

¹ Major land plant lineages respond differently to climate
² warming

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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 using data from 1174 study sites that span an elevational gradient
¹⁸ from about 200 to 3000m.
- ¹⁹ 3. We found that particularly in grasslands, the proportion of bryophytes among recorded plants (i.e.,
²⁰ bryophytes and vascular plants) strongly increased along the elevational gradient, suggesting that
²¹ bryophytes compared to vascular plants are relatively more diverse in the harsh alpine environments.
²² Presumably due to their higher sensitivity to environmental changes, their shorter live spans and
²³ their higher dispersal capacity, the temporal turnover of bryophyte species was much higher than
²⁴ the temporal turnover of vascular plant species. And as a likely consequence of higher turnover,
²⁵ bryophyte communities reacted faster to climate warming than vascular plant communities, which
²⁶ was evidenced by more pronounced thermophilisation in bryophytes. The link between a faster
²⁷ reaction of communities to climate warming and differences in live spans was further supported by
²⁸ the faster thermophilisation of short-lived bryophytes compared with long-lived bryophytes.

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

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

36 Introduction

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

45 However, range dynamics, or more specifically, how fast species track shifting isotherms vary considerably
46 between taxonomic and functional groups (Parmesan & Yohe, 2003; Essl et al., 2015; Wiens, 2016; MacLean
47 & Beissinger, 2017; Roth, Plattner & Amrhein, 2014). Especially species' life strategies are suggested to
48 reflect their potential to track shifting isotherms. For example, observed range shifts are usually larger and
49 less delayed for species with high dispersal capacities and short life cycles (Angert et al., 2011; Cotto et al.,
50 2017; MacLean & Beissinger, 2017). Furthermore, disturbance intensities that often differ between land use
51 types determine species turnover and thus have impact on thermophilisation processes (Oliver & Morecroft,
52 2014; Stevens et al., 2015).

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

59 2016; Vanneste et al., 2017).

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

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

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

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

92 Materials and methods

93 Study area and field data

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

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

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

120 Because effects of climate warming often differ along elevational gradients (e.g. Bertrand et al., 2011; Roth,
121 Plattner & Amrhein, 2014), we split our dataset according to four elevational zones based on the temperature
122 zonation of Switzerland (Schreiber et al., 1977), that is colline, montane, subalpine and alpine. The distribution
123 of plots and surveys across the elevational zones was as following: 118 plots (405 surveys) in the colline zone,
124 526 plots (1821 surveys) in the montane zone, 247 plots (873 surveys) in the subalpine zone and 283 plots
125 (988 surveys) in the alpine zone.

126 [Figure 1 about here.]

127 Community measures

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

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

¹⁴⁷ **Statistical methods and data accessibility**

¹⁴⁸ For each plot, we calculated the average and the temporal trend of species richness and temperature affinity
¹⁴⁹ based on the repeated surveys per plot. To estimate the temporal trend, we applied for each plot separately
¹⁵⁰ a linear model with species richness or temperature affinity as dependent variable and the year when the
¹⁵¹ survey has been conducted as the predictor variable. The estimated slope (given as change per decade) was
¹⁵² our measure of the temporal trend of species richness or temperature affinity, respectively, that we used in
¹⁵³ subsequent analyses.

¹⁵⁴ All analyses were done with the software R (R Core Team, 2019). We measured the temporal turnover as the
¹⁵⁵ proportion of species that differed between two time points, that is the number of species that were either only
¹⁵⁶ observed during first or only during the second survey at a given plot divided by the total number of species
¹⁵⁷ recorded during these two surveys. To estimate the temporal turnover of species we used the R package ‘simba’
¹⁵⁸ (Jurasinski & Vroni Retzer, 2012). Data and R Markdown documents to fully reproduce this manuscript
¹⁵⁹ including figures and tables are provided at <https://github.com/TobiasRoth/moss-plant-comparison>. An R
¹⁶⁰ Markdown document is written in markdown (plain text format) and contains chunks of embedded R code to
¹⁶¹ produce the figures and tables (Xie, Allaire & Grolemund, 2018). Raw data for analyses are provided in the
¹⁶² folder “data-raw” and the folder “R” contains the R-Script that was used to export the data from the BDM
¹⁶³ database. The folder “div” contains a list of all the R packages (including version number) that were in the
¹⁶⁴ workspace when the manuscript was rendered. The final version of the repository will be archived at Zenodo
¹⁶⁵ (<https://zenodo.org/>).

¹⁶⁶ **Results**

¹⁶⁷ [Table 1 about here.]

¹⁶⁸ **Species richness**

¹⁶⁹ Across all surveys, 539 bryophyte species and 1212 vascular plant species were recorded. The mean (\pm SD)
¹⁷⁰ species richness per plot was 12.87 (\pm 8.96) species for bryophytes and 27.34 (\pm 15.17) species for vascular
¹⁷¹ plants. However, species richness differed considerably between land use types, elevational zones and the two
¹⁷² land plant lineages (Table 1). For the three land use types the average species richness of vascular plants was
¹⁷³ higher than the respective species richness of bryophytes: the difference was 5.60 species (p-value based on a

¹⁷⁴ paired t-test: <0.001) in forests, 26.81 species (p-value: <0.001) in grasslands, and 7.37 species (p-value:
¹⁷⁵ <0.001) in unused open areas.

¹⁷⁶ In forests and grassland, where study plots spanned a large proportion of the elevational gradient, the species
¹⁷⁷ richness of bryophytes and vascular plants both increased from low to intermediate elevations and tended
¹⁷⁸ to decrease again at higher elevations (i.e., a mid-elevational peak, Fig. 2). This mid-elevational peak was
¹⁷⁹ particularly evident for vascular plants in grassland and less obvious to absent for vascular plants in forests
¹⁸⁰ and for bryophytes in both land use types. Consequently, in grassland the proportion of bryophytes (i.e., the
¹⁸¹ number of bryophytes divided by the total number of bryophytes and vascular plants) strongly increased
¹⁸² with elevation (Binomial-GLMM with elevation as predictor variable and site ID as random effect; slope of
¹⁸³ elevation at the logit-scale: 0.17, p-value: <0.001). This increase in the proportion of bryophyte species was
¹⁸⁴ almost absent in forests (slope of elevation at the logit-scale: 0.02, p-value: 0.118).

¹⁸⁵ [Figure 2 about here.]

¹⁸⁶ In forests, the temporal trend of species richness between 2001 and 2018 was in favour of bryophytes (Fig. 3):
¹⁸⁷ while for bryophytes the species richness increased by 5.16% (95%-credible interval: 1.92-8.40) per decade, the
¹⁸⁸ species richness of vascular plants decreased on the same plots and period by -1.35% (95%-credible interval:
¹⁸⁹ -4.32-1.62). In contrast, however, the temporal trend in species richness in grassland and unused open areas
¹⁹⁰ was in favour of vascular plants, which was particularly the case at the alpine zone (Fig. 3). In grassland
¹⁹¹ the species richness decreased in bryophytes by -5.15% (95%-credible interval: -11.30-1.01) and increased
¹⁹² in vascular plants by 0.73% (95%-credible interval: -1.15-2.61). Also in unused open areas, the increase in
¹⁹³ species richness was less strong in bryophytes than in vascular plants, with an increase of 6.10% (95%-credible
¹⁹⁴ interval: -2.79-14.98) in the former and an increase of 13.65% (95%-credible interval: 7.00-20.29) in the latter.

¹⁹⁵ [Figure 3 about here.]

¹⁹⁶ Temporal turnover

¹⁹⁷ The mean temporal turnover across all sites was higher for bryophytes than for vascular plants (mean ±
¹⁹⁸ SD for bryophytes: 0.55 ± 0.15 ; vascular plants: 0.40 ± 0.13 ; p-value based on Wilcoxon signed rank test:
¹⁹⁹ <0.001). The pattern how the temporal turnover of bryophytes changed along the elevational gradient differed
²⁰⁰ between land use types (Ancova with an interaction between land use types and elevation; F-value: 10.94;
²⁰¹ p-value: 0.001): while it decreased with elevation in forests, it tended to increase in grassland (Fig. 4). For
²⁰² vascular plants in contrast, the temporal turnover decreased from low to high elevations both in forests and
²⁰³ in grassland with only slight differences between the two land use types (Ancova with an interaction between

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

205 [Figure 4 about here.]

206 Temperature affinities and termophilisation

207 While in forests the mean temperature value of vascular plants was higher than that of bryophytes, the
208 opposite was the case for grassland and unused open areas. The difference in temperature affinity of vascular
209 plants minus the temperature affinity of bryophytes was 0.07 (p-value based on a paired t-test: <0.001) in
210 forests, -0.12 (p-value: <0.001) in grassland, and -0.30 (p-value: <0.001) in unused open areas. In grassland,
211 bryophyte communities had slightly higher temperature affinities along the entire gradient (Fig. 5). In forests,
212 however, at low elevation the temperature affinities of vascular plant communities were higher than the
213 temperature affinities of bryophyte communities whereas at higher elevations the pattern was inversed (Fig.
214 5).

215 [Figure 5 about here.]

216 Between 2001 and 2018, for both bryophyte and vascular plant communities the mean temperature value of
217 recorded species increased over time, indicating termophilisation of species communities. Termophilisation was
218 evident in all three land use types with a slightly stronger but at the same time more variable termophilisation
219 in bryophytes: in forests the average termophilisation was 0.017 (p-value based on a one sample t-test to test
220 for no termophilisation: 0.072) for bryophytes and 0.016 (p-value: <0.001) for vascular plants, in grassland
221 the average termophilisation was 0.038 (p-value: 0.102) for bryophytes and 0.012 (p-value: 0.001) for vascular
222 plants, and in unused open areas the average termophilisation was 0.059 (p-value: 0.115) for bryophytes and
223 0.031 (p-value: 0.001) for vascular plants. This tendency for higher but more variable termophilisation in
224 bryophyte communities compared to vascular plant communities was evident for all three land use types at
225 the entire elevational gradient (Fig. 6).

226 [Figure 6 about here.]

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

233 pronounced at higher elevations (Fig. 7). However, there might be a slight bias as short-lived species tend to
234 be more cryophilous (37% of all short-lived species have a T-value of 1 or 2) than long-lived species (only
235 30% have a T-value of 1 or 2). With increasing elevation, the proportion of short-lived species in bryophyte
236 communities is increasing, except for grassland, with a peak in lowlands (mainly due to communities that
237 consist of short-lived species only, presumably in disturbed habitats).

238 [Figure 7 about here.]

239 Discussion

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

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

263 persistent communities which have high resilience to vascular plant invasion (Dullinger, Dirnböck & Grabherr,
264 2004; Mark & Wilson, 2005; Grabherr, Gottfried & Pauli, 2010; Gottfried et al., 2012). Beside resilience,
265 range shifts of vascular plants towards higher elevations depend on the availability of soil. The desiccation
266 tolerance and nutrient uptake mechanisms of bryophytes, however, make them much less dependent on
267 a substrate that serves as water storage and source of nutrients (Proctor, 2009). Finally, vascular plant
268 growth and expansion at high elevations is slowed down by low temperatures, short vegetation periods and
269 positive net photosynthesis being mostly limited to the summer season (Körner, 2003; Gottfried et al., 2012).
270 Bryophytes can maintain positive net photosynthesis rates at very low temperatures (e.g., down to -10 °C in
271 *Pellia epiphylla*, a common liverwort in the study region; Pihakaski & Pihakaski, 1979) and are opportunistic
272 in their assimilation strategy. Once environmental conditions are favorable they can reassume positive net
273 photosynthesis within short (often within minutes) time intervals throughout the year (Proctor, 2009, 2011).
274 Higher termophilisation rates of bryophytes might also be due to higher extinction rates of cold-dwelling
275 bryophyte species as compared to cold-dwelling vascular plant species. Many high mountain bryophyte species
276 typically grow in the coldest microsites (e.g., in gaps between rocks on northern slopes) and another set of
277 species depends on long snow cover (Limprecht, 1890, 1895; Amann, 1928; Köckinger, 2017). These species
278 may not find suitable refugia at the same elevational level, and, in the European Alps they include endemics
279 known from a few localities only (e.g Hallingbäck et al., 2019; Schröck et al., 2019a,b). They are especially
280 threatened by climate warming (Kohler, Wehrli & Jurek, 2014; He, He & Hyvönen, 2016).
281 For vascular plants, our results expand findings of Rumpf et al. (2018) at the community level. They
282 examined range shifts of 183 vascular plant species in the Alps using data from vegetation relevés located
283 mostly between 1500 and 2700 m a.s.l., thus, roughly encompassing the subalpine and alpine zone in our
284 study. They observed decreased range size at higher elevations. The more delayed responses among alpine
285 vascular plants is supported by the decreasing temporal turnover rate of vascular plants in grassland (Fig. 4)
286 and by growing evidence that the extinction of mountain top species may be delayed by their survival in
287 colder microsite refugia (e.g. Scherrer & Körner, 2011; Maclean et al., 2015; Giezendanner et al., 2019).
288 Bryophytes are usually more diverse in the harsh alpine environments (Bruun et al., 2006; Proctor, 2011;
289 Turetsky et al., 2012; Mateo et al., 2016). Indeed, in grassland we found that the proportion of bryophytes
290 among recorded plants strongly increased along the elevational gradient. If we assume that climate warming
291 in general leads to a less harsh environments, which might be the case in regions such as Switzerland where
292 severe droughts are rare, we would expect that the proportion of bryophytes among recorded plants would
293 increase over time. This is what we found for grassland where the species richness of bryophytes tent to
294 decrease and the species richness of vascular plants increased between 2001 and 2018. While it is often

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

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

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

315 Acknowledgments

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

320 References

321 Amann J. 1928. *Bryogeographie de la Suisse*. Zürich: Fretz Frères S. A.

- 322 Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict
323 recent shifts at expanding range edges? *Ecology Letters* 14:677–689. DOI: 10.1111/j.1461-0248.2011.01620.x.
- 324 Becker Scarpitta A, Bardat J, Lalanne A, Vellend M. 2017. Long-term community change: bryophytes are
325 more responsive than vascular plants to nitrogen deposition and warming. *Journal of Vegetation Science*
326 28:1220–1229. DOI: 10.1111/jvs.12579.
- 327 Bertrand R, Lenoir J, Piedallu C, Dillon GR, De Ruffray P, Vidal C, Pierrat JC, Gégout JC. 2011. Changes
328 in plant community composition lag behind climate warming in lowland forests. *Nature* 479:517–520. DOI:
329 10.1038/nature10548.
- 330 Biodiversity IS-PP on, Ecosystem Services I. 2019. Summary for policymakers of the global assessment report
331 on biodiversity and ecosystem services. DOI: 10.5281/zenodo.3553579.
- 332 Bruun HH, Moen J, Virtanen R, Grytnes J, Oksanen L, Angerbjörn A. 2006. Effects of altitude and
333 topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of*
334 *Vegetation Science* 17:37–46. DOI: 10.1111/j.1654-1103.2006.tb02421.x.
- 335 Bühl C, Roth T. 2011. Spread of common species results in local-scale floristic homogenization in grassland
336 of Switzerland. *Diversity and Distributions* 17:1089–1098. DOI: 10.1111/j.1472-4642.2011.00799.x.
- 337 Büttner G, Feranec J, Jaffrain G, Mari L, Maucha G, Soukup T. 2004. The CORINE land cover 2000 project.
338 *EARSeL eProceedings* 3:331–346.
- 339 CH2018. 2018. *CH2018 – Climate Scenarios for Switzerland, Technical Report*. Zürich: National Centre for
340 Climate Services.
- 341 Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with
342 high levels of climate warming. *Science* 333:1024–1026. DOI: 10.1126/science.1206432.
- 343 Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology and*
344 *Evolution* 28:482–488. DOI: 10.1016/j.tree.2013.04.003.
- 345 Cotto O, Wessely J, Georges D, Klonner G, Schmid M, Dullinger S, Thuiller W, Guillaume F. 2017. A dynamic
346 eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications*
347 8. DOI: 10.1038/ncomms15399.
- 348 Devictor V, Julliard R, Couvet D, Jiguet F. 2008. Birds are tracking climate warming, but not fast enough.
349 *Proceedings of the Royal Society B: Biological Sciences* 275:2743–2748.
- 350 Dierßen K. 2002. Distribution, ecological amplitude and phytosociological-characterization of european

- 351 bryophytes. *Nova Hedwigia* 74.
- 352 Dobrowski SZ, Parks SA. 2016. Climate change velocity underestimates climate change exposure in moun-
353 tainous regions. *Nature Communications* 7:1–8. DOI: 10.1038/ncomms12349.
- 354 Dorji T, Totland Ø, Moe SR, Hopping KA, Pan J, Klein JA. 2013. Plant functional traits mediate reproductive
355 phenology and success in response to experimental warming and snow addition in Tibet. *Global Change
356 Biology* 19:459–472. DOI: 10.1111/gcb.12059.
- 357 Dullinger S, Dirnböck T, Grabherr G. 2004. Modelling climate change-driven treeline shifts: Relative effects
358 of temperature increase, dispersal and invasibility. *Journal of Ecology* 92:241–252. DOI: 10.1111/j.0022-
359 0477.2004.00872.x.
- 360 During HJ. 1979. Life strategies of bryophytes : A preliminary review. *Lindbergia* 5:2–18.
- 361 During HJ. 1992. Ecological classification of bryophytes and lichens. In: Bates JW, Farmer AM eds.
362 *Bryophytes and lichens in a changing environment*. Oxford: Clarendon Press, 1–31.
- 363 Ellenberg H. 1974. Zeigerwerte der Gefässpflanzen Mitteleuropas.
- 364 Engler R, Randin CF, Vittoz P, Czáká T, Beniston M, Zimmermann NE, Guisan A. 2009. Predicting future
365 distributions of mountain plants under climate change: Does dispersal capacity matter? *Ecography* 32:34–45.
366 DOI: 10.1111/j.1600-0587.2009.05789.x.
- 367 Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, Wilson JRU, Richardson DM. 2015. Delayed biodiversity
368 change: No time to waste. *Trends in Ecology and Evolution* 30:375–378. DOI: 10.1016/j.tree.2015.05.002.
- 369 Frahm J-P. 2007. Diversity, dispersal and biogeography of bryophytes (mosses). *Biodiversity and Conservation*
370 17:277–284.
- 371 Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL. 2018. Expanding, shifting and shrinking: The impact
372 of global warming on species' elevational distributions. *Global Ecology and Biogeography* 27:1268–1276. DOI:
373 10.1111/geb.12774.
- 374 Giezendanner J, Bertuzzo E, Pasetto D, Guisan A, Rinaldo A. 2019. A minimalist model of extinction and
375 range dynamics of virtual mountain species driven by warming temperatures. *PLoS ONE* 14:1–19. DOI:
376 10.1371/journal.pone.0213775.
- 377 Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer
378 B, Fernández Calzado MR, Kazakis G, Krajčí J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P,
379 Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A,

- 380 Theurillat JP, Tomaselli M, Villar L, Vittoz P, Vogiatzakis I, Grabherr G. 2012. Continent-wide response of
381 mountain vegetation to climate change. *Nature Climate Change* 2:111–115. DOI: 10.1038/nclimate1329.
- 382 Grabherr G, Gottfried M, Pauli H. 2010. Climate change impacts in alpine environments. *Geography Compass*
383 4:1133–1153. DOI: 10.1111/j.1749-8198.2010.00356.x.
- 384 Greaver TL, Clark CM, Compton JE, Vallano D, Talhelm AF, Weaver CP, Band LE, Baron JS, Davidson
385 EA, Tague CL, Felker-Quinn E, Lynch JA, Herrick JD, Liu L, Goodale CL, Novak KJ, Haeuber RA. 2016.
386 Key ecological responses to nitrogen are altered by climate change. *Nature Climate Change* 6:836–843. DOI:
387 10.1038/nclimate3088.
- 388 Hallingback T, Tan BC. 2014. Past and present activities and future strategy of bryophyte conservation.
389 *Phytotaxa* 9:266–274. DOI: 10.11646/phytotaxa.9.1.15.
- 390 Hallingbäck T, Hedenäs L, Huttunen S, Ignatov M, Ingerpuu N, Konstantinova N, Syrjänen K, Söderström L.
391 2019. Orthothecium chryseon. *The IUCN Red List of Threatened Species* e.T8828059.
- 392 He X, He KS, Hyvönen J. 2016. Will bryophytes survive in a warming world? *Perspectives in Plant Ecology,
393 Evolution and Systematics* 19:49–60. DOI: 10.1016/j.ppees.2016.02.005.
- 394 Henry P-Y, Lengyel S, Nowicki P, Julliard R, Clobert J, Čelik T, Gruber B, Schmeller DS, Babij V, Henle
395 K. 2008. Integrating ongoing biodiversity monitoring: Potential benefits and methods. *Biodiversity and
396 conservation* 17:3357–3382.
- 397 Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp
398 D, Larsen S, others. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for
399 conservation and monitoring. *Journal of Applied Ecology* 55:169–184.
- 400 Jurasinski G, Vroni Retzer. 2012. *Simba: A collection of functions for similarity analysis of vegetation data*.
- 401 Kohler T, Wehrli A, Jurek M. 2014. *MOUNTAINS AND CLIMATE CHANGE: A GLOBAL CONCERN. Sustainable Mountain
402 Development Series. Bern*, Centre for Development; Environment (CDE), Swiss Agency for Development;
403 Cooperation (SDC); Geographica Bernensia. DOI: 10.1017/cbo9781139023924.013.
- 404 Köckinger H. 2017. *Die Horn- und Lebermoose Österreichs (Anthocerotophyta und Marchantiophyta) Catalogus
405 Flora Austriae, Teil II, 2. Heft*. Wien: Österreichische Akademie der Wissenschaften.
- 406 Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin, Heidelberg:
407 Springer.
- 408 Landolt E. 1977. Ökologische zeigerwerte zur Schweizer Flora.

- 409 Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schwein-
410 gruber F, Theurillat J-P, others. 2010. *Flora indicativa. Ecological indicator values and biological attributes of*
411 *the flora of switzerland and the alps.* Haupt Verlag.
- 412 Lenoir J, Svenning JC. 2015. Climate-related range shifts - a global multidimensional synthesis and new
413 research directions. *Ecography* 38:15–28. DOI: 10.1111/ecog.00967.
- 414 Limprecht KG. 1890. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Abtheilung: Sphagnaceae,
415 Andreaceae, Archidiaceae, Bryineae (Cleistocarpace, Stegorcarpace [Acro- carpace]). In: *Dr. L. Rabehorsts*
416 *kryptogamen-flora von deutschland, oesterreich und der schweiz. Zweite auflage. Vierter band.* Leipzig:
417 Eduard Kummer,
- 418 Limprecht KG. 1895. *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. II. Abteilung: Bryineae.*
419 Leipzig: Eduard Kummer.
- 420 Lindo Z, Gonzalez A. 2010. The bryosphere: An integral and influential component of the Earth's biosphere.
421 *Ecosystems* 13:612–627. DOI: 10.1007/s10021-010-9336-3.
- 422 MacLean SA, Beissinger SR. 2017. Species' traits as predictors of range shifts under contemporary climate
423 change: A review and meta-analysis. *Global Change Biology* 23:4094–4105. DOI: 10.1111/gcb.13736.
- 424 Maclean IMD, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ. 2015. Microclimates buffer the responses of plant
425 communities to climate change. *Global Ecology and Biogeography* 24:1340–1350. DOI: 10.1111/geb.12359.
- 426 Mark AF, Wilson JB. 2005. Tempo and mode of vegetation dynamics over 50 years in a New Zealand
427 alpine cushion/tussock community. *Journal of Vegetation Science* 16:227–236. DOI: 10.1111/j.1654-
428 1103.2005.tb02360.x.
- 429 Martin G, Devictor V, Motard E, Machon N, Porcher E. 2019. Short-term climate-induced change in french
430 plant communities. *Biology letters* 15:20190280.
- 431 Mateo RG, Broennimann O, Normand S, Petitpierre B, Araújo MB, Svenning JC, Baselga A, Fernández-
432 González F, Gómez-Rubio V, Muñoz J, Suarez GM, Luoto M, Guisan A, Vanderpoorten A. 2016. The mossy
433 north: An inverse latitudinal diversity gradient in European bryophytes. *Scientific Reports* 6:1–9. DOI:
434 10.1038/srep25546.
- 435 Medina NG, Draper I, Lara F. 2011. Biogeography of mosses and allies: Does size matter? In: *Biogeography*
436 *of microscopic organisms: Is everything small everywhere?* Cambridge: Cambridge University Press, 209–233.
437 DOI: 10.1017/CBO9780511974878.012.

- ⁴³⁸ MeteoSwiss. 2019. Area-mean temperatures of Switzerland. DOI: 10.18751/Climate/Timeseries/CHTM/1.1.
- ⁴³⁹ Ohmura A. 2012. Enhanced temperature variability in high-altitude climate change. *Theoretical and Applied*
- ⁴⁴⁰ *Climatology* 110:499–508. DOI: 10.1007/s00704-012-0687-x.
- ⁴⁴¹ Oliver TH, Morecroft MD. 2014. Interactions between climate change and land use change on biodiversity:
- ⁴⁴² Attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change* 5:317–335.
- ⁴⁴³ DOI: 10.1002/wcc.271.
- ⁴⁴⁴ Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change. *Nature* 421:37–42. DOI:
- ⁴⁴⁵ 10.1038/nature01286.
- ⁴⁴⁶ Peñuelas J, Sardans J, Estiarte M, Ogaya R, Carnicer J, Coll M, Barbata A, Rivas-Ubach A, Llusià J,
- ⁴⁴⁷ Garbulsky M. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere.
- ⁴⁴⁸ *Global change biology* 19:2303–2338.
- ⁴⁴⁹ Pihakaski K, Pihakaski S. 1979. Effects of chilling on the ultrastructure and net photosynthesis of *Pellia*
- ⁴⁵⁰ *epiphylla*. *Annals of Botany* 43:773–781. DOI: 10.1093/oxfordjournals.aob.a085692.
- ⁴⁵¹ Plattner M, Birrer S, Weber D. 2004. Data quality in monitoring plant species richness in Switzerland.
- ⁴⁵² *Community Ecology* 5:135–143. DOI: 10.1556/comec.5.2004.1.13.
- ⁴⁵³ Proctor MCF. 2009. Physiological ecology. In: Goffinet B, Shaw J eds. *Bryophyte biology*. Cambridge:
- ⁴⁵⁴ Cambridge University Press, 237–268.
- ⁴⁵⁵ Proctor MCF. 2011. Climatic responses and limits of bryophytes : Comparisons and contrasts with vascular
- ⁴⁵⁶ plants. In: Tuba Z, Slack NG, Stark LR eds. *Bryophyte ecology and climate change*. Cambridge: Cambridge
- ⁴⁵⁷ University Press, 35–54.
- ⁴⁵⁸ Rangwala I, Sinsky E, Miller JR. 2013. Amplified warming projections for high altitude regions of the
- ⁴⁵⁹ northern hemisphere mid-latitudes from CMIP5 models. *Environmental Research Letters* 8:1–9. DOI:
- ⁴⁶⁰ 10.1088/1748-9326/8/2/024040.
- ⁴⁶¹ R Core Team. 2019. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation
- ⁴⁶² for Statistical Computing.
- ⁴⁶³ Rixen C, Wipf S. 2018. Non-equilibrium in Alpine Plant Assemblages: Shifts in Europe’s Summit Floras. In:
- ⁴⁶⁴ Catalan J, Ninot JM, Aniz MM eds. *Monitoring global change in high mountains*. Cham: Springer, 285–303.
- ⁴⁶⁵ Roth T, Kohli L, Rihm B, Achermann B. 2013. Nitrogen deposition is negatively related to species richness and
- ⁴⁶⁶ species composition of vascular plants and bryophytes in Swiss mountain grassland. *Agriculture Ecosystems*

- 467 *& Environment* 178:121–126. DOI: 10.1016/j.agee.2013.07.002.
- 468 Roth T, Plattner M, Amrhein V. 2014. Plants Birds and Butterflies: Short-Term Responses of Species
469 Communities to Climate Warming Vary by Taxon and with Altitude. *PLoS ONE* 9:e82490. DOI: 10.1371/jour-
470 nal.pone.0082490.
- 471 Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger
472 S. 2018. Range dynamics of mountain plants decrease with elevation. *PNAS* 115:1848–1853. DOI:
473 10.1073/pnas.1713936115.
- 474 Scherrer D, Körner C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant
475 diversity against climate warming. *Journal of biogeography* 38:406–416.
- 476 Schlesinger WH. 2009. On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of
477 Sciences of the United States of America* 106:203–208. DOI: 10.1073/pnas.0810193105.
- 478 Schreiber K, Kuhn N, Hug C, Häberli R, Schreiber C, Zeh W, Lautenschlager S. 1977. Wärmegliederung der
479 Schweiz. *Berne: Federal Department of Justice and Police* 69.
- 480 Schröck C, Bisang I, Caspari S, Hedenäs L, Hodgetts N, Kiebacher T, Kučera J, Štefánuť S, Vana J. 2019a.
481 Schistidium grande. *The IUCN Red List of Threatened Species* e.T8584594:1–7.
- 482 Schröck C, Bisang I, Caspari S, Hedenäs L, Hodgetts N, Kiebacher T, Kučera J, Štefánuť S, Vana J. 2019b.
483 Racomitrium nivale. *The IUCN Red List of Threatened Species* e.T8584547:1–7.
- 484 Shi Z, Sherry R, Xu X, Hararuk O, Souza L, Jiang L, Xia J, Liang J, Luo Y. 2015. Evidence for long-term
485 shift in plant community composition under decadal experimental warming. *Journal of Ecology* 103:1131–1140.
486 DOI: 10.1111/1365-2745.12449.
- 487 Soudzilovskaia NA, Elumeeva TG, Onipchenko VG, Shidakov II, Salpagarova FS, Khubiev AB, Tekeev
488 DK, Cornelissen JHC. 2013. Functional traits predict relationship between plant abundance dynamic and
489 long-term climate warming. *PNAS* 110:18180–18184. DOI: 10.1073/pnas.1310700110.
- 490 Stevens JT, Safford HD, Harrison S, Latimer AM. 2015. Forest disturbance accelerates thermophilization of
491 understory plant communities. *Journal of Ecology* 103:1253–1263.
- 492 Szyja M, Menezes A, Oliveira FD, Leal I, Tabarelli M, Büdel B, Wirth R. 2019. Neglected but potent dry
493 forest players: Ecological role and ecosystem service provision of biological soil crusts in the human-modified
494 Caatinga. *Frontiers in Ecology and Evolution* in press. DOI: doi: 10.3389/fevo.2019.00482.
- 495 Turetsky MR, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire AD, Tuittila ES. 2012. The

- 496 resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196:49–67. DOI:
497 10.1111/j.1469-8137.2012.04254.x.
- 498 Vanneste T, Michelsen O, Graae BJ, Kyrkjeeide MO, Holien H, Hassel K, Lindmo S, Kapás RE, De Frenne P.
499 2017. Impact of climate change on alpine vegetation of mountain summits in Norway. *Ecological Research*
500 32:579–593. DOI: 10.1007/s11284-017-1472-1.
- 501 Weber D, Hintermann U, Zangger A. 2004. Scale and trends in species richness: considerations for monitoring
502 biological diversity for political purposes. *Global Ecology and Biogeography* 13:97–104. DOI: 10.1111/j.1466-
503 882x.2004.00078.x.
- 504 Wiens JJ. 2016. Climate-related local extinctions are already widespread among plant and animal species.
505 *PLoS Biology* 14:1–18. DOI: 10.1371/journal.pbio.2001104.
- 506 Xie Y, Allaire J, Grolemund G. 2018. *R markdown: The definitive guide*. CRC Press.
- 507 Zhang T, Guo R, Gao S, Guo J, Sun W. 2015. Responses of plant community composition and biomass
508 production to warming and nitrogen deposition in a temperate meadow ecosystem. *PLoS ONE* 10:1–16. DOI:
509 10.1371/journal.pone.0123160.

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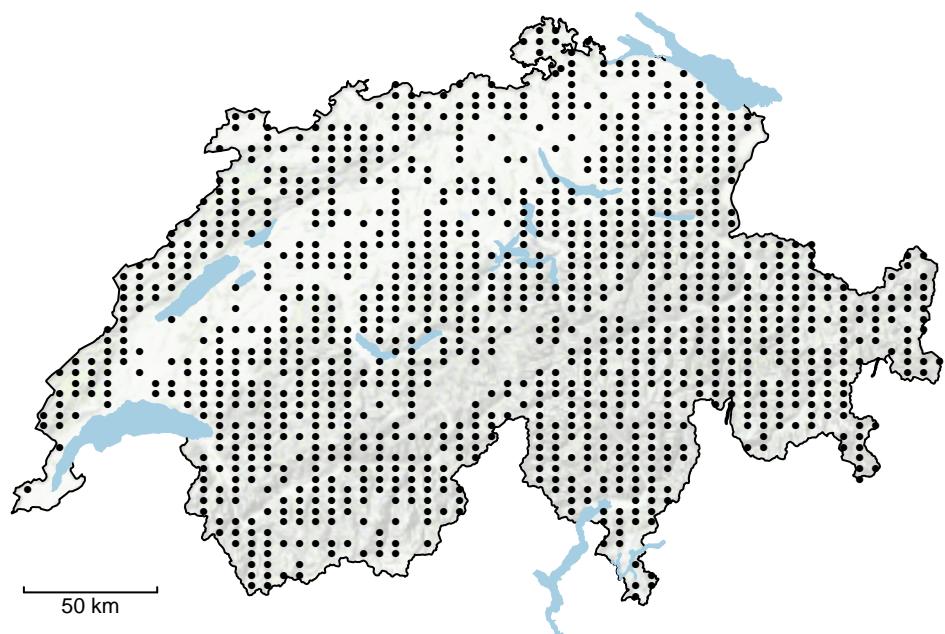


Figure 1: Distribution of the study plots across Switzerland. Only plots with land use types grassland, forest and unused open areas (in the subalpine and alpine zone) were considered. Background data source: Federal Office of Topography swisstopo.

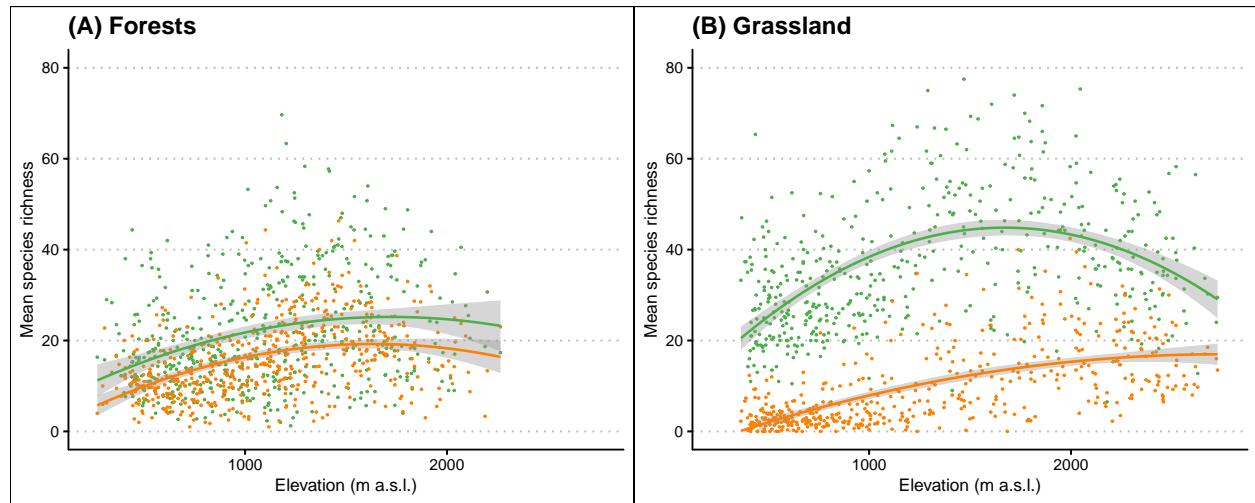


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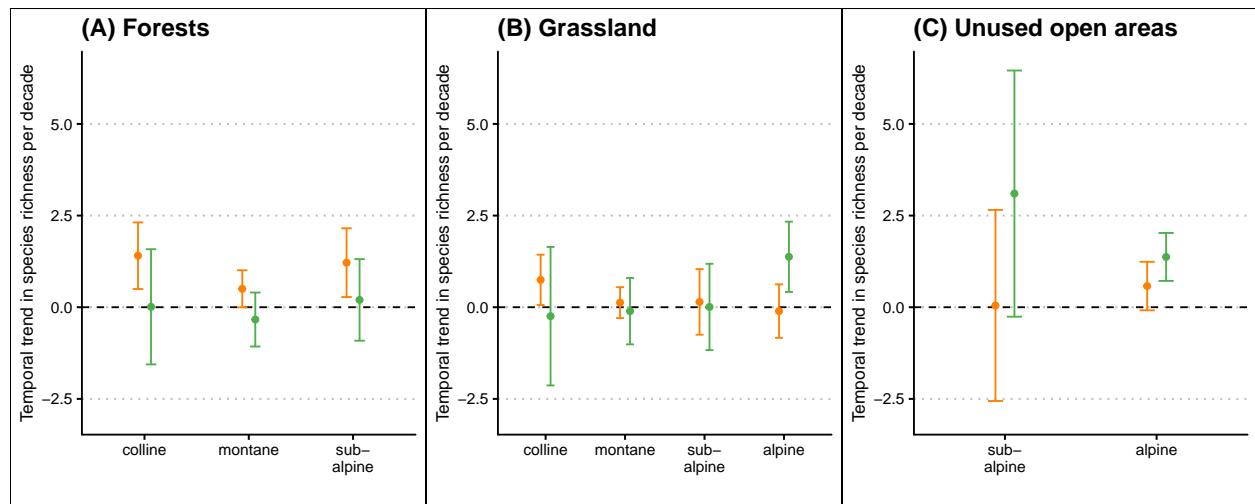


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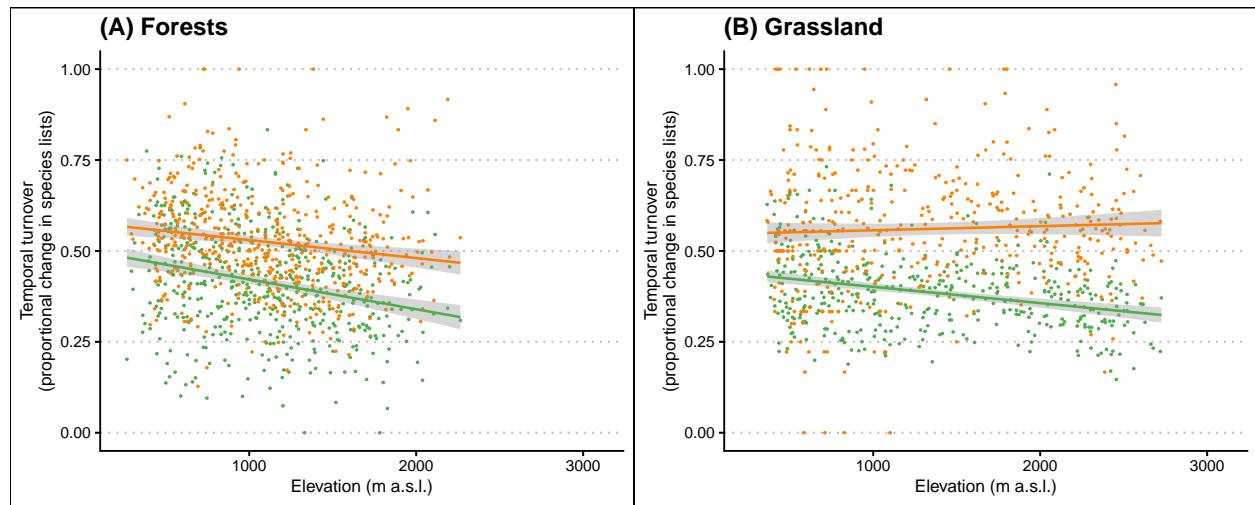


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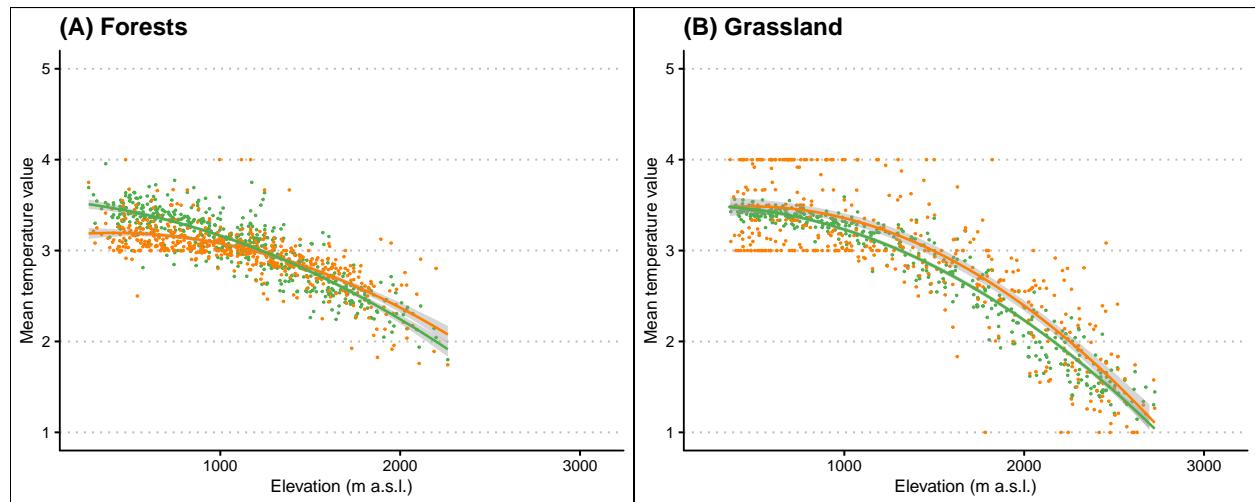


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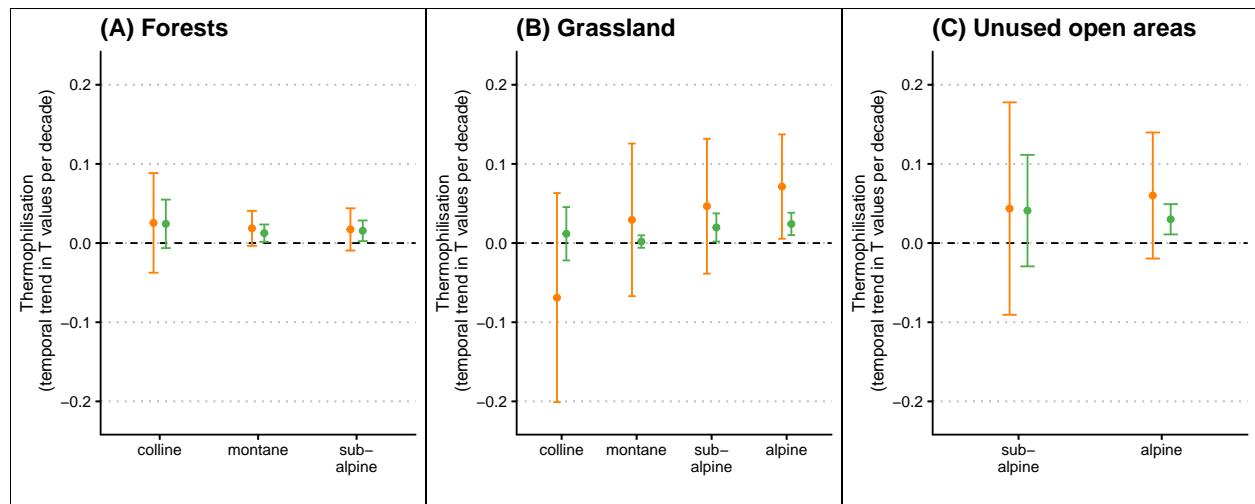


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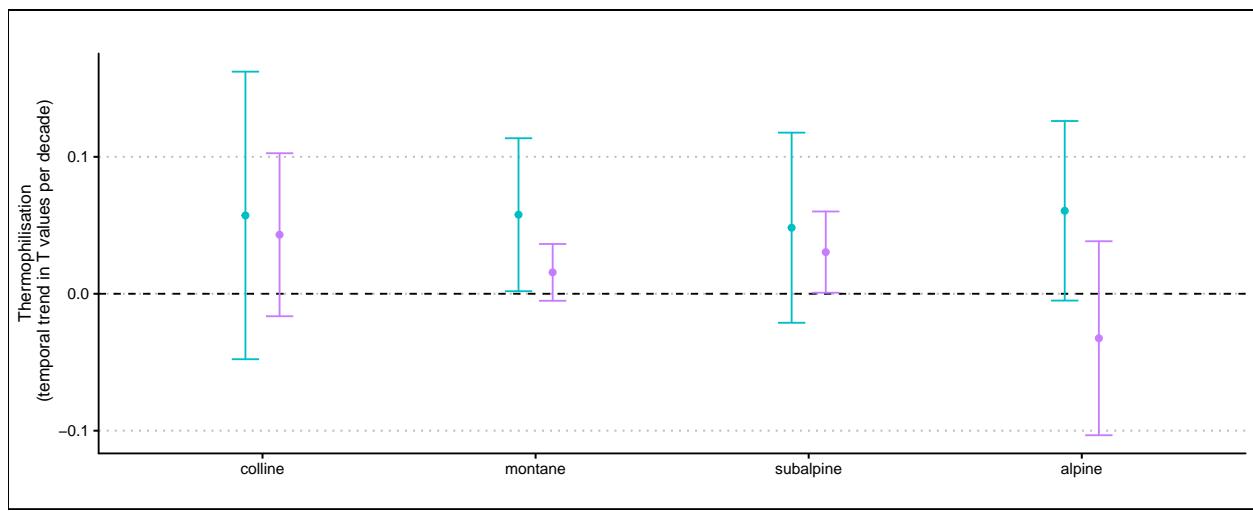


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| ⁵⁴⁰ | 1 | Community measures across land use types and elevational zones. Given are the averages from all plots in the respective category. For empty cells no data are available. | 28 |
| ⁵⁴¹ | | | |

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 |