

¹ Major land plant linages respond differently to climate
² warming

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

⁴ *¹University of Zurich, Department of Systematic and Evolutionary Botany, Zollikerstrasse
5 107, 8008 Zürich, Switzerland*

⁶ *²Hintermann & Weber AG, Austrasse 2a, 4253 Reinach, Switzerland*

⁷ *³University of Basel, Zoological Institute, Basel, Vesalgasse 1, 4051 Basel, Switzerland*

⁸

⁹ **Abstract**

¹⁰

- ¹¹ 1. Climate warming studies on plants are currently highly biased towards vascular plants. Bryophytes,
¹² the second largest group of land plants that are particularly diverse in harsh environments, however,
¹³ have received comparatively little attention.
- ¹⁴ 2. In this study we compared the temporal change of species richness, species turnover and termophilisation
¹⁵ from 2001 to 2018 between bryophytes and vascular plants within a mountainous region in
¹⁶ Central Europe. We compared differences between bryophytes and vascular plants among forests,
¹⁷ grassland and unused open areas across an elevational gradient from about 200 to 3000m.
- ¹⁸ 3. We found that particularly in grasslands, the proportion of bryophytes among recorded plants
¹⁹ (i.e., bryophytes and vascular plants) strongly increased along the elevational gradient, suggesting
²⁰ that bryophytes are relatively more diverse in the harsh alpine environments. Presumably due to
²¹ their higher sensitivity to environmental changes, their shorter live spans and their higher dispersal
²² capacity, the temporal turnover of bryophyte species was much higher than the temporal turnover
²³ of vascular plant species. And as a likely consequence of higher turnover, bryophyte communities
²⁴ reacted faster to climate warming than vascular plant communities, which was evidenced by more
²⁵ pronounced termophilisation in bryophytes. The link between a faster reaction of communities to
²⁶ climate warming and differences in live spans was further supported by the faster termophilisation
²⁷ of short-lived bryophytes compared with long-lived bryophytes.
- ²⁸ 4. *Synthesis.* We report subtle differences on how bryophytes and vascular plants communities changed
²⁹ over the last two decades and suggest that these changes are at least partly due to recent climate

*Corresponding author: thomas.kiebacher@systbot.uzh.ch

30 warming. While bryophytes were faster than vascular plants in tracking climate warming, in
31 open areas overall species richness changed in favor of vascular plants, suggesting that in sum more
32 vascular plants than bryophytes profited from recent climate warming.

33 **Keywords:** Bryophytes, disturbance, climate change, life strategies, mountain ecosystems, community
34 temperature index, vascular plants

35 **Introduction**

36 Climate warming is one of the major challenges organisms have to face and one of the major treats to
37 biodiversity in the 21th century (Peñuelas et al., 2013; Wiens, 2016; Biodiversity & Ecosystem Services,
38 2019). Changes in species range, abundance and phenology successively alter extant ecosystems (Chen et
39 al., 2011; Dorji et al., 2013; Soudzilovskaia et al., 2013; Shi et al., 2015). Spatial range shifts, poleward in
40 latitude and upslope in elevation, are among the best documented phenomena of climate warming leading to
41 the replacement of cold-dwelling with warm-dwelling species (i.e., thermophilisation) in extant communities,
42 which ultimately leads to the extinction of some of the species (Engler et al., 2009; Gottfried et al., 2012;
43 Lenoir & Svenning, 2015; Wiens, 2016; Freeman et al., 2018).

44 However, range dynamics, or more specifically, how fast species track climatic warming vary considerably
45 between taxonomic and functional groups (Parmesan & Yohe, 2003; Essl et al., 2015; Wiens, 2016; MacLean
46 & Beissinger, 2017; Roth, Plattner & Amrhein, 2014). Especially species' life strategies are suggested to
47 reflect their potential to track climatic warming. For example, observed range shifts are usually larger and
48 less delayed for species with high dispersal capacities and short life cycles (Angert et al., 2011; Cotto et al.,
49 2017; MacLean & Beissinger, 2017). Furthermore, disturbance intensities that often differ between land use
50 types determine species turnover and thus have impact on thermophilisation processes (Oliver & Morecroft,
51 2014; Stevens et al., 2015).

52 For plants, substantial time lags were observed with realised shifts being much smaller than expected given the
53 observed temperature increase; both, at the species and the community level (Bertrand et al., 2011; Corlett
54 & Westcott, 2013; Rixen & Wipf, 2018; Martin et al., 2019). Furthermore, range shifts seem to decrease with
55 increasing elevation (Angert et al., 2011; Rumpf et al., 2018) albeit at higher elevations temperature increase
56 is usually more pronounced (Ohmura, 2012; Rangwala, Sinsky & Miller, 2013) and mountain ecosystems are
57 supposed to be particularly sensitive to climate warming (Kohler, Wehrli & Jurek, 2014; Dobrowski & Parks,
58 2016; Vanneste et al., 2017).

59 Studies of the impacts of climate warming on plants are highly biased towards vascular plants. Bryophytes,

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

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

80 Here, we used a comparative approach to assess the impact of climate warming on bryophytes and vascular
81 plants in a mountainous region in Central Europe. We examined data from more than 1000 permanent
82 plots monitored 3-4 times between 2001 and 2018. Data were from the Biodiversity Monitoring Switzerland
83 (BDM; www.biodiversitymonitoring.ch) that simultaneously surveyes species diversity of bryophytes and
84 vascular plants on a systematic grid layed over entire Switzerland. To understand better how climate change
85 affectds different species groups, such real-time monitoring data using standardized schemes provide a unique
86 oportunity (Henry et al., 2008; Martin et al., 2019). We inferred the change in species richness, the temporal
87 species turnover (i.e., species exchange ratio between two points in time sensu Hillebrand et al., 2018) and
88 the average indicator values of temperature (i.e., community temperature index sensu Devictor et al., 2008)
89 between 2001 and 2018 and compared differences between bryophytes and vascular plants along the elevational
90 gradient from about 200 to 3000m.

91 Materials and methods

92 Study area and field data

93 About 70% of Switzerland is mountainous (60% Alps and 10% Jura Mountains); the altitudinal range is from
94 193 to 4634 m.a.s.l. We analyzed the presence/absence of bryophyte and vascular plant species sampled in
95 the frame of the Swiss biodiversity monitoring (BDM, www.biodiversitymonitoring.ch) program that was
96 launched in 2001 to monitor Switzerland's biodiversity (Weber, Hintermann & Zanger, 2004). Bryophytes
97 and vascular plants are investigated in a systematic sample of about 1800 circular 10 m² plots laid out as a
98 regular grid over entire Switzerland.

99 Fieldwork was highly standardized and was carried out by qualified botanists. The botanists visited each plot
100 twice a season except for the plots at high altitudes with a short vegetation period that were inspected only
101 once. During the two visits all vascular plant species detected on the plot were recorded (for more details on
102 the vascular plant surveys see Bühler & Roth, 2011; Plattner, Birrer & Weber, 2004). During the first visit,
103 bryophytes samples up to 1.5 m above ground were collected from the soil, dead wood, rocks, living trees
104 and scrubs and sent to specialists for identification. The botanists also classified the land use category using
105 a system of 32 pre-defined land use categories similar to the CORINE Land Cover system (Büttner et al.,
106 2004). For annual reporting of the BDM results, the 32 land use categories were aggregated to the six main
107 types of land use: forests, meadows and pastures, arable land, settlements, alpine pastures and unused open
108 areas. Unused open areas included mostly screes and rocks at higher elevations but also included special
109 cases at lower elevations such as gravel pits and waste lands. We thus removed the colline and montane plots
110 from the unused open areas category (which we label “unused” from now). Further, we grouped meadows,
111 pastures and alpine pastures into one group labeled “grassland”.

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

119 Because climate warming effects often differ along elevational gradients (e.g. Bertrand et al., 2011; Roth,
120 Plattner & Amrhein, 2014), we split our dataset according to four elevational bands based on the temperature

121 zonation of Switzerland (Schreiber et al., 1977), that is colline, montane, subalpine and alpine. The distribution
122 of plots and surveys across the elevational bands was as following: 118 plots (405 surveys) in the colline zone,
123 526 plots (1821 surveys) in the montane zone, 247 plots (873 surveys) in the subalpine zone and 283 plots
124 (988 surveys) in the alpine zone.

125 [Figure 1 about here.]

126 Community measures

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

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

145 Statistical methods and data accessibility

146 For each plot, we calculated the average and the temporal trend of species richness and temperature affinity
147 based on the repeated surveys per plot. To estimate the temporal trend, we applied for each plot separately a
148 linear model with species richness or temperature affinity as dependent variable and the year when the survey

¹⁴⁹ was conducted as the predictor variable. The estimated slope (given as change per decade) was our measure
¹⁵⁰ of the temporal trend of species richness and temperature affinity that we used in subsequent analyses.

¹⁵¹ All analyses were done with the software R (R Core Team, 2019). To estimate the temporal turnover of
¹⁵² species we used the package ‘simba’ (Jurasinski & Vroni Retzer, 2012). Data and R Markdown documents to
¹⁵³ 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
¹⁵⁴ chunks of embedded R code to produce the figures and tables (Xie, Allaire & Grolemund, 2018). Raw data
¹⁵⁵ for analyses are provided in the folder “data-raw” and the folder “R” contains the R-Script that was used to
¹⁵⁶ export the data from the BDM database. The folder “div” contains a list of all the R packages (including
¹⁵⁷ version number) that were in the workspace when the manuscript was rendered. The final version of the
¹⁵⁸ repository will be archived at Zenodo (<https://zenodo.org/>).

¹⁶⁰ Results

¹⁶¹ [Table 1 about here.]

¹⁶² Species richness

¹⁶³ Across all surveys, 539 bryophyte species and 1212 vascular plant species were recorded. The mean (\pm SD)
¹⁶⁴ species richness per plot was 12.87 (\pm 8.96) species for bryophytes and 27.34 (\pm 15.17) species for vascular
¹⁶⁵ plants. However, species richness was quite different between habitat types, elevational zones and species
¹⁶⁶ groups (Table 1). For the three land use types the average species richness of vascular plants was higher than
¹⁶⁷ the respective species richness of bryophytes: the difference was 5.60 species (p-value based on a paired t-test:
¹⁶⁸ <0.001) in forests, 26.81 species (p-value: <0.001) in grasslands, and 7.37 species (p-value: <0.001) in unused
¹⁶⁹ open areas.

¹⁷⁰ In forest and grassland, where study plots spanned a large proportion of the elevational gradient, the species
¹⁷¹ richness of bryophytes and vascular plants both increased from low to intermediate elevations and tent to
¹⁷² decrease again at higher elevations (i.e., a mid-elevational peak, Fig. 2). This mid-elevational peak was
¹⁷³ particularly evident for vascular plants in grassland and less obvious to absent for plants in forest and for
¹⁷⁴ bryophytes in both land use types. Consequently, in grassland the proportion of bryophytes (i.e., number of
¹⁷⁵ bryophytes divided by the total number of bryophytes and vascular plants) strongly increased with elevation
¹⁷⁶ (Binomial-GLMM with elevation as predictor variable and site ID as random effect; slope of elevation at the

₁₇₇ logit-scale: 0.17, p-value: <0.001). This increase in the proportion of bryophyte species was almost absent in
₁₇₈ forests (slope of elevation at the logit-scale: 0.02, p-value: 0.118).

₁₇₉ [Figure 2 about here.]

₁₈₀ In forest, the temporal trend of species richness between 2001 and 2018 was in favour of bryophytes: while
₁₈₁ for bryophytes the species richness increased by 5.16% (95%-credible interval: 1.92-8.40) per decade, the
₁₈₂ species richness of vascular plants decreased on the same plots and period by -1.35% (95%-credible interval:
₁₈₃ -4.32-1.62). In contrast, however, the temporal trend in species richness in grassland and unused open
₁₈₄ areas was in favour of vascular plants. In grassland the species richness decreased in bryophytes by -5.15%
₁₈₅ (95%-credible interval: -11.30-1.01) and increase in vascular plants by 0.73% (95%-credible interval: -1.15-2.61).
₁₈₆ Also in unused open areas, the increase in species richness was less strong in bryophytes than in vascular
₁₈₇ plants, with an increase of 6.10% (95%-credible interval: -2.79-14.98) in the former and an increase of 13.65%
₁₈₈ (95%-credible interval: 7.00-20.29) in the latter.

₁₈₉ **Temporal turnover**

₁₉₀ The mean temporal turnover across all sites was larger for bryophytes than for vascular plants (mean \pm
₁₉₁ SD for bryophytes: 0.55 ± 0.15 ; vascular plants: 0.40 ± 0.13 ; p-value based on Wilcoxon signed rank test:
₁₉₂ <0.001). The pattern how the temporal turnover of bryophytes changed along the elevational gradient differed
₁₉₃ between land-use types (Ancova with an interaction between land use types and elevation; F-value: 10.94;
₁₉₄ p-value: 0.001): while it decreased with elevation in forests, it tended to increase in grassland (Fig. 3). For
₁₉₅ vascular plants in contrast, the temporal turn-over decreased from low to high elevations both in forests and
₁₉₆ in grassland with only slight differences between the two land-use types (Ancova with an interaction between
₁₉₇ land use types and elevation; F-value: 6.62; p-value: 0.010; Fig. 3).

₁₉₈ [Figure 3 about here.]

₁₉₉ **Temperature affinities and termophilisation**

₂₀₀ While in forests the mean temperature value (i. e., temperature affinity) of vascular plants was higher than
₂₀₁ the mean temperature value of bryophytes, the opposite was the case for grassland and unused open areas: the
₂₀₂ difference in temperature affinity of vascular plants minus the temperature affinity of bryophytes was 0.07
₂₀₃ (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:
₂₀₄ <0.001) in unused open areas. In grassland, bryophyte communities had slightly higher temperature affinities

205 along the entire gradient (Fig. 4). In forests, however, at low elevation the temperature affinities of vascular
206 plant communities were higher than the temperature affinities of bryophyte communities whereas at higher
207 elevations the pattern was inversed (Fig. 4).

208 [Figure 4 about here.]

209 Between 2001 and 2018, for both bryophyte and plant communities the average temperature value of recored
210 species increased over time, that is termophilisation of species communities. Termophilisation was evident
211 in all three land use types with a slightly stronger but at the same time more variable termophilisation in
212 bryophytes: in forest the avearge termophilisation was 0.017 (p-value based on a one sample t-test to test for
213 no termophilisation: 0.072) for bryophytes and 0.016 (p-value: <0.001) for vascular plants, in grassland the
214 avearge termophilisation was 0.038 (p-value: 0.102) for bryophytes and 0.012 (p-value: 0.001) for vascular
215 plants, and in unused open areas the avearge termophilisation was 0.059 (p-value: 0.115) for bryophytes and
216 0.031 (p-value: 0.001) for vascular plants. This tendency for higher but more variable termophilisation in
217 bryophytes communities compared to vascular plant communities was evident for all three land use types at
218 the entire elevational gradient (Fig. 5).

219 [Figure 5 about here.]

220 Species with a short-lived life strategy are among those that colonize new habitats more rapidly, and thus
221 contribute more to thermophilisation of species communities. Temporal trends in the change of temperature
222 values were higher for short-lived bryophyte species than for bryophytes with a long-lived life strategy: the
223 difference in termophilisation of short-lived and long-lived species was 0.05 (p-value based on a paired t-test
224 to test for no differences between short-lived and long-lived species: 0.042). The difference between short-lived
225 and long-lived specieswas more pronounced at higher elevations (Fig. 6). However, there might be a slight
226 bias as short-lived species tend to be more cryophilous (37% of all short-lived species have a T-value of 1 or
227 2) than long-lived species (only 30% have a T-value of 1 or 2). With increasing elevation, the proportion
228 of short-lived species in bryophyte communities is increasing, except for grassland, with a peak in lowlands
229 (mainly due to communities that consist of short-lived species only, presumably in disturbed habitats).

230 [Figure 6 about here.]

231 Discussion

232 Climate warming is one of the major globale change impacts within the study region with an increase
233 in ambient temperature of > 0.5 K per decade since the late 1980' (CH2018, 2018; MeteoSwiss, 2019).

234 At least part of the changes in community structure of bryophytes and vascular plants that we report in
235 this study is likely related to this temperature increase. In general, both bryophyte and vascular plant
236 communities show termophilisation, that is the replacement of more cold-dwelling with more warm-dwelling
237 species. However, in eight of the nine comparisons in Fig. 5 the termophilisation was higher in bryophytes
238 than in vascular plants. If over a long period of time the termophilisation of bryophytes was indeed larger
239 than the termophilisation of vascular plants, we would expect that the average temperature values (i.e.,
240 temperature affinities) of extent bryophyte communities to be larger than the average temperature value of
241 vascular plant communities. This prediction matches particularly well with the temperature affinities of plant
242 communities we found in grasslands (Fig. 4): the temperature affinities of bryophytes were slightly higher
243 than the temperature affinities of plants along the entire elevational gradient. Although the uncertainty in
244 termophilisation particularly in bryophytes was rather high, we thus conclude that bryophyte communities
245 were faster than vascular plant communities in adapting to current climate warming.

246 The higher termophilisation rate in bryophytes compared to vascular plants might be due to higher colo-
247 nization rates of warm dwelling species and/or lower extinction rates of cold-dwelling species. We suggest
248 that ecophysiological and biological differences between the two taxonomical groups could explain higher
249 colonization rates of bryophytes as pointed out in the introduction; i.e., pokilohydry of bryophytes and
250 different life strategies. Many bryophyte species have a colonist strategy with short generation times and
251 high reproductive effort (During, 1979, 1992; Dierßen, 2002), which facilitates them to colonize sites that
252 become suitable through climate warming. By contrast and particularly in mountain areas, vascular plant
253 species are mostly long-lived species and form persistent communities which have high resilience to vascular
254 plant invasion (Dullinger, Dirnböck & Grabbherr, 2004; Mark & Wilson, 2005; Grabbherr, Gottfried & Pauli,
255 2010; Gottfried et al., 2012). Beside resilience, range shifts of vascular plants towards higher elevations
256 depend on the availability of soil. The desiccation tolerance and nutrient uptake mechanisms of bryophytes,
257 however, make them much less dependent on a substrate that serves as water storage and source of nutrients
258 (Proctor, 2009). Finally, vascular plant growth and expansion at high elevations is slowed down by low
259 temperatures, short vegetation periods and positive net photosynthesis being mostly limited to the summer
260 season (Körner, 2003; Gottfried et al., 2012). Bryophytes can maintain positive net photosynthesis rates at
261 very low temperatures (e.g., down to -10 °C in *Pellia epiphylla*, a common liverwort in the study region;
262 Pihakaski & Pihakaski, 1979) and are opportunistic in their assimilation strategy. Once environmental
263 conditions are favorable they can reassume positive net photosynthesis within short (often within minutes)
264 time intervals throughout the year (Proctor, 2009, 2011).

265 Higher termophilisation rates of bryophytes might also be due to higher extinction rates of cold-dwelling

266 bryophyte species as compared to cold-dwelling vascular plant species. Many high mountain bryophyte
267 species typically grow in the coldest microsites (e.g., in gaps between rocks on northern slopes) and another
268 set of species depends on long snow cover (Limprecht 1890, 1895, 1904, Amann 1928, Köckinger 2017). These
269 species may not find suitable refugia at the same elevational level, and, in the European Alps they include
270 endemics known from a few localities only (e.g., (Hallingbäck et al. 2019, Schröck et al. 2019a, 2019b). For
271 vascular plants, our results expand findings of (Rumpf et al. 2018) to the community level. (Rumpf et
272 al. 2018) examined range shifts of 183 plant species in the Alps using data from vegetation relevés located
273 mostly between 1500 and 2700 m, thus, roughly encompassing the subalpine and alpine zone in our study
274 and observed decreased range shifts at higher elevations. The more delayed responses among alpine vascular
275 plants is supported by the decreasing temporal turnover rate of plants in grasslands (Fig. 3) and by crowing
276 evidence that the extinction of mountain top species may be delayed by their survival in colder microsite
277 refugia (e.g. Scherrer & Körner, 2011; Maclean et al., 2015; Giezendanner et al., 2019).

278 Bryophytes are usually more diverse in the harsh alpine environments (Bruun et al., 2006; Proctor, 2011;
279 Turetsky et al., 2012; Mateo et al., 2016). Indeed, in grassland we found that the proportion of bryophytes
280 among recorded plants strongly increased along the elevational gradient. If we assume that climate warming
281 in general leads to a less harsh environments, which might be the case in areas such as Switzerland where
282 severe droughts are rare, we would expect that the proportion of bryophytes among recorded plants would
283 increase over time. This is what we found for grassland where the species richness of bryophytes tent to
284 decrease and the species richness of plants increased between 2001 and 2018. While it is often suggested that
285 communities that are faster in tracking climate warming are better able to cope with climate change (which
286 would favor bryophytes in our case), overall species richness changed in favor of vascular plants, suggesting
287 that in sum more vascular plants than bryophytes profited from climate warming.

288 However, we like to acknowledge that it is an inherent problem of observational studies such as our to ascertain
289 the drivers of observed patterns. However, climate warming is one of the major impacts the study region
290 experienced in the last decades. Since the late 1980' warming increased to rates > 0.5 K per decade (CH2018,
291 2018; MeteoSwiss, 2019). By contrast, minor changes in precipitation regimes were observed (CH2018, 2018).
292 Nonetheless, we cannot exclude that other factors than temperature have influenced our results to a certain
293 degree. For instance, nutrient enrichment, an immanent element of global- and local change in the study
294 region (Schlesinger, 2009; Roth et al., 2013), and warming may have additive effects (Zhang et al., 2015;
295 Greaver et al., 2016).

296 So far, most observational studies addressing climate warming effects encompassed time intervals > 20 years
297 and often considerably uncertainty had to be accepted because accurate relocation of historical surveys was

298 not possible (see Chen et al., 2011; Wiens, 2016; MacLean & Beissinger, 2017; Freeman et al., 2018; Rumpf
299 et al., 2018). Consequently, analyses could not address impacts on resident communities and mostly focused
300 on range shifts of common species, because a minimum number of records is required to estimate ranges.
301 Here, we can supplement research on climate warming effects with results based on an extensive dataset from
302 exactly relocated plots monitored for 10 to 15. We believe that our study is an example on how real-time
303 monitoring data using standardized schemes could allow for a better understanding of how climate change
304 influence biodiversity (Henry et al., 2008; Martin et al., 2019).

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310 References

- 311 Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict
312 recent shifts at expanding range edges? *Ecology Letters* 14:677–689. DOI: 10.1111/j.1461-0248.2011.01620.x.
- 313 Becker Scarpitta A, Bardat J, Lalanne A, Vellend M. 2017. Long-term community change: bryophytes are
314 more responsive than vascular plants to nitrogen deposition and warming. *Journal of Vegetation Science*
315 28:1220–1229. DOI: 10.1111/jvs.12579.
- 316 Bertrand R, Lenoir J, Piedallu C, Dillon GR, De Ruffray P, Vidal C, Pierrat JC, Gégout JC. 2011. Changes
317 in plant community composition lag behind climate warming in lowland forests. *Nature* 479:517–520. DOI:
318 10.1038/nature10548.
- 319 Biodiversity IS-PP on, Ecosystem Services I. 2019. Summary for policymakers of the global assessment report
320 on biodiversity and ecosystem services. DOI: 10.5281/zenodo.3553579.
- 321 Bruun HH, Moen J, Virtanen R, Grytnes J, Oksanen L, Angerbjörn A. 2006. Effects of altitude and
322 topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of*
323 *Vegetation Science* 17:37–46. DOI: 10.1111/j.1654-1103.2006.tb02421.x.

- 324 Bühler C, Roth T. 2011. Spread of common species results in local-scale floristic homogenization in grassland
325 of Switzerland. *Diversity and Distributions* 17:1089–1098. DOI: 10.1111/j.1472-4642.2011.00799.x.
- 326 Büttner G, Feranec J, Jaffrain G, Mari L, Maucha G, Soukup T. 2004. The CORINE land cover 2000 project.
327 *EARSeL eProceedings* 3:331–346.
- 328 CH2018. 2018. *CH2018 – Climate Scenarios for Switzerland, Technical Report*. Zürich: National Centre for
329 Climate Services.
- 330 Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with
331 high levels of climate warming. *Science* 333:1024–1026. DOI: 10.1126/science.1206432.
- 332 Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology and
333 Evolution* 28:482–488. DOI: 10.1016/j.tree.2013.04.003.
- 334 Cotto O, Wessely J, Georges D, Klonner G, Schmid M, Dullinger S, Thuiller W, Guillaume F. 2017. A dynamic
335 eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications*
336 8. DOI: 10.1038/ncomms15399.
- 337 Devictor V, Julliard R, Couvet D, Jiguet F. 2008. Birds are tracking climate warming, but not fast enough.
338 *Proceedings of the Royal Society B: Biological Sciences* 275:2743–2748.
- 339 Dierßen K. 2002. Distribution, ecological amplitude and phytosociological-characterization of european
340 bryophytes. *Nova Hedwigia* 74.
- 341 Dobrowski SZ, Parks SA. 2016. Climate change velocity underestimates climate change exposure in moun-
342 tainous regions. *Nature Communications* 7:1–8. DOI: 10.1038/ncomms12349.
- 343 Dorji T, Totland Ø, Moe SR, Hopping KA, Pan J, Klein JA. 2013. Plant functional traits mediate reproductive
344 phenology and success in response to experimental warming and snow addition in Tibet. *Global Change
345 Biology* 19:459–472. DOI: 10.1111/gcb.12059.
- 346 Dullinger S, Dirnböck T, Grabherr G. 2004. Modelling climate change-driven treeline shifts: Relative effects
347 of temperature increase, dispersal and invasibility. *Journal of Ecology* 92:241–252. DOI: 10.1111/j.0022-
348 0477.2004.00872.x.
- 349 During HJ. 1979. Life strategies of bryophytes : A preliminary review. *Lindbergia* 5:2–18.
- 350 During HJ. 1992. Ecological classification of bryophytes and lichens. In: Bates JW, Farmer AM eds.
351 *Bryophytes and lichens in a changing environment*. Oxford: Clarendon Press, 1–31.
- 352 Ellenberg H. 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas.

- 353 Engler R, Randin CF, Vittoz P, Czáká T, Beniston M, Zimmermann NE, Guisan A. 2009. Predicting future
354 distributions of mountain plants under climate change: Does dispersal capacity matter? *Ecography* 32:34–45.
355 DOI: 10.1111/j.1600-0587.2009.05789.x.
- 356 Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, Wilson JRU, Richardson DM. 2015. Delayed biodiversity
357 change: No time to waste. *Trends in Ecology and Evolution* 30:375–378. DOI: 10.1016/j.tree.2015.05.002.
- 358 Frahm J-P. 2007. Diversity, dispersal and biogeography of bryophytes (mosses). *Biodiversity and Conservation*
359 17:277–284.
- 360 Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL. 2018. Expanding, shifting and shrinking: The impact
361 of global warming on species' elevational distributions. *Global Ecology and Biogeography* 27:1268–1276. DOI:
362 10.1111/geb.12774.
- 363 Giezendanner J, Bertuzzo E, Pasetto D, Guisan A, Rinaldo A. 2019. A minimalist model of extinction and
364 range dynamics of virtual mountain species driven by warming temperatures. *PLoS ONE* 14:1–19. DOI:
365 10.1371/journal.pone.0213775.
- 366 Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer
367 B, Fernández Calzado MR, Kazakis G, Krajčí J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P,
368 Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A,
369 Theurillat JP, Tomaselli M, Villar L, Vittoz P, Vogiatzakis I, Grabherr G. 2012. Continent-wide response of
370 mountain vegetation to climate change. *Nature Climate Change* 2:111–115. DOI: 10.1038/nclimate1329.
- 371 Grabherr G, Gottfried M, Pauli H. 2010. Climate change impacts in alpine environments. *Geography Compass*
372 4:1133–1153. DOI: 10.1111/j.1749-8198.2010.00356.x.
- 373 Greaver TL, Clark CM, Compton JE, Vallano D, Talhelm AF, Weaver CP, Band LE, Baron JS, Davidson
374 EA, Tague CL, Felker-Quinn E, Lynch JA, Herrick JD, Liu L, Goodale CL, Novak KJ, Haeuber RA. 2016.
375 Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change* 6:836–843. DOI:
376 10.1038/nclimate3088.
- 377 Hallingback T, Tan BC. 2014. Past and present activities and future strategy of bryophyte conservation.
378 *Phytotaxa* 9:266–274. DOI: 10.11646/phytotaxa.9.1.15.
- 379 He X, He KS, Hyvönen J. 2016. Will bryophytes survive in a warming world? *Perspectives in Plant Ecology,*
380 *Evolution and Systematics* 19:49–60. DOI: 10.1016/j.ppees.2016.02.005.
- 381 Henry P-Y, Lengyel S, Nowicki P, Julliard R, Clobert J, Čelik T, Gruber B, Schmeller DS, Babij V, Henle
382 K. 2008. Integrating ongoing biodiversity monitoring: Potential benefits and methods. *Biodiversity and*

- 383 *conservation* 17:3357–3382.
- 384 Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp
385 D, Larsen S, others. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for
386 conservation and monitoring. *Journal of Applied Ecology* 55:169–184.
- 387 Jurasinski G, Vroni Retzer. 2012. *Simba: A collection of functions for similarity analysis of vegetation data.*
- 388 Kohler T, Wehrli A, Jurek M. 2014. *Mountains and climate change: A global concern. Sustainable Mountain*
389 *Development Series. Bern*, Centre for Development; Environment (CDE), Swiss Agency for Development;
390 Cooperation (SDC); Geographica Bernensia. DOI: 10.1017/cbo9781139023924.013.
- 391 Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin, Heidelberg:
392 Springer.
- 393 Landolt E. 1977. Ökologische zeigerwerte zur Schweizer Flora.
- 394 Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schwein-
395 gruber F, Theurillat J-P, others. 2010. *Flora indicativa. Ecological indicator values and biological attributes of*
396 *the flora of switzerland and the alps*. Haupt Verlag.
- 397 Lenoir J, Svenning JC. 2015. Climate-related range shifts - a global multidimensional synthesis and new
398 research directions. *Ecography* 38:15–28. DOI: 10.1111/ecog.00967.
- 399 Lindo Z, Gonzalez A. 2010. The bryosphere: An integral and influential component of the Earth's biosphere.
400 *Ecosystems* 13:612–627. DOI: 10.1007/s10021-010-9336-3.
- 401 MacLean SA, Beissinger SR. 2017. Species' traits as predictors of range shifts under contemporary climate
402 change: A review and meta-analysis. *Global Change Biology* 23:4094–4105. DOI: 10.1111/gcb.13736.
- 403 Maclean IMD, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ. 2015. Microclimates buffer the responses of plant
404 communities to climate change. *Global Ecology and Biogeography* 24:1340–1350. DOI: 10.1111/geb.12359.
- 405 Mark AF, Wilson JB. 2005. Tempo and mode of vegetation dynamics over 50 years in a New Zealand
406 alpine cushion/tussock community. *Journal of Vegetation Science* 16:227–236. DOI: 10.1111/j.1654-
407 1103.2005.tb02360.x.
- 408 Martin G, Devictor V, Motard E, Machon N, Porcher E. 2019. Short-term climate-induced change in french
409 plant communities. *Biology letters* 15:20190280.
- 410 Mateo RG, Broennimann O, Normand S, Petitpierre B, Araújo MB, Svenning JC, Baselga A, Fernández-
411 González F, Gómez-Rubio V, Muñoz J, Suarez GM, Luoto M, Guisan A, Vanderpoorten A. 2016. The mossy

- 412 north: An inverse latitudinal diversity gradient in European bryophytes. *Scientific Reports* 6:1–9. DOI:
413 10.1038/srep25546.
- 414 Medina NG, Draper I, Lara F. 2011. Biogeography of mosses and allies: Does size matter? In: *Biogeography
415 of microscopic organisms: Is everything small everywhere?* Cambridge: Cambridge University Press, 209–233.
416 DOI: 10.1017/CBO9780511974878.012.
- 417 MeteoSwiss. 2019. Area-mean temperatures of Switzerland. DOI: 10.18751/Climate/Timeseries/CHTM/1.1.
- 418 Ohmura A. 2012. Enhanced temperature variability in high-altitude climate change. *Theoretical and Applied
419 Climatology* 110:499–508. DOI: 10.1007/s00704-012-0687-x.
- 420 Oliver TH, Morecroft MD. 2014. Interactions between climate change and land use change on biodiversity:
421 Attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change* 5:317–335.
422 DOI: 10.1002/wcc.271.
- 423 Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change. *Nature* 421:37–42. DOI:
424 10.1038/nature01286.
- 425 Peñuelas J, Sardans J, Estiarte M, Ogaya R, Carnicer J, Coll M, Barbata A, Rivas-Ubach A, Llusià J,
426 Garbulsky M. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere.
427 *Global change biology* 19:2303–2338.
- 428 Pihakaski K, Pihakaski S. 1979. Effects of chilling on the ultrastructure and net photosynthesis of *Pellia
429 epiphylla*. *Annals of Botany* 43:773–781. DOI: 10.1093/oxfordjournals.aob.a085692.
- 430 Plattner M, Birrer S, Weber D. 2004. Data quality in monitoring plant species richness in Switzerland.
431 *Community Ecology* 5:135–143. DOI: 10.1556/comec.5.2004.1.13.
- 432 Proctor MCF. 2009. Physiological ecology. In: Goffinet B, Shaw J eds. *Bryophyte biology*. Cambridge:
433 Cambridge University Press, 237–268.
- 434 Proctor MCF. 2011. Climatic responses and limits of bryophytes : Comparisons and contrasts with vascular
435 plants. In: Tuba Z, Slack NG, Stark LR eds. *Bryophyte ecology and climate change*. Cambridge: Cambridge
436 University Press, 35–54.
- 437 Rangwala I, Sinsky E, Miller JR. 2013. Amplified warming projections for high altitude regions of the
438 northern hemisphere mid-latitudes from CMIP5 models. *Environmental Research Letters* 8:1–9. DOI:
439 10.1088/1748-9326/8/2/024040.
- 440 R Core Team. 2019. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation

- ⁴⁴¹ for Statistical Computing.
- ⁴⁴² Rixen C, Wipf S. 2018. Non-equilibrium in Alpine Plant Assemblages: Shifts in Europe's Summit Floras. In:
- ⁴⁴³ Catalan J, Ninot JM, Aniz MM eds. *Monitoring global change in high mountains*. Cham: Springer, 285–303.
- ⁴⁴⁴ Roth T, Kohli L, Rihm B, Achermann B. 2013. Nitrogen deposition is negatively related to species richness and
- ⁴⁴⁵ species composition of vascular plants and bryophytes in Swiss mountain grassland. *Agriculture Ecosystems*
- ⁴⁴⁶ & Environment 178:121–126. DOI: 10.1016/j.agee.2013.07.002.
- ⁴⁴⁷ Roth T, Plattner M, Amrhein V. 2014. Plants Birds and Butterflies: Short-Term Responses of Species
- ⁴⁴⁸ Communities to Climate Warming Vary by Taxon and with Altitude. *PLoS ONE* 9:e82490. DOI: 10.1371/jour-
- ⁴⁴⁹ nal.pone.0082490.
- ⁴⁵⁰ Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger
- ⁴⁵¹ S. 2018. Range dynamics of mountain plants decrease with elevation. *PNAS* 115:1848–1853. DOI:
- ⁴⁵² 10.1073/pnas.1713936115.
- ⁴⁵³ Scherrer D, Körner C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant
- ⁴⁵⁴ diversity against climate warming. *Journal of biogeography* 38:406–416.
- ⁴⁵⁵ Schlesinger WH. 2009. On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of*
- ⁴⁵⁶ *Sciences of the United States of America* 106:203–208. DOI: 10.1073/pnas.0810193105.
- ⁴⁵⁷ Schreiber K, Kuhn N, Hug C, Häberli R, Schreiber C, Zeh W, Lautenschlager S. 1977. Wärmegliederung der
- ⁴⁵⁸ Schweiz. *Berne: Federal Department of Justice and Police* 69.
- ⁴⁵⁹ Shi Z, Sherry R, Xu X, Hararuk O, Souza L, Jiang L, Xia J, Liang J, Luo Y. 2015. Evidence for long-term
- ⁴⁶⁰ shift in plant community composition under decadal experimental warming. *Journal of Ecology* 103:1131–1140.
- ⁴⁶¹ DOI: 10.1111/1365-2745.12449.
- ⁴⁶² Soudzilovskaia NA, Elumeeva TG, Onipchenko VG, Shidakov II, Salpagarova FS, Khubiev AB, Tekeev
- ⁴⁶³ DK, Cornelissen JHC. 2013. Functional traits predict relationship between plant abundance dynamic and
- ⁴⁶⁴ long-term climate warming. *PNAS* 110:18180–18184. DOI: 10.1073/pnas.1310700110.
- ⁴⁶⁵ Stevens JT, Safford HD, Harrison S, Latimer AM. 2015. Forest disturbance accelerates thermophilization of
- ⁴⁶⁶ understory plant communities. *Journal of Ecology* 103:1253–1263.
- ⁴⁶⁷ Szyja M, Menezes A, Oliveira FD, Leal I, Tabarelli M, Büdel B, Wirth R. 2019. Neglected but potent dry
- ⁴⁶⁸ forest players: Ecological role and ecosystem service provision of biological soil crusts in the human-modified
- ⁴⁶⁹ Caatinga. *Frontiers in Ecology and Evolution* in press. DOI: doi: 10.3389/fevo.2019.00482.

- 470 Turetsky MR, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire AD, Tuittila ES. 2012. The
471 resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196:49–67. DOI:
472 10.1111/j.1469-8137.2012.04254.x.
- 473 Vanneste T, Michelsen O, Graae BJ, Kyrkjeeide MO, Holien H, Hassel K, Lindmo S, Kapás RE, De Frenne P.
474 2017. Impact of climate change on alpine vegetation of mountain summits in Norway. *Ecological Research*
475 32:579–593. DOI: 10.1007/s11284-017-1472-1.
- 476 Weber D, Hintermann U, Zangger A. 2004. Scale and trends in species richness: considerations for monitoring
477 biological diversity for political purposes. *Global Ecology and Biogeography* 13:97–104. DOI: 10.1111/j.1466-
478 882x.2004.00078.x.
- 479 Wiens JJ. 2016. Climate-related local extinctions are already widespread among plant and animal species.
480 *PLoS Biology* 14:1–18. DOI: 10.1371/journal.pbio.2001104.
- 481 Xie Y, Allaire J, Golemund G. 2018. *R markdown: The definitive guide*. CRC Press.
- 482 Zhang T, Guo R, Gao S, Guo J, Sun W. 2015. Responses of plant community composition and biomass
483 production to warming and nitrogen deposition in a temperate meadow ecosystem. *PLoS ONE* 10:1–16. DOI:
484 10.1371/journal.pone.0123160.

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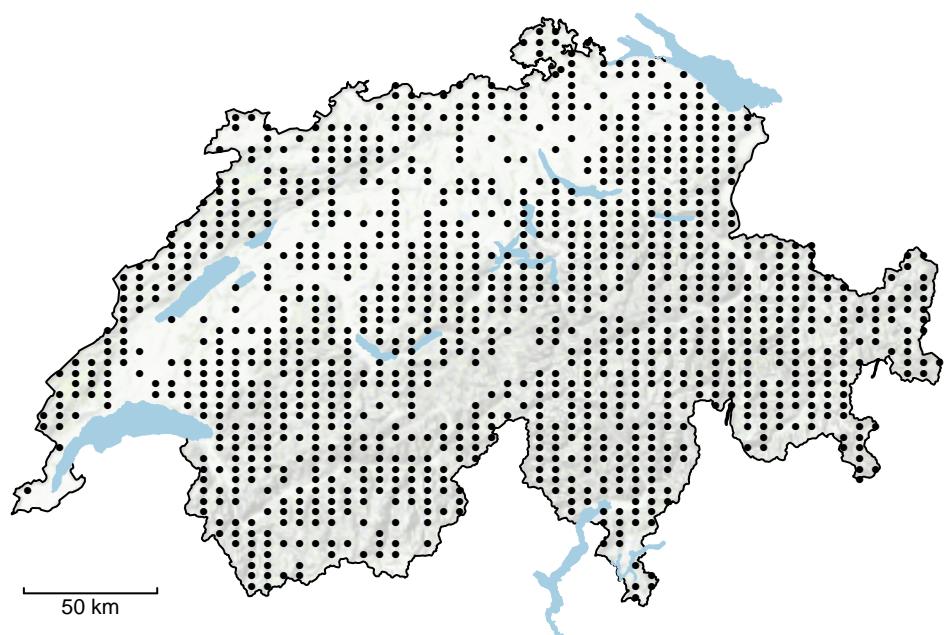


Figure 1: Distribution of the study plots accross Switzerland. Background data source: Swisstopo, Federal Office of Topography.

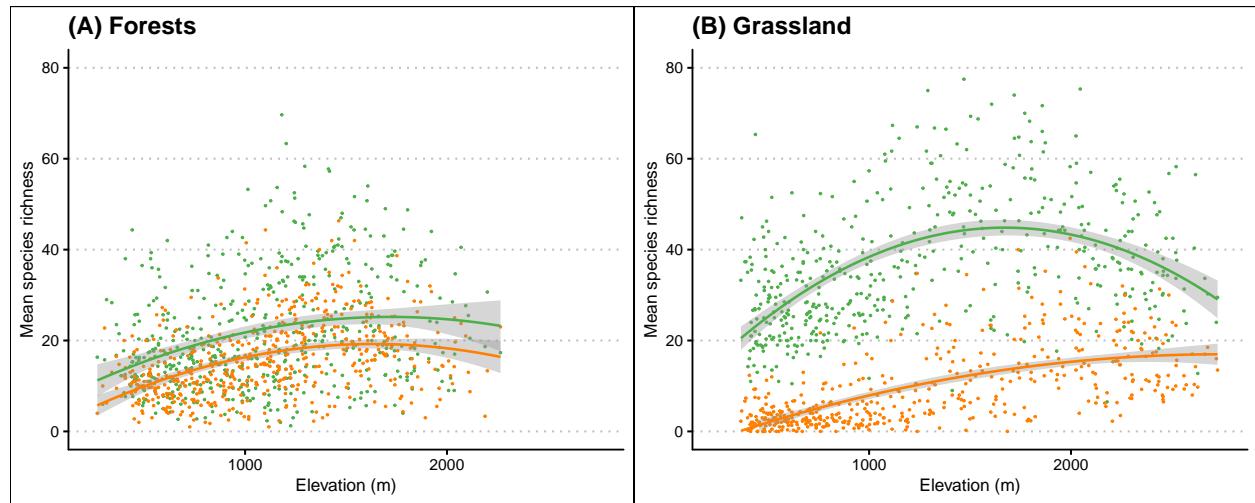


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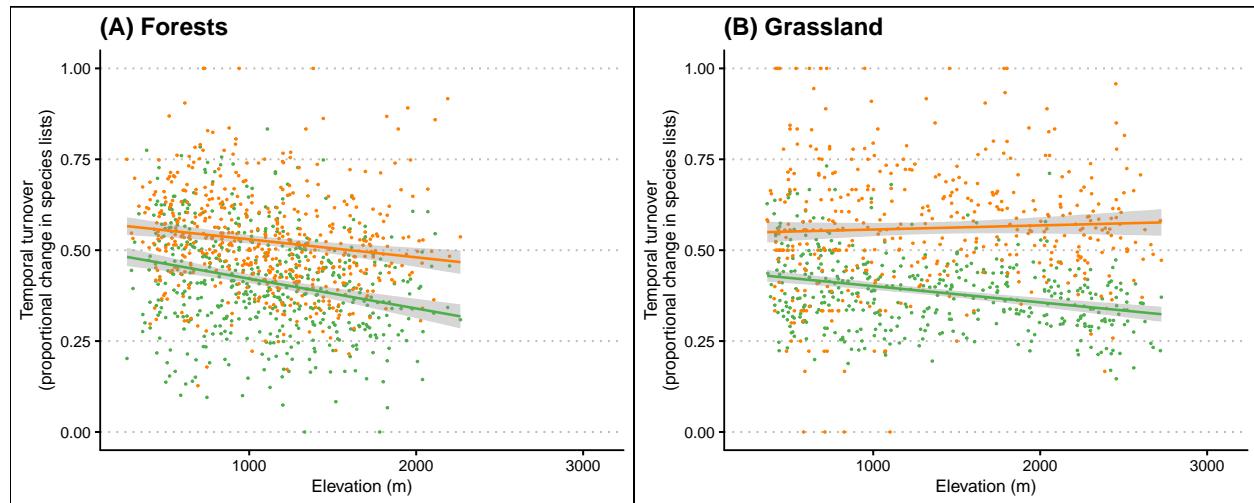


Figure 3: Temporal turnover of bryophytes (orange) and vascular plants (green) along the elevational gradient for plots that were (A) forests and (B) grassland according to the first survey to each plot. Each point represents the proportional difference in the species lists of the surveys at one study plot. The lines represent the regression of temporal turnover on elevation (linear trend) with grey areas indicating the corresponding 95%-credible intervals.

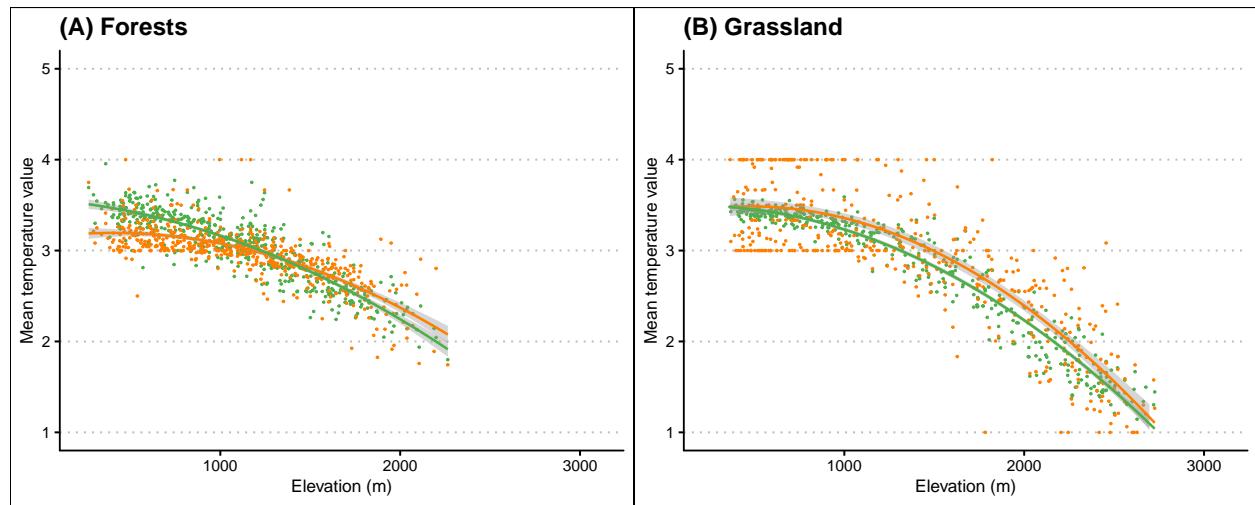


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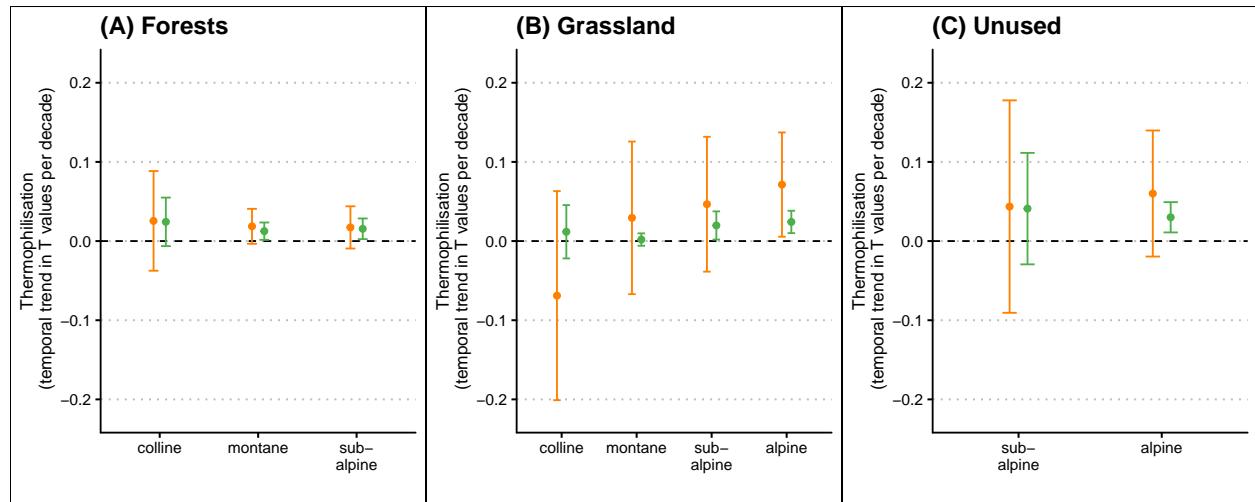


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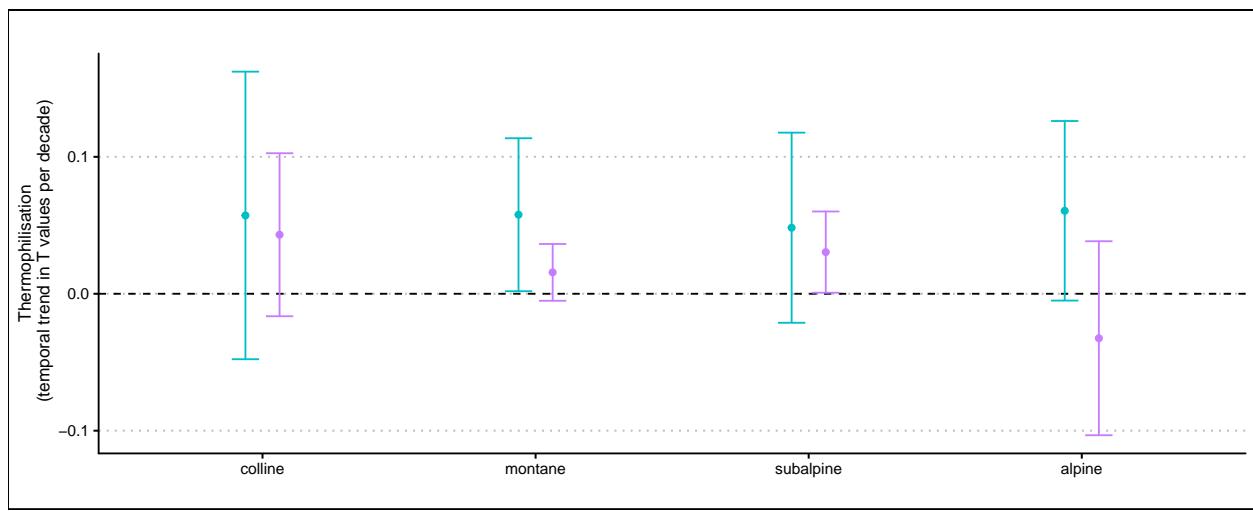


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| 510 1 | Community measures across land use types and elevational zones. Given are the averages 511 from all plots in the respective category. For empty cells no data are available. | 26 |
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Table 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 |