treeline ecotones are vegetation transitions strongly controlled by climate. In many mountains, they are additionally controlled by land-use practices. As they delineate two major mountain ecosystems, it is important to understand how they function. In spite of significant scientific progress, many questions about alpine treelines are still open, including: Why do climatic treelines exist? How will treeline ecotones respond to climatic change? How do land use and land-use changes affect treeline-ecotone vegetation dynamics? And what are the implications for designing and implementing mountain conservation, restoration and management strategies? The focus of this session are the mechanisms, patterns and consequences of alpine treeline ecotone vegetation dynamics. We welcome research from all disciplines, addressing questions on treeline ecophysiology, ecology, history, spatial patterns and human dimensions, using diverse approaches, including experiments, monitoring, modelling, remote sensing, palaeoecology, dendroecology, and comparative analyses.

Presentations

Advantages and limitations of stringent logics applied to the global treeline phenomenon

Körner, Christian

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After A. von Humboldt's genuine idea of an isotherm connecting the mountains of the world, the bioclimatic stratification of vegetation belts became an accepted biogeographic framework. The climatic treeline represents the overarching reference line for this stratification. Next year we can celebrate hundred years after Däniker's first attempt at a unifying explanation of the low temperature range limit of the life form tree, although inevitably, he had a temperate zone perspective and very limited data. Over these 100 years, the topic saw its ups and downs, largely tied to definition issues, available methods and concepts rooted in different disciplines. For instance, one may question whether rating a tree by its stem's usefulness as timber bears ecological meaning. In this presentation I will illustrate how stringent scientific logics can both advance and constrain this field of research. Scale is a central issue. Some seemingly divergent ideas converge, depending on the scale applied. I will focus on the global dimension, the underlying physical principles and the potential biases of static concepts in comparison to dynamic ones. I will conclude that a dynamic forest line concept will make static categories superfluous, and it opens the floor to generalization. However, such a concept also bears conflict with attempts at applying stringent explanatory criteria, physiological ones in particular. Impressions of site visits and short-term demographic assessments are likely to give weight to a random state on a multi-century chronology of forest dynamics at the edge. I will illustrate cases of rapid current advances of tree limits and provide data for the likely global land area that will become encroached by advancing uppermost montane forests in response

to ongoing climatic warming. Further reading: Körner C (2021) The cold range limit of trees. Trends Ecol Evol 36: 979, <https://doi.org/10.1016/j.tree.2021.06.011>

Poster flash talks:

Drought resistance and recovery of Norway spruce seedlings

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Climate change substantially alters temperature and precipitation patterns, leading to more frequent and/or intense drought events in Central Europe and the Alpine region. Increasing drought stress can have severe influences on tree productivity, carbon and water relations, and may cause species range shifts. Severe and/or prolonged droughts can impair tree water transport via emboli in xylem tissue with potential long-term consequences on tree fitness. However, knowledge of resilience and recovery potential under and after different drought stress intensities/durations of juvenile trees is scarce.

In this study, tree hydraulic traits were combined with gas exchange measurements on an alpine tree species (*Picea abies*). We used specially designed greenhouse gas exchange chambers for individual seedlings and compared drought effects on, and recovery patterns of juvenile Norway spruce trees under long-term (DD), intermitted (DR) and short-term drought (CD). Measurements of water potential, gas exchange fluxes and non-structural carbohydrates (NSC; starch and soluble sugars) in combination with climate data, soil water content, and high-resolution stem increment data allowed for evaluation of detailed drought and recovery patterns.

During the first drought period, critical water potentials induced reduction in increment, net photosynthesis, and caused emboli in DD and DR trees. This resulted in an even faster drop in water potentials during the second drought period. DR trees recovered within a few days between droughts. However, in the second drought period they showed a faster drop in water potentials and net photosynthesis compared CD trees. Drought led to a depletion of starch in branches and needles. Stress release resulted in a fast recovery of water potentials, except for DR trees which did not reach levels of control trees after 10 days. NSC storages recovered within 10 days. Albeit the recovery of photosynthesis was delayed in the long-term drought treatments (DD, DR), and even CD trees did not reach levels of control trees within 10 days after re-watering.

Incomplete recovery of net photosynthesis and water potential indicate long-term impairments in the water transport system of drought-treated trees. Low water and carbon storage of juvenile trees might not be sufficient to repair damages induced by embolized vessels and the limited hydraulic capacity thus lowered the potential of full recovery. Especially long-term and intermitted long-term droughts render juvenile Norway spruce trees susceptible to long-term impairments. Limited recovery potential may ultimately become decisive for tree survival in face of repeated drought events as expected due to climate change.

Improving macroevolutionary studies of alpine plant groups by accurately assigning species to biomes based on imperfect data

Bätscher, Livio; de Vos, Jurriaan

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Macroevolutionary studies to understand niche evolution in plants usually rely on classifying species as belonging to particular biomes, even though occurrence data is typically noisy and boundaries of biomes may be poorly defined both spatially and climatically. For diverse plant clades (e.g., all species of a genus) that have broad geographic distributions, such assignment need to consider imperfect, rasterized global climatic data. Moreover, spatial datasets of millions of point-localities require a fully automated approach. Accurately assigning species to biomes then becomes a challenging task that is often not fully addressed but may bias downstream evolutionary inference.

Here we present an approach to automatically classify species to thermal belts (e.g. alpine or non-alpine) using the climatic proxies for the treeline and the ruggedness of the terrain. We account for poorly geo-referenced point-localities and bias due to rasterized data in topographically highly heterogeneous mountainous areas. Specifically, to classify a record, we combine digital elevation

models and climatic data to model the elevation of a local treeline and use it to adjust a "raw" classification of a record. To reconstruct the evolution of biome shifts, we then use phylogeny-explicit methods and well-sampled phylogenies of species-rich genera that contain species in all thermal belts.

We demonstrate that accurately defining biomes positively impacts the accuracy of reconstructed biome shifts, underlining the importance of our approach. Furthermore, this study is among the few that considers the local differences of the treeline, through by the mass elevation effect (causing the isotherms to move upslope in larger mountain systems) and latitude.

Decadal alpine treeline dynamics modelled using Landsat timeseries amidst rapid climate change in Australia: a song of ice and fire

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Alpine ecosystems are characterised by low temperatures and short growing seasons, but the stability of these ecosystems is threatened by climate change. Climate-induced dynamics in alpine vegetation have been recorded globally with changes in diversity, vegetation cover type, and composition, including in the Australian Alps. However, insights into these dynamics in Australia have been gleaned solely from field studies at small spatial scales. Here, climate data and LANDSAT imagery were assessed for Australia's highest and most diverse alpine area that surrounds Mount Kosciuszko (455 km²). Climatic changes were assessed using gridded climate data (5 x 5 km) for mean annual temperature (1910-2019) and seasonal precipitation (1900-2019), and changes in snow cover were assessed from snow course records (1954-2021). A vegetation cover timeseries (1990, 2000, 2010, 2020) was modelled with an optimised RandomForest supervised classification using recursive feature selection. Over time, mean temperatures (0.1 °C/decade) and summer precipitation (6.5 mm/decade) have increased whereas snow cover (12.74 metre-days/decade) and winter precipitation (9.7 mm/decade) have declined. Subsequently, there were considerable vegetation dynamics between 1990 and 2020 with the cover of treeline snowgum woodlands increasing (+134.8%) via densification and in-filling at lower elevations, but not treeline advance. Treeline subalpine woodlands replaced large tracts of dry alpine heath (36.4 km²) and wet alpine heath (38.0 km²) while there was less change in cover of grassland vegetation types. The study area also experienced a landscape-level fire in 2003 (268.4 km² burnt or 59%), with the cover of treeline subalpine woodlands increasing at a greater rate in burnt (+1.70 km² per annum) versus unburnt (+0.73 km² per annum) areas between 2000 and 2020. Evidently, the rate of change in the climate of the study area has increased through time and is mirrored by vegetation cover and zonation dynamics with the proliferation of treeline subalpine woodlands (+70.6 km²) and advance of dry (+33.5 m) and wet (+12.89 m) shrubline, while in burnt areas there was treeline retreat (-9.2 m) as well as dry (-16.5 m) and wet (-5.3 m) shrubline suppression. Warmer temperatures, variable precipitation, and declining snow cover also increase the frequency and severity of fires, which may be compounded by increasing fuel loads from the proliferation and advance of woody vegetation in alpine areas. In the coming decades, alpine vegetation may be impacted by climate change both incrementally, through relatively gradual changes in abiotic conditions, and transformatively, through landscape-level disturbance from fire.

Alpine treeline spatial patterns revealed through proximal and remote sensing techniques

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Alpine treeline ecotones are facing an exceptional change due to both climatic and land use changes. Elevational treelines of Southern Alps are mostly constrained by regional-scale climate, landscape-scale human legacy and fine-scale microsite conditions.

10 treeline ecotones of the Italian Alps were randomly selected along the uppermost forestline extracted from a tree cover density Copernicus dataset (year 2018), spanning from west to east of

the mountain range. In these treeline ecotones, we integrated proximal and UAV-based remote sensing data to obtain a stem-mapped dataset of seedlings within 9 ha plots. In particular, proximal data included the position of all seedlings taller than 50 cm and their height. Regarding remote sensing data, we employed UAV photogrammetry to derive a 4 cm digital elevation model (DEM) and a canopy height model (CHM). Moreover, we coupled object-based image analysis (OBIA) and random forest (RF) to classify RGB very-high resolution orthomosaics into land cover classes, including tree species. We adopted multivariate statistical analysis to assess site-scale environmental and anthropogenic drivers. At a singletree scale, we used first- and second-order point pattern analysis (PPA) to assess species distribution and facilitation mechanisms and statistical modeling to assess micro-topographic drivers on tree encroachment.

Coupling proximal and remote sensing techniques allowed us to map accurately (average RMSE = 30 cm) 90 ha of alpine treeline ecotone. Results highlighted common patterns and some peculiarities. *Larix decidua* was the dominant species at the treeline, but *Pinus cembra*, *Picea abies*, *Pinus sylvestris* and *Pinus uncinata* were locally abundant. All the measured treeline ecotones showed a common legacy of human impact, but with locally different intensities and patterns. Pure larch treelines of western Alps were at lower elevations and mostly associated with intense pastoral historical use.

Our fine-scale approach is a powerful and low-cost tool to efficiently obtaining precise and spatially explicit data on forest dynamics occurring at treeline ecotones. The comprehensive dataset that we obtained for relatively large study areas allowed us to explore the role of biotic and abiotic drivers of tree establishment and growth at the treeline. An integration of landscape-scale diachronic analysis is planned to disentangle the role of land use legacy on treeline ecotone dynamics.

Acceleration of subalpine forest limit upward shift and densification in the French Pyrenees

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The upper subalpine forest limit is characteristic of mountain landscapes. This limit is influenced by global change. We studied subalpine forest in its extent with its upper limit shift, and in its structure with the transition from closed to open forest. The studied period goes from the forest minimum to its current maximum. We focused on the French Pyrenees because it is the first digitized area in the map which dates back to 1840 ("Etat-Major" map). We used two other maps from 1996 and 2010, made by the National Forest Inventory according to aerial photographs interpretation. We estimated the altitude of open and closed subalpine forest limits for each municipal district and each date. We then calculated the difference in altitude between these dates. We observed a positive altitudinal shift of open forest limit between 1840 and 1996 in most of the municipal districts (84 %), and of open and closed forest limits after 1996 (78 % and 88 % of municipal districts). On average, the open forest limit raised of about 180 m between 1840 and 1996, and open and closed forest limits raised of about 50 m and 100 m respectively after 1996. Hence, the open forest limit raised on average of 13 m per decade between 1840 and 1996 and of 35 m per decade after 1996, while the closed forest limit raised on average of 65 m per decade after 1996. Our study shows an acceleration of upward shift and densification. Since land abandonment have been constant during the studied period, this acceleration may be due to climate change acceleration. Moreover, these results suggest a need to consider both subalpine forest upward shift and densification in studies quantifying impacts of forest expansion on carbon cycle.

Branch water uptake and redistribution in two conifers growing at the alpine treeline

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Under harsh winter conditions, conifers growing at the alpine treeline suffer dramatic losses of hydraulic conductivity, which can be successfully recovered during late winter. Branch and needles water uptake have been observed to support hydraulic recovery.

We analyzed water absorption and redistribution in *Picea abies* and *Larix decidua* growing at the alpine treeline by *in situ* exposure of branches to $\delta^2\text{H}$ -labelled water.

Both species suffered high winter embolism rates (>40-60% loss of conductivity) and recovered in late winter (< 20%). Isotopic analysis showed water to be absorbed over branches and redistributed within the crown during late winter for over 425 ± 5 cm within the axes system and shifted to the trunk, as well as to lower and higher branches (tree height 330 ± 40 cm).

Results demonstrated relevant branch water uptake and re-distribution in treeline conifers. *L. decidua* showed higher rates of water absorption and re-distribution, indicating species-specificity in this process. At the alpine treeline, melting snow might be the main source for absorbed and redistributed water, enabling embolism repair and restoration of water reservoirs prior to the vegetation period. Pronounced water uptake in the deciduous *L. decidua* indicated bark to participate in the process of water absorption.

Xylem characteristics and formation dynamics under long-term drought: A study on conifers at the Alpine treeline

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Trees in mountain forest systems are exposed to extreme climatic conditions with high spatial and temporal variation. Factors such as low air and soil temperatures, intense frost or long snow coverage and associated short vegetation periods are challenging for trees at high elevation. Additionally, also mountain ecosystems will have to face pronounced change in mean climate conditions and an increasing risk of climate extremes (e.g. heat waves, extended drought periods) with ongoing global warming. However, our current knowledge of how trees at the treeline respond to changing climatic conditions (especially to pronounced summer droughts) is scarce.

To gain new insights into the eco-physiology of drought-stressed trees at the treeline, we studied two coniferous species (*Picea abies*; *Larix decidua*) growing at an experimental field site located at ~2000 m asl (Kaserstattalm, Tyrol, Austria), where through-fall was excluded from trees during vegetation periods since 2016. With a main focus on the hydraulic system (i.e. xylem), drought-induced structural and functional changes were assessed: we studied tracheid characteristics and xylogenesis dynamics of stressed and control trees as well as seasonal and annual changes in hydraulic traits (e.g. sap flow, hydraulic conductivity, water potential). In micro-CT observations of branch samples, we quantified the trees' vulnerability to drought-induced embolism and relevant anatomical traits.

Results demonstrate species-specific changes in the dynamics of xylem formation under long-term drought stress. Drought stress also affected structural traits of wood cells which in consequence led to changes in hydraulic efficiency and/or hydraulic vulnerability.

Conifers dominate the treeline ecotone and a better understanding how future climatic conditions affect their xylem formation and functionality will help to better anticipate individual tree responses and ecosystem dynamics at high altitude.

Simulating landscape-scale treeline dynamics under climate and land-use change to support forest management strategies

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Forests are long-lived ecosystems, very sensible to rapid environmental changes. In mountain areas, the effect of climate warming on the upper treeline and the subalpine forest belt can already be

observed today. Although rising temperature may improve forest growth and promote treeline expansion towards new elevation ranges, other aspects such as water availability, soil conditions, incoming radiation as well as land-use and management activities may alter these effects. So far, many studies have focused on single effects of climate variability on treeline forest dynamics. Nonetheless, only few have attempted to project the future response of treeline ecotone using dynamic vegetation models, with a spatially explicit approaches that allow evaluating landscape-scale patterns that could deliver meaningful insights to ecosystem managers. Focusing on a mountain forest landscape in the Central Alps (Stubai Valley, Austria), we aimed at evaluating the effects of climate and land-use change on the treeline ecotone by simulating forest dynamics from the stand to the landscape scale. We applied a process-based forest landscape model (iLand) under different climate and forest management scenarios. Additionally, we compared two land-use scenarios that might affect treeline dynamics, namely business-as-usual versus land abandonment. Our preliminary results showed that the upper treeline will generally advance in elevation promoted by rising temperature, but this effect is highly heterogeneous and contingent on multiple factors across such a complex mountain terrain. The treeline reached highest elevations under the high emission climate scenario, but its expansion was highly modulated by different land-use, which strongly influenced forest regeneration patterns across the landscape. Overall, we observed an expansion of the forest area in the subalpine belt which was considerably greater under the abandonment scenario. Heterogeneous soil conditions also affected the future spatial pattern of treeline dynamics. Although modelling future treeline dynamics remains a challenge due to the complexity of multiple interacting factors acting at different scales, our study highlights the potential of dynamic forest landscape models to project future treeline development. Such modelling approaches also allow exploring future spatial patterns of the upper treeline with a landscape perspective. This can be useful for decision makers in the context of forest management planning, particularly to alpine ecotone biodiversity, improving conservation strategies and to maintain the provision of future ecosystem services.

Seven years of seedling survival and growth in a recruitment experiment at treeline
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Treelines are predicted to move upward and poleward globally due to increasing temperatures under the ongoing climate change. The establishment of new tree populations above the current treeline depends on the up-slope transport of viable tree seeds, their successful germination and the long-term survival of seedlings. In the framework of the Global Treeline Range Expansion Experiment (G-TREE), we conducted a multifactorial long-term field experiment to quantify biotic and abiotic recruitment drivers in an alpine treeline ecotone in the Swiss Alps. In 2013, two experimental sites - at and above the current treeline - were established. At each site, we applied a combination of vegetation removal and seeding treatments with low and high elevation provenances of *Picea abies* L. Karst (Norway spruce) and *Larix decidua* MILL. (European larch) in two consecutive years. Seedling survival and growth were monitored annually since then. Over the whole study period, natural recruitment only rarely occurred in the study plots. Only 21% of the totally 1'715 emerged seedlings survived the first winter. Thereafter, the number of surviving seedlings continuously decreased to 4% in 2021. Vegetation removal had a positive effect on seedling survival, especially in the first years, while this influence became slightly less important in the longer-term. Above treeline, only *L. decidua* seedlings survived, while at treeline equal numbers of both species survived. Average seedling heights at and above treeline were similar except for the last two years of the study, when seedling growth above treeline even exceeded growth at the lower elevation site. Our results demonstrate that tree seedlings can establish several hundred meters above the current treeline when viable seeds and suitable microsities are available. After passing the bottleneck of first winter survival, some seedlings survived for at least seven years. Enhanced seedling survival in the presence of open ground in the immediate surrounding indicates a positive effect of light availability and higher soil temperatures. Our findings also show an advantage for the pioneer species *L.*

decidua, which had higher survival rates. The strong seed source limitation in the alpine treeline ecotone suggests that individual survivors may become stepping stones for treeline advance.

Quantifying changes in alpine treeline ecotone spatial patterns in the Pyrenees: proposal for a standardized methodological protocol

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Alpine treeline ecotones are particularly sensitive to environmental changes. In the absence of other disturbances, this ecotone is controlled by climatic constraints. It should thus respond, theoretically, to the current rise in temperatures by an elevational shift of the subalpine forest. Nevertheless, various studies indicate that these elevational changes are not systematic, somewhere regressive or stagnant, reflecting the complexity of the mechanisms at work¹. In addition, the ecotone spatial dynamics can be characterized by processes other than elevational change, such as the tree population densification without elevational shift, or changes in spatial pattern. These structures characterize the ecotone's shape in plan: rectilinear, diffuse, islands, etc. Recently, Bader et al² proposed a typology of these structures and associated them with underlying ecological processes such as natural or anthropogenic disturbances (grazing, fire, etc.).

Thus, these spatial dynamics inform us about how the ecotone responds to different forcings. Therefore, quantifying this shape pattern change and then relating it to potential determinants is a meaningful contribution to treeline studies. However, such a quantification also raises some methodological issues that need to be addressed. The aim of the present study is to propose a methodological protocol for quantifying this change in shape in a multidimensional space, applied to the eastern part of the French Pyrenees. After mapping the treeline at two dates (1953 and 2015) from historical and current orthophotographs, we characterized its shape within 648 plots using 19 landscape metrics computed using the R package *landscapemetrics*³. We then applied a PCA incorporating the 1953 metrics and obtained a factor space defined by the first two components. The observational plots (each characterized by a specific factorial score in 1953 and in 2015) could then be projected into this space, thus forming a map of the 648 pairs of points. Finally, the distance between the points of each pair was estimated, then considered as the dependent variable of a subsequent correlative model including climatic, anthropogenic and topo-geomorphological exogeneous variables.

References

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- [3] Hesselbarth et al. 2019. *landscapemetrics*: an open-source R tool to calculate landscape metrics. - *Ecography* 42:1648-1657.

Evaluation of high-elevation afforestation

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In alpine regions, mountain forests are important to protect people and infrastructure against frequently recurring natural hazards. In this context, and particularly to mitigate the effects of deforestation in the 19th century, more than 5,000 high elevation afforestation sites have been established in Austria since 1906. Today, the question of future development strategies for such afforestation sites arises, which makes an assessment of their effectiveness necessary. Typically,

such assessments are usually done by collecting forest data through time-consuming and costly field surveys. However, in recent years, the automatic detection of forest parameters with remote sensing data has been successively improved and has already been applied in numerous forestry issues. Here, we focus on the usability of RGB-orthophotos - covering 30 afforestation sites located in the Paznaun and Stanzervalley, Tyrol, Austria. Five different recent land cover classes as well as actual tree species were classified by combining the remote information (RGB) with the random forest ensemble learning method.

Land cover classification results were assessed by using overall, producer and user accuracies, dividing the number of correctly classified pixels by the total number of pixels, the number of pixels in the respective class and the number of pixels predicted for the respective class. In total, an accuracy of more than 90 % could be achieved in 26 cases and an accuracy between 80 and 90 % in three other cases. Producer and user accuracies above 80 % were obtained in the classification of the individual classes, making them comparable to other studies. Furthermore, the proportion and spatial distribution of the predicted land cover classes showed results close to reality.

For the classification of the tree species, the typical high-elevation tree species Norway spruce, European larch, Cembran pine, Scots pine, Mountain pine, and deciduous trees were considered. For almost all sites, the classification based on a spectral analysis of the RGB information showed accuracies between 72-95 % and thus predicted realistic tree species proportions comparable with similar studies.

We conclude that the accuracy of classifying land cover and tree species from RGB orthophotos is sufficient, making it a cost-effective option for assessing the protective effects of existing afforestation sites at high elevations. Remote sensing in combination with the presented ensemble learning methodology can facilitate the assessment of high-elevation afforestation sites, especially for locations that are difficult to access.

Long- and short-term climatic controls of tree growth at the forest line

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Tree species in high elevation may react differently to climate change with consequences for the composition and vitality of future mountain forests. We used tree ring analysis and automatic dendrometers to analyze long- and short-term growth dynamics of *Larix decidua*, *Picea abies*, and *Pinus cembra* and their relation to climatic drivers in the subalpine zone and at the forest line in the LTSER platform Matsch|Mazia in the Italian Alps. With increasing temperatures since the 1980s, tree ring widths increased stronger in *Larix* and *Picea* than in *Pinus*. *Larix* and *Picea* also showed a stronger positive correlation of tree ring width and temperature than *Pinus* while correlations with precipitation were hardly found. However, in short-term dendrometer data, we observed a distinct limitation of growth by vapor pressure deficit in *Pinus* but not in *Larix* which could be an explanation for the difference in long-term growth responses. Overall, our study indicates that *Larix decidua* and *Picea abies* might actually benefit from climate warming at high elevation at the expense of *Pinus cembra*.

Microhabitat preferences of seedlings of *Larix decidua*, *Pinus uncinata* and *P. cembra* in calcareous and siliceous treeline sites in the French Alps

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Seedling establishment is crucial for elevational shifts and local increases of tree cover in treeline ecotones, but the characteristics and availability of safe sites for tree-species establishment in alpine ecosystems are not well understood. The conditions that constitute a safe site are likely to vary between tree species, e.g. in edaphically dry sites only topographically wet microsites may be "safe". We aimed at describing the microhabitat preferences of the conifers *Larix decidua*, *Pinus uncinata*

and *Pinus cembra* on mountain slopes of two different geologic origins in the French Alps. We selected two sites with calcareous and two with siliceous parent material. At each site, we selected 50 individuals at the upper treeline ecotone and compared their microsites with 50 randomly-placed reference microsites in terms of the substrate, ground cover, meso- and microtopography, and the type, size, direction and distance to the nearest shelter. A microsite was spatially defined as a circle of 0.6 m radius around the individual. We found that seedlings were not randomly located at the study sites: at the siliceous sites, seedlings preferred growing among rocks or on bare ground, or surrounded by dwarf shrubs or other low vegetation, while at the calcareous sites, only a preference for rocks and low vegetation was found. Rocks were the main type of shelter at all sites. Terraces and shrubby vegetation played a smaller role, and the direction of the shelter seemed to have no clear pattern. Our results show that microsite preferences are consistent between sites with different bedrock types and hence edaphic conditions as well as between species. Generally, our results emphasize the importance of safe sites for successful tree regeneration in the treeline ecotone. This implies, on the one hand, treeline advance patterns are modified by microtopographic features, and on the other hand, that trees can take advantage of the great variety of environmental conditions found in the alpine zone. However, although tree individuals were found abundantly at our high-elevation study sites, the majority of them were either only a few years old or showed a krummholz growth form, staying within 1 m from the ground. Yet with the warming climate, growth into tree stature is expected to become increasingly feasible in the alpine zone, so that tree-species establishment may increasingly lead to an advance of forest into formerly tree-less alpine vegetation.

Modelling demographic processes to understand spatial patterns in alpine-treeline ecotones

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Tree populations in alpine-treeline ecotones are characterized by shifts in tree density, spatial distribution, size and shape. The nature of these shifts may reveal what underlying demographic processes shape the treeline and control its dynamics. To study the link between these processes and spatial patterns in alpine-treeline ecotones, we are developing an individual-based spatial model of treeline tree populations. In the first version of this model, we focus on the effects of imposed elevational gradients in demographic processes (growth, dieback and mortality) on the emerging spatial treeline patterns. Even though the general parameterization is based on field data from several Pyrenean alpine-treeline sites, this version is used mainly to study how hypothetical demographic gradients lead to conceptual treeline types. For example, we test if survival gradients, together with simplified facilitative neighborhood interactions (i.e. higher survival of seedlings near established trees) is sufficient to produce island-type treelines, or if growth gradients only will produce treelines with a gradually declining tree height and a discrete edge.

In future versions of the model, the demographic gradients will no longer be imposed but will emerge from tree-environment interactions. The model aims to serve researchers as a tool to test hypotheses on pattern formation at alpine treelines around the globe, and to help predict future dynamics in these ecotones in the context of the ongoing global change.

Monitoring high-mountain shrubs and land-cover change with remote sensing and deep learning

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High mountains can serve as natural laboratories to disentangle the effects of different global change drivers, such as climate and land-use change, on biodiversity distribution and vegetation cover. The fusion of remote sensing data and artificial intelligence can facilitate the automated analysis and

monitoring of these changes. This work presents two main studies within the projects DETECTOR and LIFEWATCH ERIC SmartEcoMountains in the Sierra Nevada (Spain): (1) automatic change detection in high mountain shrubs (*Juniperus* sp.) by applying deep learning to historical orthophotography and very high-resolution satellite imagery; and (2) automatic land-use and land-cover (LULC) mapping by applying deep learning to coarse (MODIS) and high (Sentinel-2) resolution satellite imagery. In the first study, we digitized 1000 individuals of *Juniperus* sp. from six zones using orthophotography between 1977 and 2020. The digitized images were used to train state-of-the-art segmentation models based on Convolution Neural Networks (CNNs) to automatically detect high mountain juniper shrubs. The created models were then deployed on images from different decades to analyze the overall change in the plant size, distribution, expansion, and decay. Shrubs near human infrastructures experienced higher growth than in natural environments while lower growth rate occurred in higher altitudes surrounded by bare soil. The reported increase in temperatures does not seem to have favored growth at higher elevations more than at lower elevations, but the other way around. In the second study, we created the TimeSpec4LULC dataset containing a 22-year monthly multispectral time series extracted from merging Terra and Aqua data of Modis sensor at 500 m resolution. In addition, the Sentinel2GlobalLULC dataset was created using RGB images of size 224x224 pixels from Sentinel-2 at 10 m resolution. Both datasets were preprocessed to eliminate the disruptions created by atmospheric conditions, then were annotated using spatial-temporal consensus over 15 global LULC products available in Google Earth Engine. Afterward, these datasets were employed to train deep learning-based models for LULC mapping at 10 m resolution.

This work is part of Smart EcoMountains, the Thematic Center on Mountain Ecosystems of LifeWatch-ERIC.

Towards an open solution for high-resolution mapping of mountain vegetation using remote sensing

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Mountain plants can respond to climate change by shifting populations uphill or locally to suitable microsites, functioning as local refugia. Such shifts reduce the risk of species going extinct and reshuffle the alpine vegetation, sometimes even causing an expansion of forest. Current spatial vegetation patterns can provide strong indications of the processes controlling plant distributions, and therefore of future shifts. Accurately describing such patterns is therefore important for predicting and monitoring vegetation change. Very-high-resolution remote sensing (i.e. with spatial resolutions < 0.5 m) offers great promise to map the fine-grained alpine vegetation above the closed forest. However, two big challenges need to be solved before this potentially fantastic resource can be applied to map and monitor vegetation patterns in mountains globally: the availability of and access to these data, and the analysis of the images in terms of recognising and delineating vegetation types and, in the case of larger species like shrubs, trees, cushion plants and giant rosettes, individuals.

In an open-format synthesis workshop, co-funded by the Mountain Research Initiative (MRI), we discussed these challenges and potential solutions. We will present the preliminary output of this workshop, hoping to contribute to a freely-accessible solution to very-high-resolution mapping of alpine vegetation, including alpine-treeline ecotones, in mountains worldwide.

Tropical-Andean treelines in a global context

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Alpine treeline ecotones are expected to shift uphill due to climate and land-use changes, but not all treelines are shifting. Treeline ecotones in the tropical Andes differ in several ways from alpine treeline ecotones in temperate and boreal climates, for example in the near-absence of snow effects and temperature seasonality and in the very high tree diversity. Very little is known about whether or where Andean treelines are shifting or what can be expected in the future, or what processes control

these shifts. It is important to gain more insight here, since the distribution of forest and páramo vegetation, which are delineated by the treeline ecotone, is highly relevant for biodiversity, ecological processes and climatic and hydrological regulation. We are therefore developing a research collaboration to design and test methods to gain a better understanding of the functioning and dynamics of tropical-Andean treelines and to determine similarities and differences compared to treelines in different climate zones. In particular, we aim to develop methods to describe treeline spatial patterns (including vegetation cover, structure and diversity) at different scales, such that the data can be used to understand the ecological processes that shape these patterns and that control treeline dynamics and shifts in tropical-Andean ecosystems. Since the project is young and has not produced concrete results yet, we will present the concepts and ideas behind it, introducing tropical alpine treelines and their particularities and the challenges faced when studying them.

Montane forest species can respond to climate change both with vertical and horizontal range shifts

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The ability of a species to track favourable conditions by shifting its range may be crucial to cope with global warming. Vertical (upslope) range shifts are frequently reported as the main mechanism for tracking climate change in mountainous areas. However, horizontal range shifts from sun-exposed to shaded habitats at constant elevations are an often neglected alternative mechanism. In the present study, we quantify the vertical and horizontal dimensions of species ranges in temperate European mountain forests. We investigate the potential of horizontal range shifts to counteract upslope shifts and how this changes our understanding of novel species assemblages under climate change.

We used data from biodiversity surveys in the Bavarian Forest National Park and adjacent areas in 2006 and 2016 at locations between 660-1400 meters above sea-level. The area features dynamic montane forests with a variety of microclimatic regimes. Elevation and canopy cover served as proxies for the local climate and microclimate, respectively. We calculated species-specific elevation (vertical) and canopy cover (horizontal) optima (abundance-weighted mean) and niche breadths (abundance-weighted standard deviation) for species that occurred in both survey years. We then used generalized linear models to compare the links between species abundance, niche optima, and niche breadths among several taxonomic groups.

Most species exhibited a shift in either their elevation or canopy cover optimum, or both of them. Most taxonomic groups showed mean shifts towards cooler climates, i.e., upslope or towards higher canopy cover, although responses were highly diverse at species level. Niche breadths increased with both horizontal and vertical shifts to cooler climates, indicating species experienced range-expansion at their upper range boundaries rather than range-contraction at their lower range boundaries. We found a negative correlation between vertical and horizontal range shifts, confirming our hypothesis that shifting towards higher canopy cover offers an alternative mechanism to track climate change besides shifting upslope.

Using a two-dimensional concept of antagonistic horizontal and vertical range shifts can improve predictions about future species assemblages, as response trajectories entail both dimensions to a species-specific extent. Our findings imply an increased likelihood of community reassembly both at the vertical and the horizontal dimension, potentially resulting in novel species interactions or impaired ecosystem functioning. However, the possibility of a species to track climate change within a given elevation may increase its overall ability to track climate change, highlighting the importance of diverse landscapes to safeguard mountain biodiversity.

Session 3

FS 05-II: Alpine Treeline Ecotones under Global Change II

Time:

**Tuesday, 13/Sept/2022:
4:00pm - 5:30pm**

Location: **THEOLOGIE - Madonnensaal**

Theologie - Madonnensaal, second floor

Presentations

Spatio-temporal dynamics of Apennines treeline ecotones under global change

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Human activities and natural processes over millennia have shaped the forest landscapes of European mountain ranges. In the Apennines, the second largest range in Italy, the post-World War II abandonment of traditional activities has led to a widespread forest expansion with a different declination from valley bottoms to upper treelines ecotones. Firstly, we examined the available literature about the land-use/cover change in the Apennines (57 case studies), that revealed a clear trend of forest expansion (+78%) and the reduction of croplands (-49%) and grasslands (-19%). Secondly, we investigated the landscape configurational shifts comparing different slope exposures and altitudinal zones. We selected two paired study landscapes (North-East vs South-West slopes) for each of 10 selected sites. Computing the reforestation dynamics with historical (1954) and recent aerial images (2012), we found that landscape mosaics generally experienced a structural simplification and specifically a diffuse fragmentation of grasslands at higher elevations. Most treeline ecotones in the Apennines are human-shaped. Here we assessed the major drivers of the highest treeline location and their species composition. Human impact, geomorphology, and environmental conditions acted in synergy to determine tree species distribution. The mean treeline altitude is 1755 m a.s.l. and *Fagus sylvatica* is the dominant species (94%), forming the typical abrupt transition from forest to grassland. We also found several *Pinus nigra* plantations and very limited *Pinus mugo* shrublands and *Pinus heldreichii* stands in the central and south Apennines, respectively. Treelines at lower elevations were associated to human presence and sunny exposures. The depressed and monospecific features of Apennines treelines suggested a widespread severe human pressure. Examining the species-specific ecotones with remote sensing data, we reported that beech treelines slowly shifted upslope in the last 60 years. The common spatio-temporal dynamics of beech is characterized by infilling processes, canopy enlargement of preexisting trees and microtopography-dependent upward shift of new stems. The presence of shrub species acted as facilitation driver for the establishment of new forest patches. Oppositely, the faster successional processes of *Pinus nigra* were reported as rapid upward shift controlled by microsite topography and guaranteed by the proximity to seed source plantations. The presence of reproductive pines above the treeline, could indicate an increasing tree recruitment in the future. The role played by climate on growth and recruitment processes seems to be overrun by anthropogenic-processes. These secondary successions could induce a significant long-term decline in plant diversity in species-rich grasslands and the loss of cultural landscapes.

Land-use and climate change induced alteration in tree- and forestline location, structure and composition in the Eastern (Julian) Alps, Slovenia

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Mountain forests in the Alps are an important natural resource enabling man to persist in this area for centuries. In the past, mountain forests even at the forest and treeline have been subjected to intensive exploitation, first by slash-and-burn techniques and grazing, and later by extensive timber exploitations, lowering tree- and forest lines and changing forests' structure and composition. Posterior socio-economic changes led to abandonment of this intensive use, first and especially in the upper-mountain elevation belt. The Alps are also significantly impacted by climate change, mainly through increased average annual temperature, the Julian Alps experiencing one of the highest increases. Additionally, mountain forests are one of the most susceptible forest types for climate induced influences.

This contribution tackles land-use and climate change induced shifts of the tree- and forest line in the strictly protected Triglav Lakes valley (≈1100ha), as well as with changes in forest cover, forest

structure and composition of mountain forests in the transition zone and just under the forest line. Changes of the upper forest- and treelines were analysed by interpreting a series of aerial photographs from the mid-20th century till now. An intensive monitoring of forest ecosystems was established in 1983 to study the long-term dynamics of forest structure and composition.

Most recent analyses showed that during the last century both the upper treeline and forest line moved upwards to higher altitudes and forest cover increased. In the transition zone between forest and treeline trees and small cohorts are widely spaced, dominated by *Larix decidua* and *Picea abies*; the average stand volume was 116 m³ha⁻¹, thin trees up to 35 cm prevailed. Regeneration was extremely rare. Forest stands just below the forest line exhibited opened canopy closure with lots of canopy gaps, stand structure was uneven-sized and uneven-aged, stand volume was significantly higher than in the transition zone (515 m³ha⁻¹), but was decreasing with increasing altitude. *Picea abies* predominated in the growing stock, regeneration was rare and occurred sporadically.

The showed dynamics of treeline and analysed alpine mountain forests may reflect combined influences of land-use change (i.e. abandoned pasture, strict protection) and climate change (i.e. increased annual temperature); forests have been gradually returning to abandoned pastures on deforested areas, occurred after the last heavy harvests in 1883. Due to slow dynamics and possible impact of climate change in mountain forests, long-term monitoring is decisive, representing an important starting point for sustainable forest management.

Soil nutrient cycling shapes treeline dynamics of Russian mountains

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Treelines are striking vegetation boundaries. In unmanaged regions, treeline position is mainly attributed to low temperatures limiting growth processes. Treeline shifts due to climate change are observed to lag behind climate warming, which is primarily related to species interaction. Belowground processes remain largely understudied, but as nutrient mineralization from soil organic matter is highly temperature sensitive, the resulting changes in nutrient availability may also affect plant growth and species competition and thus, treeline dynamics. In our study, we explored how nitrogen and phosphorus availability and cycling in the soil changed across forest-tundra ecotones and how this is linked to plant traits and treeline productivity. In three Russian mountain ranges (South and Polar Urals, Khibiny mountains on Kola Peninsula), we sampled and analyzed plants and entire soil profiles along elevation gradients across treeline reaching from the closed forest to the tundra.

In all three regions, indices for nutrient availability (foliage nutrient concentration, natural ¹⁵N abundance, soil extractable N and P concentrations) showed pronounced increases from tundra to the forest. Mineralization experiments indicate that the improved N and P availability in the forest is related to a greater release of N and P from litter layers and soils in the forest than in the tundra, very likely due to tighter C-to-nutrient ratios in decomposing organic matter. We suggest that this pattern in nutrient cycling stabilizes existing vegetation patterns: while the slow nutrient cycle and the low nutrient availability in the tundra contributes to the restricted tree establishment, the several fold higher nutrient supply in the forested soil possibly contributes to the abrupt growth enhancement below treeline once the thermal limitation for tree growth is relieved. These results indicate that belowground processes play an important but underexplored role in treeline dynamics.

Low recruitment success limits the upward range shift of a broad-leaved evergreen eucalypt at alpine treeline despite a warming climate and fire disturbance.

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The alpine treeline on mainland Australia is dominated by various subspecies of *Eucalyptus pauciflora*; broad-leaved evergreen trees with a mallee (multi-stemmed) growth form, affectionally known as snowgums. They can re-sprout after fire from a basal lignotuber and may live for up to 300-400 years.

We collected empirical data across a range of early life-history recruitment stages to determine how recruitment may limit range expansion at alpine treeline. We estimated canopy-stored seed, seed rain, soil seed bank germination and tracked the survival of naturally occurring seedlings down 30 m into the sub-alpine woodland. After wildfire, naturally occurring seedlings were tracked and compared between burnt and un-burnt sites, above and below treeline. Field germination and seedling survival was assessed via seed and seedling transplants above and below treeline and in experimentally warmed plots using open-top chambers. Germination potential was assessed in the laboratory under different warming treatments. Seedling frost resistance was also assessed from transplants above and below the treeline.

We incorporated this empirical recruitment data into the LANDIS-II framework, a spatially explicit landscape simulation model, with flexible temporal and spatial resolution that is designed to simulate vegetation community succession with the incorporation of disturbances, such as fire. Here, we specifically parameterised LANDIS-II for the study region to simulate snowgum stand dynamics and disturbances and then estimated the probability of snowgum range expansion over set time periods and environmental scenarios.

The change in elevation after 20 years of simulations, where the probability of snowgums occurring was 50%, indicated only a 2 m shift in elevation. However, in different areas of the treeline, there was a simulated shift 8 - 40 m in elevation after 100 years. The migration rates per year for snowgum across diffuse treelines between 1640 m and 1890 m where snowgum currently exist show similarly very small increases in elevation (0.5 – 1.0 m), but only when fire disturbance and climate change are included in the models. In-filling within diffuse snowgum stands near treeline is more likely, rather than an upward migration of the alpine treeline.

Our results concur with other local studies indicating that snowgum recruitment and subsequent range expansion is limited by very low recruitment success under natural conditions, despite ample seed production and high seed viability. Given that snowgums may live for hundreds of years, and are rarely killed by fire, recruitment every 100 years or so may be sufficient to maintain high elevation populations.

Growth response of green alder (*Alnus alnobetula*) to climate at an alpine treeline ecotone

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Green alder (*Alnus alnobetula* (Ehrh.) K. Koch = *Alnus viridis* (Chaix) DC) is an early successional shrub species that is widely distributed at the alpine treeline ecotone in the northern hemisphere. Due to changes in land management green alder is currently the most expanding shrub species in the Alps. As it forms dense monospecific thickets which are known to impair establishment and development of trees, a better understanding of how climate affects growth of green alder is therefore essential for improved predictions of forest dynamics at the alpine treeline under climate change. Here, we make use of ring width data from >50 *A. alnobetula* stems sampled from 8 plots at the treeline ecotone on Mt. Patscherkofel (2246 m asl., Central Tyrolean Alps, Austria) to identify the main climate drivers of radial stem growth and to determine the influence of climate warming on growth. As expected, response function analysis revealed that radial stem growth of *A. alnobetula* is primarily controlled by temperature during the growing season. However, no strong response to climate warming during the period 1991–2020 is discernible from ring width time series, most likely indicating that carbon is preferably used to promote clonal propagation, i.e., formation of root suckers and adventitious shoots rather than stem growth. A comparison of growth rates with those of co-existing Swiss stone pine (*Pinus cembra*) and the evaluation of time series of aerial photographs confirms this interpretation, because *A. alnobetula* shows strikingly lower radial growth rates than *P. cembra* but has spread rapidly within the study area since the 1980s (c. 370 m² ha⁻¹ decade⁻¹), respectively. We conclude that the preference for clonal growth over stem growth turns out to be an advantageous strategy at the alpine treeline ecotone, where height growth is increasingly constrained by low air temperature.

The research was funded by the Austrian Science Fund (FWF; project number P34706-B).

Increasing impacts of recurrent summer drought on tree growth, xylem sap flow and dehydration dynamics of *Larix decidua* and *Picea abies* in a subalpine forest

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The severity and frequency of drought events is expected to increase in a future climate, but consequences for ecosystems that were previously not affected by drought are highly uncertain. At a subalpine forest site in the Austrian Central Alps, we experimentally exposed mature trees of *Larix decidua* and *Picea abies* to multiple years of recurrent summer drought. We continuously monitored tree growth, xylem sap flow and tree water deficit and analyzed xylem anatomy and non-structural carbohydrate (NSC) concentrations and their carbon isotope signature ($d^{13}C$).

We found that tree growth was limited from the first year of drought in both species, and that the drought effects on growth increased with recurrent drought in *P. abies*, and to a lesser extent in *L. decidua*. Both species showed pronounced tree water deficits already shortly after the onset of drought, *L. decidua* exhibiting larger relative tree water deficits. Xylem anatomy was affected by drought only in *P. abies*, reflecting a comparatively higher sensitivity to reduced stem water content. Furthermore, while total NSC and soluble sugar concentrations were increased in needles and branches of drought-exposed *P. abies* trees and starch concentrations reduced in branches of *P. abies* under drought, NSC concentrations of *L. decidua* remained largely unaffected. In both species, $d^{13}C$ of soluble sugars of drought exposed trees was increased already at the onset of the third drought, indicating a sustained imprint of previous droughts on water-use efficiency. In contrast to our expectations, the drought response of xylem sap flow did not differ between the two species, which were previously suggested to differ in their water-use strategy. Drought effects on xylem sap flow tended to increase with recurrent drought in both species.

Our study suggests that recurrent drought progressively impairs the functioning of the two treeline species, with species-specific responses likely owing to differences in rehydration capacity and / or cambial tissue sensitivity to water deficit. We conclude that even under comparatively low evaporative demand, typical for most treelines, tree functioning may be strongly impacted by summer drought, especially if such drought events recur during two or more consecutive years.