

Major land plant lineages respond differently to climate warming

Thomas Kiebacher^{*1}, Tabea Kipfer², Tobias Roth^{2,3}

¹*University of Zurich, Department of Systematic and Evolutionary Botany, Zollikerstrasse 107, 8008 Zürich, Switzerland*

²*Hintermann & Weber AG, Austrasse 2a, 4253 Reinach, Switzerland*

³*University of Basel, Zoological Institute, Basel, Vesalgasse 1, 4051 Basel, Switzerland*

Abstract

1. Climate warming studies on plants are currently highly biased towards vascular plants. Bryophytes, the second largest group of land plants that are particularly diverse in harsh environments, however, have received comparatively little attention.
2. In this study we compared the temporal change of species richness, species turnover and thermophilisation from 2001 to 2018 between bryophytes and vascular plants within a mountainous region in Central Europe. We compared differences between bryophytes and vascular plants among forests, grassland and unused open areas using data from 1174 study sites that span an elevational gradient from about 200 to 3000m.
3. We found that particularly in grasslands, the proportion of bryophytes among recorded plants (i.e., bryophytes and vascular plants) strongly increased along the elevational gradient, suggesting that bryophytes compared to vascular plants are relatively more diverse in the harsh alpine environments. Presumably due to their higher sensitivity to environmental changes, their shorter live spans and their higher dispersal capacity, the temporal turnover of bryophyte species was much higher than the temporal turnover of vascular plant species. And as a likely consequence of higher turnover, bryophyte communities reacted faster to climate warming than vascular plant communities, which was evidenced by more pronounced thermophilisation in bryophytes. The link between a faster reaction of communities to climate warming and differences in live spans was further supported by the faster thermophilisation of short-lived bryophytes compared with long-lived bryophytes.

^{*}Corresponding author: thomas.kiebacher@systbot.uzh.ch

4. *Synthesis.* We report subtle differences on how bryophytes and vascular plants communities changed over the last two decades and suggest that these changes are at least partly due to recent climate warming. While bryophytes were faster than vascular plants in tracking climate warming, in open areas overall species richness changed in favor of vascular plants, suggesting that in sum more vascular plants than bryophytes profited from recent climate warming.

Keywords: Bryophytes, climate change, life strategy, mountain ecosystems, community temperature index, vascular plants

Introduction

Climate warming is one of the major challenges organisms have to face and one of the major threats to biodiversity in the 21st century (Peñuelas et al., 2013; Wiens, 2016; Biodiversity & Ecosystem Services, 2019). Changes in species range, abundance and phenology successively alter extant ecosystems (Chen et al., 2011; Dorji et al., 2013; Soudzilovskaia et al., 2013; Shi et al., 2015). Spatial range shifts, poleward in latitude and upslope in elevation, are among the best documented phenomena of climate warming leading to the replacement of cold-dwelling with warm-dwelling species (i.e., thermophilisation) in extant communities, which ultimately leads to the extinction of some of the species (Engler et al., 2009; Gottfried et al., 2012; Lenoir & Svenning, 2015; Wiens, 2016; Freeman et al., 2018).

However, range dynamics, or more specifically, how fast species track shifting isotherms vary considerably between taxonomic and functional groups (Parmesan & Yohe, 2003; Essl et al., 2015; Wiens, 2016; MacLean & Beissinger, 2017; Roth, Plattner & Amrhein, 2014). Especially species' life strategies are suggested to reflect their potential to track shifting isotherms. For example, observed range shifts are usually larger and less delayed for species with high dispersal capacities and short life cycles (Angert et al., 2011; Cotto et al., 2017; MacLean & Beissinger, 2017). Furthermore, disturbance intensities that often differ between land use types determine species turnover and thus have impact on thermophilisation processes (Oliver & Morecroft, 2014; Stevens et al., 2015).

For plants, substantial time lags were observed with realised shifts being much smaller than expected given the observed temperature increase; both, at the species and the community level (Bertrand et al., 2011; Corlett & Westcott, 2013; Rixen & Wipf, 2018; Martin et al., 2019). Furthermore, range shifts seem to decrease with increasing elevation (Angert et al., 2011; Rumpf et al., 2018) albeit at higher elevations temperature increase is usually more pronounced (Ohmura, 2012; Rangwala, Sinsky & Miller, 2013) and mountain ecosystems are supposed to be particularly sensitive to climate warming (Kohler, Wehrli & Jurek, 2014; Dobrowski & Parks,

2016; Vanneste et al., 2017).

Studies of the impacts of climate warming on plants are highly biased towards vascular plants. Bryophytes, the second largest group of land plants after flowering plants, hitherto received little attention (Corlett & Westcott, 2013; He, He & Hyvönen, 2016), although they often constitute a large part of the local and regional plant biodiversity and provide key ecosystem services (Lindo & Gonzalez, 2010; Hallingback & Tan, 2014). Bryophytes play a significant role in nutrient, carbon and water cycling and the resilience of ecosystems (Turetsky et al., 2012; Szyja et al., 2019). Compared to vascular plants they are generally more diverse and abundant in harsh environments, e.g. at high latitudes and elevations (Bruun et al., 2006; Proctor, 2011; Turetsky et al., 2012; Mateo et al., 2016).

Bryophytes fundamentally differ in their ecophysiological properties from vascular plants and are expected to be differently affected by climate warming (He, He & Hyvönen, 2016). They are poikilohydric (i.e., the lack to regulate the water content) and absorb humidity and nutrients directly from the atmosphere, hence, they are more directly linked to the abiotic environment and are usually more sensitive to environmental changes (Proctor, 2009; Hallingback & Tan, 2014; Becker Scarpitta et al., 2017). Furthermore, many bryophyte species do not depend on a well-developed soil layer and some of them can grow directly on bare rock surfaces. This makes them excellent pioneer species, able to colonise newly formed habitat where competing vascular plants are absent. Furthermore, the life strategy types of bryophytes encompass a wide range, from fugative and very short-lived (a few weeks) types inhabiting transient habitats, to competitive and long-lived types that dominate persistent communities. Bryophytes often differ from vascular plants in their high dispersal capacity via small diaspores (Frahm, 2007; Medina, Draper & Lara, 2011). Short life cycles and high dispersal capacities are likely to be positively related to the magnitude of range shifts under recent climate warming (corlett_2013; MacLean & Beissinger, 2017).

Here, we used a comparative approach to assess the impact of climate warming on bryophytes and vascular plant communities in a mountainous region in Central Europe. We examined data from more than 1000 permanent plots monitored 3-4 times between 2001 and 2018 in the frame of the Biodiversity Monitoring Switzerland (BDM; www.biodiversitymonitoring.ch). This monitoring programme simultaneously surveys species diversity of bryophytes and vascular plants on a systematic grid laid over entire Switzerland. To gain a better understanding on how climate change affects different species groups, such real-time monitoring data using standardized schemes provide a unique opportunity (Henry et al., 2008; Martin et al., 2019). We calculated changes in species richness, the temporal species turnover (i.e., species exchange ratio between two points in time sensu Hillebrand et al., 2018) and changes in average indicator values of temperature (i.e., community temperature index sensu Devictor et al., 2008) and compared differences between the two land

plant lineages along an elevational gradient from about 200 to 3000 m a.s.l.

Materials and methods

Study area and field data

About 70% of Switzerland is mountainous (60% Alps and 10% Jura Mountains); the altitudinal range is from 193 to 4634 m a.s.l. We analysed data on the presence/absence of bryophyte and vascular plant species recorded in the frame of the Swiss biodiversity monitoring programme (BDM, www.biodiversitymonitoring.ch). This programme has been launched in 2001 to monitor Switzerland's biodiversity (Weber, Hintermann & Zangger, 2004). Bryophytes and vascular plants are investigated using a systematic sample of about 1800 circular 10 m^2 plots laid out as a regular grid over entire Switzerland.

Fieldwork was highly standardized and was carried out by qualified botanists. The botanists visited each plot twice a season except for the plots at high altitudes with a short vegetation period that were inspected only once. During the two visits all vascular plant species detected on the plot were recorded (for more details on the vascular plant surveys see Bühler & Roth, 2011; Plattner, Birrer & Weber, 2004). During the first visit, bryophytes samples up to 1.5 m above ground were collected from the soil, dead wood, rocks, living trees and scrubs and sent to specialists for identification. The botanists also classified the land use category using a system of 32 pre-defined land use categories similar to the CORINE Land Cover system (Büttner et al., 2004). For annual reporting of the BDM results, the 32 land use categories were aggregated to the six main types of land use: forests, meadows and pastures, arable land, settlements, alpine pastures and unused open areas. Unused open areas included mostly screes and rocks at higher elevations but also comprised special cases at lower elevations such as gravel pits and waste lands. We thus removed the colline and montane plots from the unused open areas category. Further, we aggregated meadows, pastures and alpine pastures into one group labeled "grassland".

BDM field work started in 2001 and we analysed all data from start until 2018. Each year, about a fifth of the sample plots are surveyed and every plot is resampled every five years. In this study, we only analysed the data of surveys that were classified as forests, grassland or unused open areas and only data from surveys for which both the bryophyte and vascular plant surveys met our standards of data collection. The final sample included the data from 1174 study plots (Fig. 1) and 4087 surveys (that is in average 3.5 surveys per plot). Of all the surveys, 1865 (46%) of the surveys were conducted in forests, 1639 (40%) of the surveys were conducted in grassland, and 583 (14%) of the surveys were conducted in unused open areas.

Because effects of climate warming often differ along elevational gradients (e.g. Bertrand et al., 2011; Roth, Plattner & Amrhein, 2014), we split our dataset according to four elevational zones based on the temperature zonation of Switzerland (Schreiber et al., 1977), that is colline, montane, subalpine and alpine. The distribution of plots and surveys across the elevational zones was as following: 118 plots (405 surveys) in the colline zone, 526 plots (1821 surveys) in the montane zone, 247 plots (873 surveys) in the subalpine zone and 283 plots (988 surveys) in the alpine zone.

[Figure 1 about here.]

Community measures

To describe the bryophyte and vascular plant communities and their change between time points we used three different measures: (1) the total number of species recorded (i.e., species richness) as a measure of community richness, (2) the temporal turnover (i.e., species exchange ratio between two points in time sensu Hillebrand et al., 2018) to describe colonisation and extinction of species between different time points, and (3) the temperature affinities of plant communities measured as the average Landolt et al. (2010) temperature indicator values of recorded species (i.e., the community temperature index sensu Devictor et al., 2008). Similar to the Ellenberg indicator values (Ellenberg, 1974), the Landolt values are ordinal numbers that express the realized ecological optima of species. For vascular plants, they range from 1 (cryophilous species) to 5 (thermophilous species) with steps of 0.5 in between. The Landolt indicator values were developed for the specific situation in Switzerland, published the first time in Landolt (1977) and recalibrated in Landolt et al. (2010). For bryophytes, a comparable system of indicator values has been developed by E. Urmi, published in Landolt et al. (2010). In contrast to the Landolt indicator values for vascular plants, those of bryophytes comprise only integers between 1 and 5. We speak of “termophilisation” if the mean temperature value of a community increases over time.

To assign bryophyte species to life strategies we use the system proposed by During (1979) and During (1992) and the species’ classification given by Dierßen (2002) with few edits and additions for species not covered. We assembled the strategy types into two groups: fugatives, annual shuttles, colonists and ephemeral were summarized as short-lived life strategy, and long-lived shuttles, perennial stayers and dominants were grouped as long-lived life strategy.

Statistical methods and data accessibility

For each plot, we calculated the average and the temporal trend of species richness and temperature affinity based on the repeated surveys per plot. To estimate the temporal trend, we applied for each plot separately a linear model with species richness or temperature affinity as dependent variable and the year when the survey has been conducted as the predictor variable. The estimated slope (given as change per decade) was our measure of the temporal trend of species richness or temperature affinity, respectively, that we used in subsequent analyses.

All analyses were done with the software R (R Core Team, 2019). We measured the temporal turnover as the proportion of species that differed between two time points, that is the number of species that were either only observed during first or only during the second survey at a given plot divided by the total number of species recorded during these two surveys. To estimate the temporal turnover of species we used the R package ‘simba’ (Jurasinski & Vroni Retzer, 2012). Data and R Markdown documents to fully reproduce this manuscript including figures and tables are provided at <https://github.com/TobiasRoth/moss-plant-comparison>. An R Markdown document is written in markdown (plain text format) and contains chunks of embedded R code to produce the figures and tables (Xie, Allaire & Golemund, 2018). Raw data for analyses are provided in the folder “data-raw” and the folder “R” contains the R-Script that was used to export the data from the BDM database. The folder “div” contains a list of all the R packages (including version number) that were in the workspace when the manuscript was rendered. The final version of the repository will be archived at Zenodo (<https://zenodo.org/>).

Results

[Table 1 about here.]

Species richness

Across all surveys, 539 bryophyte species and 1212 vascular plant species were recorded. The mean (\pm SD) species richness per plot was 12.87 (\pm 8.96) species for bryophytes and 27.34 (\pm 15.17) species for vascular plants. However, species richness differed considerably between land use types, elevational zones and the two land plant lineages (Table 1). For the three land use types the average species richness of vascular plants was higher than the respective species richness of bryophytes: the difference was 5.60 species (p-value based on a

paired t-test: <0.001) in forests, 26.81 species (p-value: <0.001) in grasslands, and 7.37 species (p-value: <0.001) in unused open areas.

In forests and grassland, where study plots spanned a large proportion of the elevational gradient, the species richness of bryophytes and vascular plants both increased from low to intermediate elevations and tended to decrease again at higher elevations (i.e., a mid-elevational peak, Fig. 2). This mid-elevational peak was particularly evident for vascular plants in grassland and less obvious to absent for vascular plants in forests and for bryophytes in both land use types. Consequently, in grassland the proportion of bryophytes (i.e., the number of bryophytes divided by the total number of bryophytes and vascular plants) strongly increased with elevation (Binomial-GLMM with elevation as predictor variable and site ID as random effect; slope of elevation at the logit-scale: 0.17, p-value: <0.001). This increase in the proportion of bryophyte species was almost absent in forests (slope of elevation at the logit-scale: 0.02, p-value: 0.118).

[Figure 2 about here.]

In forests, the temporal trend of species richness between 2001 and 2018 was in favour of bryophytes (Fig. 3): while for bryophytes the species richness increased by 5.16% (95%-credible interval: 1.92-8.40) per decade, the species richness of vascular plants decreased on the same plots and period by -1.35% (95%-credible interval: -4.32-1.62). In contrast, however, the temporal trend in species richness in grassland and unused open areas was in favour of vascular plants, which was particularly the case at the alpine zone (Fig. 3). In grassland the species richness decreased in bryophytes by -5.15% (95%-credible interval: -11.30-1.01) and increased in vascular plants by 0.73% (95%-credible interval: -1.15-2.61). Also in unused open areas, the increase in species richness was less strong in bryophytes than in vascular plants, with an increase of 6.10% (95%-credible interval: -2.79-14.98) in the former and an increase of 13.65% (95%-credible interval: 7.00-20.29) in the latter.

[Figure 3 about here.]

Temporal turnover

The mean temporal turnover across all sites was higher for bryophytes than for vascular plants (mean \pm SD for bryophytes: 0.55 ± 0.15 ; vascular plants: 0.40 ± 0.13 ; p-value based on Wilcoxon signed rank test: <0.001). The pattern how the temporal turnover of bryophytes changed along the elevational gradient differed between land use types (Ancova with an interaction between land use types and elevation; F-value: 10.94; p-value: 0.001): while it decreased with elevation in forests, it tended to increase in grassland (Fig. 4). For vascular plants in contrast, the temporal turnover decreased from low to high elevations both in forests and in grassland with only slight differences between the two land use types (Ancova with an interaction between

land use types and elevation; F-value: 6.62; p-value: 0.010; Fig. 4).

[Figure 4 about here.]

Temperature affinities and termophilisation

While in forests the mean temperature value of vascular plants was higher than that of bryophytes, the opposite was the case for grassland and unused open areas. The difference in temperature affinity of vascular plants minus the temperature affinity of bryophytes was 0.07 (p-value based on a paired t-test: <0.001) in forests, -0.12 (p-value: <0.001) in grassland, and -0.30 (p-value: <0.001) in unused open areas. In grassland, bryophyte communities had slightly higher temperature affinities along the entire gradient (Fig. 5). In forests, however, at low elevation the temperature affinities of vascular plant communities were higher than the temperature affinities of bryophyte communities whereas at higher elevations the pattern was inversed (Fig. 5).

[Figure 5 about here.]

Between 2001 and 2018, for both bryophyte and vascular plant communities the mean temperature value of recorded species increased over time, indicating termophilisation of species communities. Termophilisation was evident in all three land use types with a slightly stronger but at the same time more variable termophilisation in bryophytes: in forests the average termophilisation was 0.017 (p-value based on a one sample t-test to test for no termophilisation: 0.072) for bryophytes and 0.016 (p-value: <0.001) for vascular plants, in grassland the average termophilisation was 0.038 (p-value: 0.102) for bryophytes and 0.012 (p-value: 0.001) for vascular plants, and in unused open areas the average termophilisation was 0.059 (p-value: 0.115) for bryophytes and 0.031 (p-value: 0.001) for vascular plants. This tendency for higher but more variable termophilisation in bryophyte communities compared to vascular plant communities was evident for all three land use types at the entire elevational gradient (Fig. 6).

[Figure 6 about here.]

Species with a short-lived life strategy are among those that colonise new habitats more rapidly, and thus are expected to contribute more to termophilisation of species communities. Temporal trends in the change of temperature values were higher for short-lived bryophyte species than for bryophytes with a long-lived life strategy: the difference in termophilisation of the part of species communities with short-lived and long-lived species, respectively, was 0.05 (p-value based on a paired t-test to test for no differences between short-lived and long-lived species: 0.042). This difference between short-lived and long-lived species was more

pronounced at higher elevations (Fig. 7). However, there might be a slight bias as short-lived species tend to be more cryophilous (37% of all short-lived species have a T-value of 1 or 2) than long-lived species (only 30% have a T-value of 1 or 2). With increasing elevation, the proportion of short-lived species in bryophyte communities is increasing, except for grassland, with a peak in lowlands (mainly due to communities that consist of short-lived species only, presumably in disturbed habitats).

[Figure 7 about here.]

Discussion

Climate warming is a major global change impact within the study region with an increase in ambient temperature of > 0.5 K per decade since the late 1980' (CH2018, 2018; MeteoSwiss, 2019). At least part of the changes in community structure of bryophytes and vascular plants that we report in this study is likely to be related to this temperature increase. In general, both bryophyte and vascular plant communities show termophilisation, that is the replacement of more cold-dwelling with more warm-dwelling species. However, in eight of the nine comparisons in Fig. 6 the termophilisation was higher in bryophytes than in vascular plants. This is in accordance with the higher temporal turnover of bryophyte communities we found in this study (Fig. 4). If for bryophyte communities species replacement towards more thermophilous species was higher, in the long run, than for vascular plants, we would expect the average temperature value (i.e., temperature affinity) of extant bryophyte communities to be higher than the average temperature value of vascular plant communities. This prediction matches particularly well with the temperature affinities of plant communities we found in grassland (Fig. 5): the temperature affinities of bryophytes were slightly higher than the temperature affinities of plants along the entire elevational gradient. Although the uncertainty in termophilisation particularly in bryophytes was rather high, we thus conclude that bryophyte communities were faster than vascular plant communities in adapting to current climate warming.

The higher termophilisation rate in bryophytes compared to vascular plants might be due to higher colonisation rates of warm-dwelling species and/or higher extinction rates of cold-dwelling species. We suggest that ecophysiological and biological differences between the two taxonomical groups could explain higher colonisation rates of bryophytes as pointed out in the introduction; i.e., poikilohydry of bryophytes and different life strategies. Many bryophyte species have a colonist strategy with short generation time and high reproductive effort (During, 1979, 1992; Dierßen, 2002), which facilitates them – together with higher dispersal capacities than vascular plants – to colonize sites that become suitable through climate warming. By contrast and particularly in mountainous areas, vascular plant species are mostly long-lived species and form

persistent communities which have high resilience to vascular plant invasion (Dullinger, Dirnböck & Grabherr, 2004; Mark & Wilson, 2005; Grabherr, Gottfried & Pauli, 2010; Gottfried et al., 2012). Beside resilience, range shifts of vascular plants towards higher elevations depend on the availability of soil. The desiccation tolerance and nutrient uptake mechanisms of bryophytes, however, make them much less dependent on a substrate that serves as water storage and source of nutrients (Proctor, 2009). Finally, vascular plant growth and expansion at high elevations is slowed down by low temperatures, short vegetation periods and positive net photosynthesis being mostly limited to the summer season (Körner, 2003; Gottfried et al., 2012). Bryophytes can maintain positive net photosynthesis rates at very low temperatures (e.g., down to -10 °C in *Pellia epiphylla*, a common liverwort in the study region; Pihakaski & Pihakaski, 1979) and are opportunistic in their assimilation strategy. Once environmental conditions are favorable they can reassume positive net photosynthesis within short (often within minutes) time intervals throughout the year (Proctor, 2009, 2011). Higher thermophilisation rates of bryophytes might also be due to higher extinction rates of cold-dwelling bryophyte species as compared to cold-dwelling vascular plant species. Many high mountain bryophyte species typically grow in the coldest microsites (e.g., in gaps between rocks on northern slopes) and another set of species depends on long snow cover (Limpricht, 1890, 1895; Amann, 1928; Köckinger, 2017). These species may not find suitable refugia at the same elevational level, and, in the European Alps they include endemics known from a few localities only (e.g. Hallingbäck et al., 2019; Schröck et al., 2019a,b). They are especially threatened by climate warming (Kohler, Wehrli & Jurek, 2014; He, He & Hyvönen, 2016).

For vascular plants, our results expand findings of Rumpf et al. (2018) at the community level. They examined range shifts of 183 vascular plant species in the Alps using data from vegetation relevés located mostly between 1500 and 2700 m a.s.l., thus, roughly encompassing the subalpine and alpine zone in our study. They observed decreased range size at higher elevations. The more delayed responses among alpine vascular plants is supported by the decreasing temporal turnover rate of vascular plants in grassland (Fig. 4) and by growing evidence that the extinction of mountain top species may be delayed by their survival in colder microsite refugia (e.g. Scherrer & Körner, 2011; Maclean et al., 2015; Giezendanner et al., 2019).

Bryophytes are usually more diverse in the harsh alpine environments (Bruun et al., 2006; Proctor, 2011; Turetsky et al., 2012; Mateo et al., 2016). Indeed, in grassland we found that the proportion of bryophytes among recorded plants strongly increased along the elevational gradient. If we assume that climate warming in general leads to a less harsh environments, which might be the case in regions such as Switzerland where severe droughts are rare, we would expect that the proportion of bryophytes among recorded plants would increase over time. This is what we found for grassland where the species richness of bryophytes tend to decrease and the species richness of vascular plants increased between 2001 and 2018. While it is often

suggested that communities that are faster in tracking climate warming are better able to cope with climate change (which would favour bryophytes in our case), overall species richness changed in favour of vascular plants, suggesting that in sum more vascular plants than bryophytes profited from climate warming.

However, we like to acknowledge that it is an inherent problem of observational studies such as our to ascertain the drivers of observed patterns. At a regional scale, climate warming is one of the major changes the study region experienced in the last decades. Since the late 1980' warming increased to rates > 0.5 K per decade (CH2018, 2018; MeteoSwiss, 2019). By contrast, minor changes in precipitation regimes were observed (CH2018, 2018). Nonetheless, we cannot exclude that other factors than temperature such as for example the change in land-use intensity have influenced our results to a certain degree. For instance, nutrient enrichment, an immanent element of global and local change in the study region (Schlesinger, 2009; Roth et al., 2013), and warming may have additive effects (Zhang et al., 2015; Greaver et al., 2016).

So far, most observational studies addressing climate warming effects encompassed time intervals > 20 years and often considerably uncertainty had to be accepted because accurate relocation of historical surveys was not possible (see Chen et al., 2011; Wiens, 2016; MacLean & Beissinger, 2017; Freeman et al., 2018; Rumpf et al., 2018). Consequently, analyses could not address impacts on resident communities and mostly focused on range shifts of common species, because a minimum number of records is required to estimate ranges. Here, we can supplement research on climate warming effects with results based on an extensive dataset from exactly relocated plots monitored for 10 to 15. We believe that our study is an example on how real-time monitoring data using standardized schemes could allow for a better understanding of how climate change influence biodiversity (Henry et al., 2008; Martin et al., 2019).

Acknowledgments

The Swiss Federal Office for the Environment (FOEN) kindly provided the BDM data, the topographic data of the BDM plots and financial support to do the analyses. We thank the many dedicated botanists for their field work, the people at swissbryophytes for the bryophyte determination and Christine Föhr for helpful comments on the interpretation of the results.

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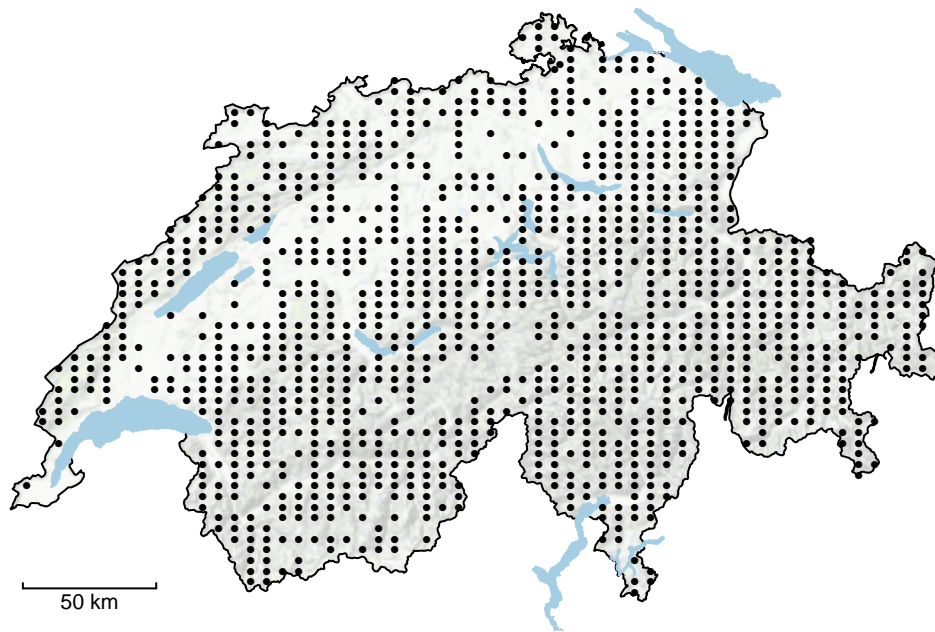


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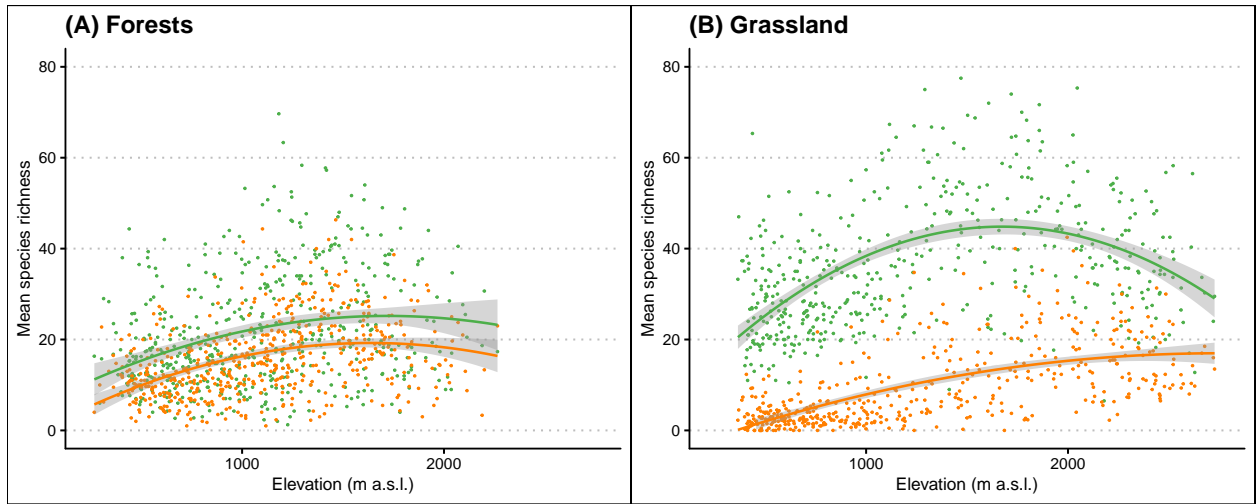


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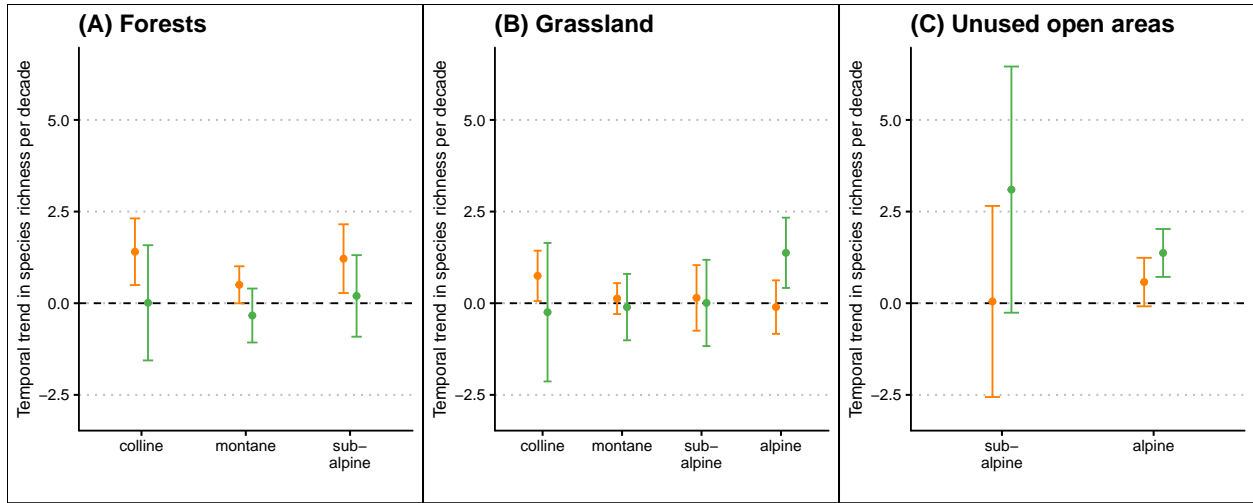


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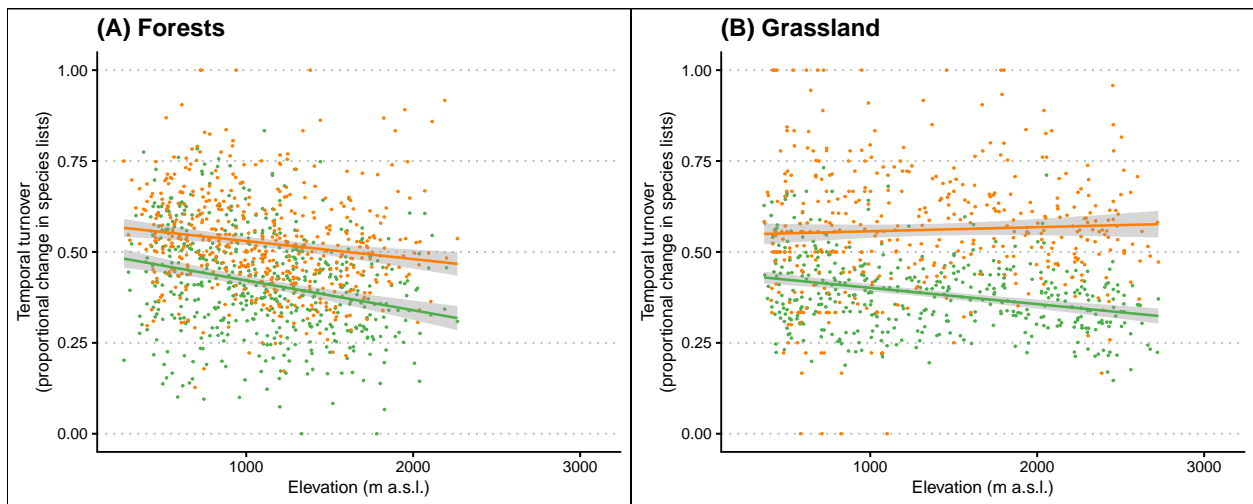


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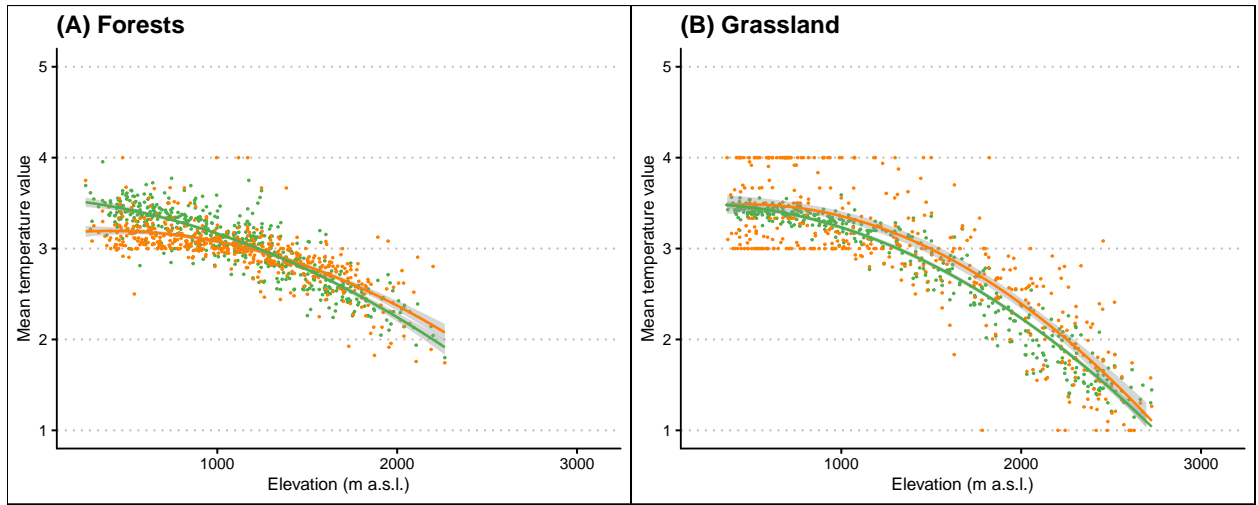


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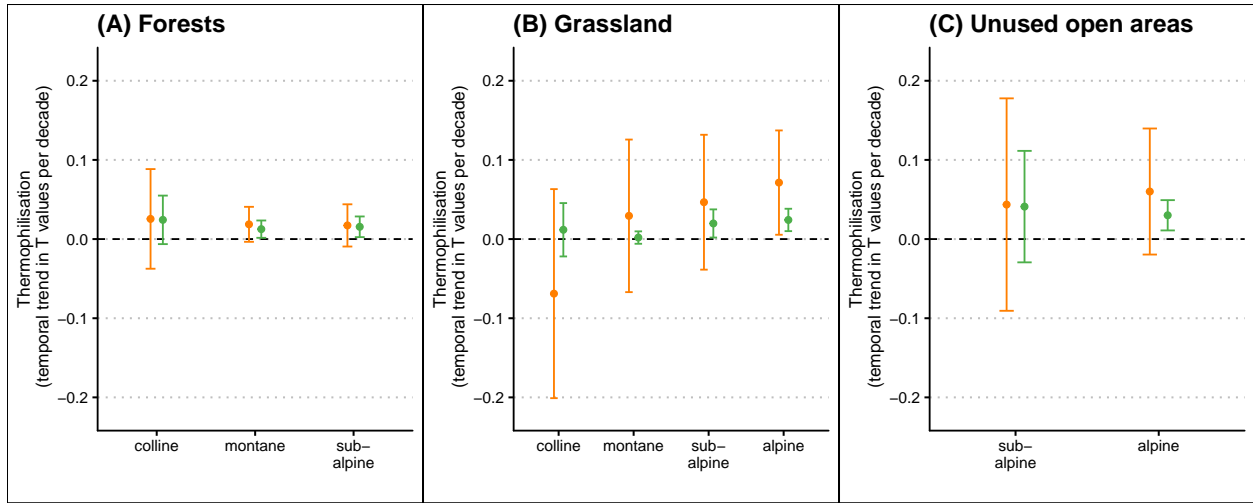


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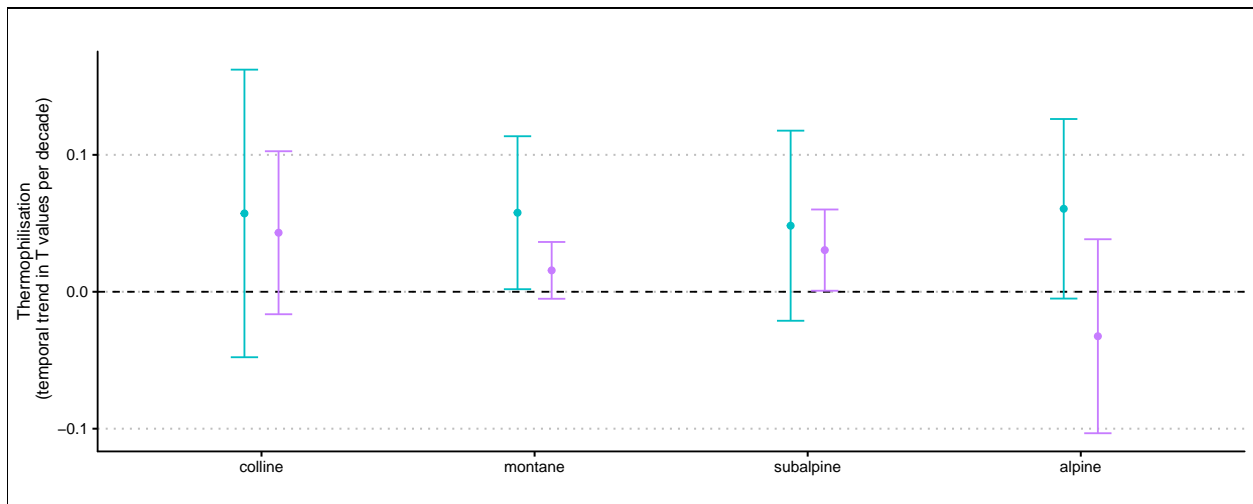


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Table 1: Community measures across land use types and elevational zones. Given are the averages from all plots in the respective category. For empty cells no data are available.

Measure	Land use type	colline	montane	subalpine	alpine
<i>(a) Measures of bryophyte communities</i>					
Species richness	forest	11.29	14.55	20.06	
Species richness	grassland	3.85	4.96	12.77	16.92
Species richness	unused			16.66	13.91
Temporal turnover	forest	0.57	0.53	0.50	
Temporal turnover	grassland	0.54	0.55	0.60	0.55
Temporal turnover	unused			0.51	0.57
Termophilisation	forest	0.03	0.02	0.02	
Termophilisation	grassland	-0.07	0.03	0.05	0.07
Termophilisation	unused			0.04	0.06
<i>(b) Measures of vascular plant communities</i>					
Species richness	forest	18.05	19.40	27.05	
Species richness	grassland	28.76	32.19	45.26	39.30
Species richness	unused			33.36	20.37
Temporal turnover	forest	0.48	0.43	0.36	
Temporal turnover	grassland	0.46	0.40	0.38	0.35
Temporal turnover	unused			0.43	0.40
Termophilisation	forest	0.02	0.01	0.02	
Termophilisation	grassland	0.01	0.00	0.02	0.02
Termophilisation	unused			0.04	0.03