

Threatened and specialist species suffer from increased wood cover and productivity in Swiss steppes

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Abstract

In Switzerland, steppe vegetation is restricted to dry soils in inner alpine dry valleys in the West (Valais) and the East (Grisons). They harbour many specialist and threatened species. In 2011, a long-term program was established to monitor changes in Swiss habitats of national importance. Here, we studied patterns of vascular plant diversity in a subset of 148 steppe plots of 10 m² from this program. Plots were either grazed or abandoned. On average, we found 23.3 species per plot. The proportion of steppe specialists and of threatened species out of the total species richness was 29.3% and 12.2%, respectively. The total number of species increased with elevation and peaked at intermediate productivity levels. In contrast, the proportion of threatened and steppe specialist species was generally negatively related to higher productivity and wood cover – two factors considered as indicators of habitat degradation. Abandonment vs. pasture had no effects on total species richness. Productivity was positively related to ecological indicator values for moisture, competition and ruderality, as well as the community mean traits of plant height and specific leaf area, but negatively with the indicator value for light. Similarly, wood cover was positively associated with higher ecological indicator values for productivity, moisture and competition, as well as the community mean trait of plant height, but negatively with the indicator value for light and ruderality. The negative response of threatened and steppe specialist vascular plant species to habitat degrading factors suggests their proportional richness to be a better indicator of habitat quality than the total species richness. We conclude that management regimes which guarantee low productivity and wood cover and avoid intensification by fertilization and irrigation are essential for the conservation of steppe habitats. Beside periodic clearing of woody species, low-intensity grazing might prevent shrub encroachment.

Keywords: Elevational gradient, ecological indicator values, functional traits, remote sensing, steppe vegetation, vascular plant diversity

1. Introduction

Since 1945, approximately 95 % of the dry grassland area in Switzerland has been lost, mainly due to land-use intensification and abandonment (Lachat et al., 2010) and habitat quality is still decreasing particularly in higher elevated areas (Boch et al., 2019). These major drivers of habitat degradation and loss cause a general decline in biodiversity and are responsible for the threatening of a large number of species (Visconti et al., 2018). In Switzerland, 35 % of about 350 dry grassland species are considered threatened and many formerly unthreatened species have recently been re-classified as potentially threatened (Bornand et al., 2016).

To protect its biodiversity as well as to prevent further habitat loss and the extinction of endangered species, Switzerland designated about 7000 sites of national importance since the early 1990s. These nationally important sites are legally protected and include fens, bogs, dry grasslands, riparian areas, flood plains and amphibian breeding sites. The dry grasslands of national importance comprise 3631 sites and consist of meadows and pastures of various vegetation types, representing about 0.5% of the country's land area. Between 1995 and 2006 predefined key species were surveyed in more than 10,000 vegetation plots within these sites. On the basis of this inventory, conservation objectives and measures were defined. To maintain the habitat quality and the typical species composition of managed sites (e.g. dry grasslands and fens), land owners and farmers are under contract with the particular canton, including limitation of intensification, e.g. low-intensity grazing and no fertilizer use is compulsory (Eggenberg et al., 2001; BAFU, 2017a, b, c).

In Switzerland, steppe vegetation is restricted to dry soils on sediment deposits, moraine tracts or rocks and grows mainly on steep southern-facing slopes in inner alpine dry valleys in the West (Canton Valais) and the East (Canton Grisons) up to about 3000 m a.s.l. These xerothermic vegetation complexes harbour a particular rich flora, comprising different elements such as steppic species at their westernmost range outposts, sub-Mediterranean

species, dealpine and European dry grassland species (Dengler et al., 2019). In other regions of Switzerland, outside of the inner alpine dry valleys, steppe-like vegetation types occur, but rather represent transitions to other more mesic dry grassland types than steppes. Steppe vegetation similar to those of Switzerland are found in adjacent inner alpine dry valleys such as Aosta or Venosta in Italy. Braun-Blanquet (1961) therefore mentioned Swiss steppes to substantially diverge from “real” climatic steppes of the Iberian Peninsula or in eastern Europe, as they mostly are defined by orography, pedology and human land use, occur in isolated patches within a climatic forest zone and thus represent a mixture of different floristic elements. Despite a low biomass productivity and quality (Klötzli et al., 2010), Swiss steppes are traditionally grazed with sheep, goat or even cattle (Frey, 1934; Delarze et al., 2015), sometimes in combination with traditional irrigation via artificial open water channel systems (Christ, 1879; Crook and Jones, 1999). The abandonment of these traditional land-use system, particularly in less accessible areas, is still proceeding (Graf et al., 2014) and leads to habitat degradation, i.e. encroachment by woody species (Volkart-Duperret and Godat, 2008; Erdős et al., 2013; Riedener et al., 2014). Besides abandonment, additional threats to the steppes in inner alpine dry valleys are the expansion of vineyards and settlements, but also land-use intensification by fertilization and modern irrigation methods such as aerial sprinkler systems (Delarze et al., 2015; Humbert et al., 2016; Boch et al., 2018a), which distribute water much more efficiently and homogeneously than the traditional water-channel systems (Crook and Jones, 1999). While the negative effects of intensification on grassland diversity and composition are well explored (Allan et al., 2014; Gossner et al., 2016), land-use abandonment effects might differ among vegetation types (Kämpf et al., 2016; Valkó et al., 2018) and are largely unexplored in Swiss steppes (but see Riedener et al., 2014). Despite their well-known floristic uniqueness, literature on Swiss steppes is scarce and mainly restricted to descriptive books and book chapters or to less accessible grey literature, mainly focusing on vegetation classification and the floristic and ecological characterization of steppe

vegetation types (Christ, 1879; Frey, 1934; Braun-Blanquet, 1961; Dengler, 2018; reviewed in Schwabe and Kratochwil, 2004). Systematic studies on diversity patterns along environmental gradients, among land-use types or regarding functional traits are largely missing (but see Schwabe and Kratochwil, 2004). For instance, elevational gradients reflect a transition from warmer low-elevation to colder high-elevation conditions corresponding with – at least in the European Alps – increasing mean annual precipitation. Elevational gradients are thus a substitute for complex climatic gradients and can be used to investigate diversity and species composition patterns. Such species richness-elevation relationships are well explored for various habitats and taxa, with a mid-elevational peak being the most common relationship (McCain and Grytnes, 2010). However, biodiversity patterns along elevational gradients have not been studied among Swiss steppes.

Similarly, species richness of vascular plants is commonly used as biodiversity indicator. Total species richness does, however, not necessarily reflect the conservation status or the habitat quality of a site, different indicators such as proportional richness of threatened or specialist species might be better indicators (Boch et al., 2013a, b). In addition, vascular plant species may be further classified according to their ecological preferences, i.e., by using ecological indicator values (Ellenberg et al., 2001; Landolt et al., 2010). Ecological indicator values are an important and widely used tool to characterise site conditions and temporal changes of vegetation plots (Diekmann, 2003; Czortek et al, 2018). They describe the realised niche of a plant taxon on an ordinal scale. Averaging values over all taxa yields information on the environmental conditions of a site (Tölgyesi et al., 2014). Mean ecological indicator values were even proposed to better describe longer-term site conditions than exact point measurements do (Wamelink et al., 2002).

Furthermore, plant functional traits represent morpho-physio-phenological characteristics of plant taxa which are related to resource acquisition, growth, reproduction, competition and survival. Functional traits can be used to understand vegetation changes along environmental

gradients, which are often not reflected by diversity or species richness patterns. Similar to mean indicator values, community mean trait values are widely used in ecological studies, as they provide mechanistic insights in local vegetation and biodiversity patterns (Díaz et al., 2007; Pfestorf et al., 2013; Heer et al., 2018; Soliveres et al., 2018; Busch et al., 2018, 2019; Boeddinghaus et al., 2019). Again, neither patterns of specialist or threatened vascular plant species nor of differences in mean indicator values or community mean traits along environmental gradients have been studied in Swiss steppes.

In this article, we study patterns of species richness as well as differences of mean indicator values and community mean traits along elevational gradients, land-use types and temporal changes in wood cover. First, we hypothesized higher species richness and a lower proportion of steppe specialists with increasing elevation because of more mesic conditions at higher elevation. Based on the humped-back model hypothesis (Fraser et al., 2015), we further assumed species richness to peak at intermediate productivity levels, i.e., intermediate nutrient conditions (Pitarello et al., 2018). Second, we further hypothesized that land-use abandonment also promotes more mesic conditions, leading to the immigration of tall plant and woody species (Valkó et al., 2018). This immigration might result in increased competition, productivity, plant height and specific leaf area, a reduced number of steppe specialists and threatened plants, as well as decreasing light conditions, ruderality and leaf dry matter content.

2. Methods

2.1 The Monitoring of the nationally important habitats of Switzerland

In 2011, the program “Monitoring the effectiveness of habitat conservation in Switzerland” was initiated by the Swiss Federal Office for the Environment BAFU and the WSL Swiss Federal Research Institute. It monitors changes in habitats of national importance. Using remote sensing, changes of structures such as tree and shrub cover or infrastructures such as

roads and buildings of all 7000 sites of national importance are measured. Of these 7000 sites about 900 are selected for vegetation surveys, weighting rare habitat types higher in a random selection process to avoid overrepresentation of frequent habitat types (for details see Tillé and Ecker, 2014). Each plot is surveyed once in a six-year cycle (Boch et al., 2018b). The first phase of the project lasted from 2012 to 2017, the second phase started in 2018.

2.2 Vegetation data, vegetation classification and selection of plots for analysis

Within the 900 sites of national importance selected for vegetation surveys, we conducted about 7000 vegetation relevés in circular plots of 10 m². All plots were permanently marked belowground with strong magnets, which ensures relocation with a metal detector (Boch et al., 2018b). From 2012 to 2017, we recorded all vascular plant species and estimated their abundance (cover) in each plot using a modified Braun-Blanquet scale ($r \triangleq <0.1\%$, $+$ $\triangleq 0.1\% - <1\%$, $1 \triangleq 1\% - <5\%$, $2 \triangleq 5\% - <25\%$, $3 \triangleq 25\% - <50\%$, $4 \triangleq 50\% - <75\%$, $5 \triangleq 75\% - <100\%$). Nomenclature of vascular plants followed Lauber et al. (2012). About 2800 of the plots were situated in 403 dry grasslands.

To separate steppe and non-steppe plots in the dry grassland data set, we manually sorted plots by using character species listed in Braun-Blanquet (1961) for different steppe vegetation types occurring in Switzerland. In particular, these species were character species of the order Festucetalia vallesiaca, the alliances Stipeto-Poion carniolicae (in the West) and Stipeto-Poion xerophilae (in the East) and the ten associations Ephedreto-Koelerietum vallesiaca, Stipeto-Koelerietum vallesiana, Brometum-Pulsatilletum montanae, Brachipodieto-Astgragaletum exscapi, Jasionetum-Festucetum vallesiaca, Festuco-Pulsatilletum halleri, Xerobrometum rhaeticum, Astragalo-Brometum, Koelerio-Poetum xerophilae, Artemisio-Agropyretum (nomenclature of syntaxa according to Braun-Blanquet, 1961; for details see Appendix S1). This approach revealed a clearer selection of typical steppe plots than using numerical methods such as the Van-der-Maarel similarity measure

(Wildi and Orlóci, 1996). This resulted in a total of 148 steppe plots at 40 sites of national importance (142 plots in the West (Valais) and 6 in the East (Grisons) of Switzerland), which we used for analysis. The plots covered an elevational gradient from 384 m to 1719 m a.s.l. (Figs. 1,2).

2.3 Species richness data

We calculated the total species number per plot. Excluding uncertainly identified taxa (cf. taxa), we further calculated the proportion of threatened species (RE, CR, EN, VU, NT; Bornand et al., 2016; for details on the Red List status of species see Appendix S1), of neophyte species (Juillerat et al., 2017; for details on occurring neophyte species see Appendix S1), and of steppe specialist species out of the total species richness. As neophytes were negligible in our plots (136 of our 148 plots were without neophyte species, 11 plots had one and one plot had two neophyte species), we did not further analyze patterns of neophyte proportions in our plots. As steppe specialist species (for details on included species see Appendix S1), we considered the character species of orders and alliances of steppe vegetation types listed in Braun-Blanquet (1961; for included orders and alliances see previous paragraph). We further included all *Stipa* species as steppe specialists and taxon aggregates of which all taxa are occurring in steppes (e.g. *Fumana ericoides* agg. comprising *F. ericoides* and *F. procumbens*). However, we likely underestimated the number of steppe specialists, as we did not include broad species aggregates, which comprise many taxa that occur outside steppes (e.g. *Achillea millefolium* agg. comprises few character species of steppes such as *A. setacea* and *A. tomentosa* that were, however, rarely identified to the species level).

2.4 Community weighted mean traits and ecological indicator values

We requested data from TRY – Plant Trait Database (Kattge et al., 2011) to calculate community mean values of traits related to resource acquisition, growth, competition and grazing intensity, i.e. specific leaf area (SLA; leaf area per leaf dry mass [mm^2/mg]), leaf dry matter content (LDMC; leaf dry mass per leaf fresh mass, [g/g]) and plant height (height, [meter]) (Wright et al., 2004; Díaz et al., 2007; Bernhardt-Römermann et al., 2011; Pfestorf et al., 2013; Reich, 2014; Busch et al., 2018). For the TRY request, we first translated our species list to the nomenclature used in TRY and set subspecies to species level to maximize the number of matches. This resulted in a total of 334 species of which for 328 species trait data were available. Excluding records without data (NAs) resulted in a total of 58023 TRY records for the three requested traits. We then merged the three separate SLA traits (Trait ID: 3115 petiole excluded, 3116 petiole included, 3117 undefined if petiole was included or not) and the two plant height traits (Trait ID: 3106 plant height vegetative, 3107 plant height generative) to a compound SLA and a compound plant height trait, respectively. SLA was available for 275 of all taxa (82.3%), LDMC for 268 taxa (80.2%) and plant height for 327 taxa (97.9%). We finally calculated the median value per trait based on all database records and used the abundance-weighted community mean of each trait per plot for further analysis. We also calculated abundance-weighted indicator values for moisture, nutrients/productivity, light, competition and ruderality for each plot using Landolt et al. (2010). As the indicator value for nutrients is weakly related to mere soil nutrient content and rather reflects site productivity as measured by plant biomass (Schaffers and Sykora, 2000) or nitrogen concentrations in the biomass (Klaus et al., 2012), we call it “indicator value for productivity” throughout the manuscript. We transformed the nominal measures of competition and ruderality given in Landolt et al. (2010), which are based on Grime’s C-S-R triangle (Grime, 1974), into a numerical value ranging from 0 to 3. For instance, a taxon with ‘rrr’, indicating highest ruderality, was assigned a ruderality value of 3 and a competition value of 0, or a taxon with ‘crr’ got a competition value of 1 and a ruderality value of 2.

226

227 2.5 Plot data

228 For each of the 148 plots, we measured its central GPS coordinates (using a Trimble Geo 7X
229 H-Star with 10 cm precision after post processing) in the field and later computed the
230 corresponding elevation from a LIDAR data-derived digital terrain model (DTM-AV DOM-
231 AV © 2017 swisstopo 5704 000 000). We additionally recorded land-use at two levels per
232 plot, namely non-intensively grazed vs. abandoned. We further estimated the percentage
233 cover of tree and shrub species.

234

235 2.6 Site data

236 Digital aerial pictures from the 1990s of all 7000 assigned sites of national importance were
237 visually compared to recent aerial pictures (Fig. 3) in up to 50 m × 50 m large polygons.
238 Changes in tree and shrub cover or infrastructures such as roads and buildings were recorded
239 using an ordinal scale with 11 classes ($1 \triangleq <0\%$, $2 \triangleq 1-10\%$, $3 \triangleq 11-20\%$, $4 \triangleq 21-30\%$, $5 \triangleq$
240 $31-40\%$, $6 \triangleq 41-50\%$, $7 \triangleq 51-60\%$, $8 \triangleq 61-70\%$, $9 \triangleq 71-80\%$, $10 \triangleq 81-90\%$, $11 \triangleq 91-$
241 100% cover). Here, we used the change in cover of woody species in those 50 m × 50 m grid
242 cells in which the 148 plots were situated (referred as change of wood cover on the site level
243 henceforth). The remotely-sensed values therefore do not necessarily refer to the situation in a
244 particular plot. They rather can be used as an indicator for restoration activities (clearing of
245 woody species) or land-use abandonment (tree and shrub encroachment) in the close
246 proximity of a plot.

247

248 2.7 Statistical analysis

249 All statistical tests were performed in R version 3.5.1 (R Core Team, 2018). To avoid large
250 differences in variances among factors and to improve model convergence, we standardized
251 all continuous variables to a mean of 0 and a standard deviation of 1. Factors were not

confounded ($r < 0.7$). We then used linear mixed-effect models (lmerTest package; Kuznetsova et al., 2017) fitting the site code (often several plots occur in one site) as a random factor to correct for site-specific differences. We included elevation, land use (57 pasture plots vs. 91 abandoned plots), mean indicator values for productivity, cover of woody species (cumulative cover of trees and shrubs based on field estimates) and remotely sensed changes in wood cover as fixed factors to test for the effects on the number of all species and the proportion of threatened and steppe specialist species out of the total species richness as well as mean indicator values and community mean traits. We excluded the indicator value for productivity from models when fitting it as response variable. We further included the quadratic term of the indicator value for productivity when testing its effect on species richness, as we expected a hump-shaped relationship between species richness and productivity (Pitarello et al., 2018). We did not use the quadratic term of the indicator value for productivity in all other models, because it yielded no major improvement in the amount of variation explained and because there was no plausible hypothesis to test for non-linear relationships. We also included elevation as quadratic term because of common non-linear relationships between elevation and species richness (McCain and Grytnes, 2010). However, as the quadratic term of elevation was not significant in any model, we excluded it from all models. To test for differences in the strength of the effects along the elevational gradient, we included the interaction between other factors and elevation. Again, as the interactions were never significant, we also excluded interactions from the models. For all models, we calculated R^2 as the marginal coefficient of determination for mixed models, which represents the variance explained by the fixed effects (MuMin package; Barton, 2018).

3. Results

3.1 Species richness patterns

Mean species richness per plot was 23.3 (± 7.4 SD) and ranged from 5 to 45 taxa. The proportion of steppe specialists out of the total species richness was 29.3% that of threatened species 12.2%. Species richness increased by 0.7 species per 100 m increase in elevation. Overall, species numbers and proportions did not differ between pastures and abandoned sites. Vascular plant species richness peaked at intermediate levels of indicator values for productivity (Tab. 1, Fig. 4), while the proportion of threatened and steppe specialist species was negatively related to indicator values for productivity. Wood cover in plots had no effect on the total species richness, but was negatively related to the proportion of threatened and steppe specialist species. Interestingly, the temporal increase of wood cover at the site level (remote sensing-based values) had a positive effect on the proportion of threatened species (Tab. 1).

3.2 Effects on community mean ecological indicator values

Surprisingly, elevation had no effect on mean indicator values, while abandonment decreased mean indicator values for productivity and ruderality by 3.6% and 23.2%, respectively. The indicator value for productivity was positively associated with mean indicator values for moisture, competition and ruderality and negatively with the light value (Tab. 2). Wood cover in the plots was positively related to mean indicator values for productivity, moisture and competition and negatively with light and ruderality values. Overall, temporal wood cover change at the site level had no effects on any mean indicator values (Tab. 2).

3.3 Effects on community mean traits

We found only little and few significant effects on community mean traits. Mean plant height was positively related to productivity and wood cover (Tab. 3). These patterns even remained when woody species were excluded from the community mean trait calculations and when presence/absence data was used instead of abundance weighted community mean plant height

(results not shown). Specific leaf area was positively associated with elevation and productivity. Increasing wood cover at the site level had no effects on functional traits (Tab. 3). LDMC was not at all affected by the factors and the amount of variation explained by the model was very poor (Tab. 3).

4. Discussion

4.1 Patterns of species richness

The average number of 23.3 vascular plant species found in this study is below the values reported for Festuco-Brometea communities in most European countries for 10-m² plots (Dengler et al., 2012, 2016; Pedashenko et al., 2013; Kuzemko et al., 2016). However, they were similar to the values of species richness found by Dengler et al. (unpublished data) at one location in the Canton of Valais in Switzerland (26.8 species), to those found by Wiesner et al. (2015) in the nearby Aosta valley in Italy (27.8 species) and the species numbers reported in Schwabe and Kratochwil (2004) from extremely dry Festuco-Brometea communities in the Aosta valley and Valais (range from 24 to 28). The lower species richness of our plots compared with those in other European regions is not surprising as the latter refer to basiphilous grasslands of the Brachypodietalia order (Dengler et al., 2016) which grow under more mesophilous conditions. They strongly differ from steppe communities of the Festucetalia valesiacae on dry and shallow soils. The pool of species that can cope with the rather harsh conditions in steppe grasslands is limited (Tóth et al., 2018), and species richness within steppes in the Alps at small spatial scales is generally low (Braun-Blanquet, 1961; Dengler et al., unpublished data). This is also a possible explanation for the positive species richness-elevation relationship. As mean annual temperature decreases and mean annual precipitation tends to increase with elevation in the European Alps (Körner, 2003), conditions are getting more mesic at higher elevations enabling more species to persist in less extreme

steppe vegetation. This is in line with Schwabe and Kratochwil (2004), who found a positive plant diversity-humidity relationships in various vegetation types of inner alpine dry valleys. As hypothesized, we found a species richness peak at intermediate indicator values for productivity. This confirmed the results of Pitarello et al. (2018), who found a similar relationship in pastures of the Western Italian Alps. This humped-back curve suggests on the one hand that species richness is limited by abiotic stress under unproductive conditions and, on the other hand, that species richness declines under highly productive conditions because of competitive exclusion of many species by a small number of strongly competitive species (Fraser et al., 2015). However, the proportion of threatened and steppe specialist species generally declined with increasing indicator values for productivity, indicating a major threat of the overall diversity and in particular of typical steppe vegetation of the inner alpine dry valleys by land-use intensification, and notably by fertilisation (Allan et al., 2014; Bornand et al., 2016; Boch et al., 2018a; Visconti et al., 2018).

In contrast to Riedener et al. (2014), who found a higher number of threatened species in abandoned compared to managed species-rich grasslands in the Swiss Canton of Valais, abandonment had no effects on species richness or the proportion of threatened and steppe specialist species in our study. This finding contradicted the expectation of abandonment generally being a major threat for species richness and threatened species (Valkó et al., 2018; Visconti et al., 2018). However, it might well be that in most cases the time since abandonment was rather short and thus not long enough for local species extinction, influencing the number of species or the floristic composition of communities. In fact, the effects of abandonment will take time to become visible on low-productivity steppe sites with their rather sparse vegetation and harsh environmental conditions to become visible.

Moreover, as the wood cover was confounded with land use, i.e., higher values in abandoned than grazed plots ($8.47\% \pm 2.34$ vs. $5.90\% \pm 2.08$ SE, respectively), the effect of wood cover might have masked the abandonment effect in our study: shrub and tree cover was negatively

related to the proportion of threatened and steppe specialist species. This finding was in line with previous studies showing negative effects of shrub encroachment on single species, species groups such as threatened or specialist species or overall species richness (e.g. Černý et al., 2011; Hegedúšová and Senko, 2011; Deák et al., 2016; Elias et al., 2018a, b). The effects of both, abandonment and shrub encroachment are similar and can often not be disentangled. Both lead to litter accumulation, reduced light availability and often an increase in a small number of dominant and competitive species (Valkó et al., 2018). These effects of abandonment and wood encroachment hinder the germination and establishment of light-demanding seeds of grassland species and lead to competitive exclusion of small-statured and light demanding species (Deák et al., 2016; Valkó et al., 2018). However, as the extinction of species is a rather slow process (Helm et al., 2006), there is a high restoration potential of encroached grasslands, i.e., by directed grazing and removal of woody species (Elias et al., 2018a).

Unexpectedly, we found a positive effect of the remotely-sensed change of wood cover on the proportion of threatened species in our plots. However, as the remote sensing data used in this study reflect the situation at the site and not necessarily of the 10 m² plot surveyed, this finding might be simply be caused by the consideration of different spatial scales and by the fact that abandonment and increase in wood cover can temporarily lead to a higher habitat diversity at the site level (Diacon-Bolli et al. 2012) and under particular circumstances might even positively affect total species richness and the richness of diagnostic species (Tölgyesi et al., 2018). In addition, abandonment might occur more frequently at low productivity sites and under extreme dry conditions. Both will likely increase the proportion of threatened species.

4.2 Effects on community mean ecological indicator values

In contrast to our expectation, elevation had no effect on any of the mean indicator values. As the growing season is shorter, solar radiation and precipitation are higher (at least in the European Alps) and mineralization rate and airborne N deposition is lower in higher elevation areas (Körner, 2003), we assumed lower productivity and competition but higher moisture values at higher sites (Güsewell et al., 2012). Mean indicator values for productivity and ruderality were lower in abandoned than in grazed plots. Ruderal species are mainly nitrophilous and constitute a characteristic component of grazed dry grasslands (Brandes and Pfützenreuther, 2013). Similarly, Elias et al. (2018a) in Central Germany and Dostálek and Frantík (2008) in the Czech Republic found a trend of a higher number of nitrophilous and ruderal species in grazing treatments compared to unmanaged control plots in dry grasslands. The studies thus support our findings for inner alpine steppe vegetation. The results of an increasing wood cover being negatively related to light and ruderality values and positively associated with productivity, moisture and competition values in the plots are intuitive, because shading promotes tall growing, rather nitrophilous and competitive species at the expense of small-statured, light-demanding species (Ellenberg 2001).

4.3 Effects on community mean traits

We found few significant relationships between elevation, land use, productivity or wood cover and community mean functional traits. For instance, we expected clear differences among abandoned and grazed plots, such as on average smaller plants under grazing because plant height constitutes a trade-off between competition capacity, reflected by comparatively high growth, and grazing resistance via durable plant tissue (Bernhardt-Römermann et al., 2011). The latter often goes along with a lower mean SLA and higher mean LDMC in pastures, as slow growing species with a lower biomass quality and stronger grazing resistance are promoted by grazing (Díaz et al., 2007; Busch et al., 2018). In fact, Pfestorf et

al. (2013) proposed LDMC to be the best indicator for grazing intensity when analyzing the relationship between land-use intensity, species diversity and a set of community mean traits in a large number of differently managed grasslands in Germany. However, in the study we neither found effects on plant height nor on LDMC. It might well be the case that the mean LDMC differences among the abandoned and pasture plots were too small to be detected, as the land-use gradient between abandoned and pastures was possibly too small because grazing intensity was generally very low. Moreover, as most vascular plant species of inner alpine steppe vegetation are adapted to both drought and grazing, the differences in LDMC values among our plots were rather small. This also corresponds to the findings of Zheng et al. (2015), showing that traits corresponding to grazing are largely mediated by soil moisture and plant functional group identity.

Pfester et al. (2013) found plant height (vegetative and reproductive) as well as SLA to be positively associated with fertilization, i.e., productivity. Their results correspond to ours of plant height and SLA being positively associated with productivity, complemented by our finding of shading by increased wood cover promoting taller vascular plant species (see section 4.2).

6. Conclusions

Biodiversity of steppe vegetation in inner-alpine valleys in general and in Swiss steppe vegetation in particular are not well known. Our findings extend the knowledge on diversity patterns of such steppes and also have important implications for conservation management. The decreasing proportion of threatened and steppe specialist species with higher productivity and wood cover found in the present study first clearly suggests the proportion of these species groups as suitable indicators for the conservation status of steppes. Second, it further highlights the need of maintaining traditional low-intensity management regimes including extensive grazing and shrub removal to keep wood cover at low levels in inner alpine steppe

vegetation and to thus counteract abandonment. Third and at the same time, intensification by fertilization and modern irrigation systems should be avoided in order to maintain low productivity in inner alpine steppes. To ensure early detection of such negative changes in the sites of national importance in Switzerland, such as wood encroachment, and to conduct prompt conservation measures, we implemented a remote sensing-based online colour-coded warning system, which can be assessed by the responsible federal and cantonal conservation authorities. This online early warning system informs them about negative developments in the Swiss habitats of national importance – including sites with steppe vegetation – on a yearly basis.

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8. Literature

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Tab. 1: Results of linear mixed-effect models with site as random factor separating the effects of elevation, productivity (indicator value for nutrients was used as proxy for productivity; including a quadratic term), land use (pasture vs. abandoned), percentage wood cover and remote sensing-based change of wood cover at the site level on the number of all species and the proportions of threatened and steppe specialist species per plot. Significant differences are indicated in bold. R^2 denotes the marginal coefficient of determination representing the variance explained by fixed effects.

	df	Number of species		Proportion of species			
		Slope	P	Red list		Specialists	
				Slope	P	Slope	P
Intercept	1	0.02	0.891	-0.21	0.198	0.18	0.259
Elevation	1	0.36	<0.001	-0.06	0.522	-0.17	0.074
Pasture [y/n]	1	0.19	0.343	0.29	0.150	-0.31	0.114
Productivity	1	0.11	0.357	-0.21	0.021	-0.27	0.002
Productivity ²	1	-0.18	<0.001	—	—	—	—
Wood cover	1	0.08	0.260	-0.19	0.011	-0.22	0.003
Change wood cover	1	0.01	0.920	0.16	0.044	-0.01	0.901
		$R^2 = 0.19$		$R^2 = 0.15$		$R^2 = 0.17$	

Tab. 2: Results of linear mixed-effect models with site as random factor separating the effects of elevation, productivity (indicator value for nutrients was used as proxy for productivity), land use (pasture vs. abandoned), percentage wood cover per plot and remote sensing-based change of wood cover at the site level on mean indicator values for productivity, moisture, light, competition and ruderality per plot. Productivity was excluded from the model when testing this factor as response variable. Significant differences are indicated in bold. R^2 denotes the marginal coefficient of determination representing the variance explained by fixed effects.

	df	Indicator value for									
		Productivity		Moisture		Light		Competition		Ruderality	
		Slope	P	Slope	P	Slope	P	Slope	P	Slope	P
Intercept	1	0.43	0.020	-0.06	0.632	0.02	0.913	-0.02	0.906	0.18	0.213
Elevation	1	0.03	0.792	0.09	0.182	0.02	0.829	-0.01	0.931	0.04	0.603
Pasture [y/n]	1	-0.62	0.001	0.12	0.409	0.03	0.860	0.06	0.746	-0.36	0.037
Productivity	1	–	–	0.64	<0.001	-0.31	<0.001	0.21	0.018	0.44	<0.001
Wood cover	1	0.14	0.021	0.20	<0.001	-0.30	<0.001	0.22	0.003	-0.18	0.005
Wood cover change	1	-0.07	0.312	-0.01	0.778	0.00	0.987	0.02	0.782	-0.07	0.293
		$R^2 = 0.10$		$R^2 = 0.52$		$R^2 = 0.23$		$R^2 = 0.10$		$R^2 = 0.31$	

Tab. 3: Summary of linear mixed-effect models with site as random factor separating the effects of elevation, productivity (indicator value for nutrients was used as proxy for productivity), land use (pasture vs. abandoned), percentage wood cover per plot and remote sensing-based change of wood cover at the site level on community mean traits of plant height, specific leaf area (SLA) and leaf dry matter content (LDMC). Significant differences are indicated in bold. R^2 denotes the marginal coefficient of determination for generalized mixed models which represents the variance explained by the fixed effects.

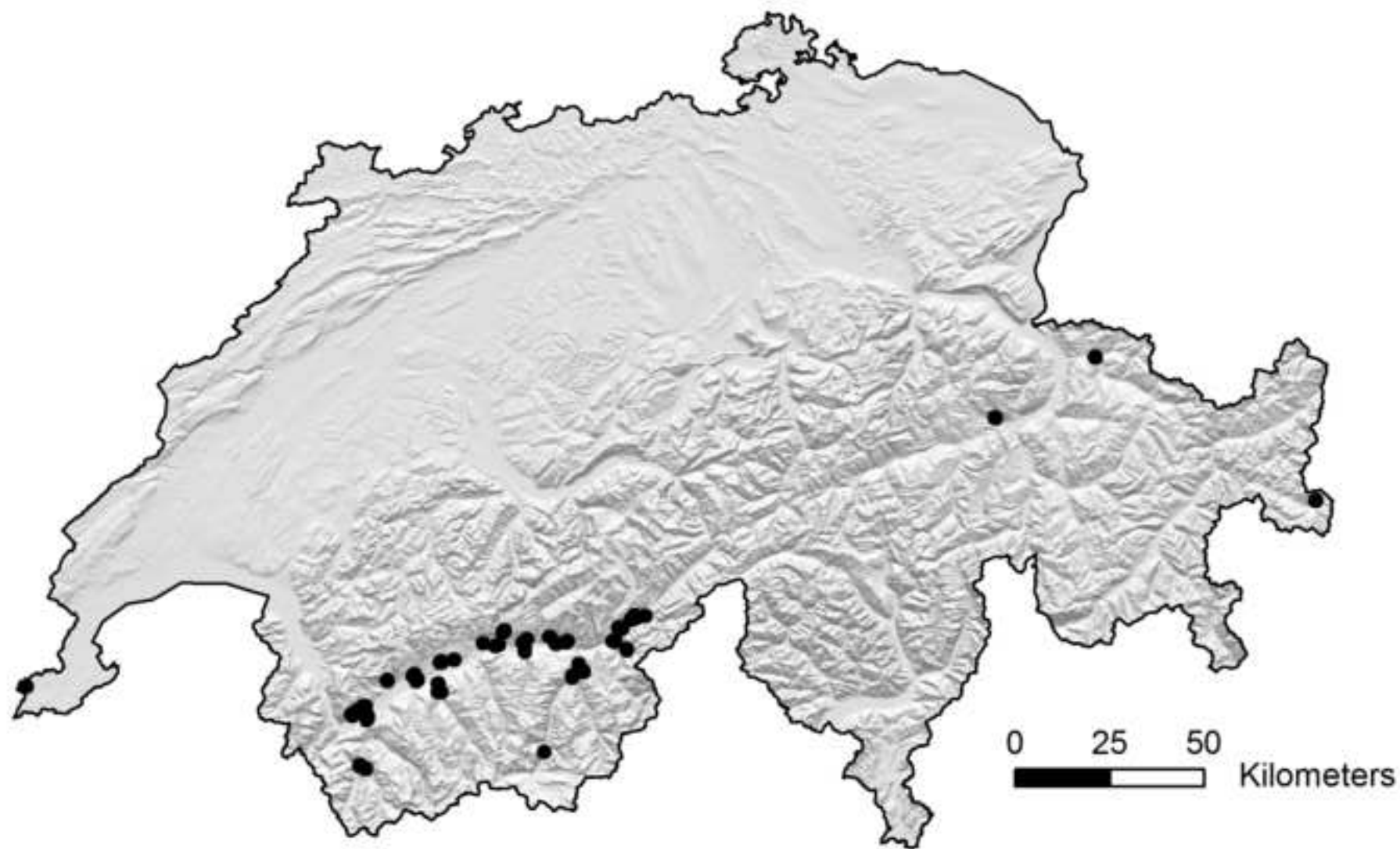
	df	Community mean trait of					
		Height		SLA		LDMC	
		Slope	P	Slope	P	Slope	P
Intercept	1	-0.26	0.040	0.13	0.289	0.01	0.934
Elevation	1	-0.06	0.464	0.16	0.027	-0.19	0.058
Pasture [y/n]	1	0.31	0.058	-0.20	0.181	-0.14	0.480
Productivity	1	0.37	<0.001	0.57	<0.001	-0.06	0.505
Wood cover	1	0.15	0.027	0.04	0.469	0.01	0.907
Wood cover change	1	0.11	0.104	-0.05	0.375	0.05	0.507
		$R^2 = 0.21$		$R^2 = 0.47$		$R^2 = 0.05$	

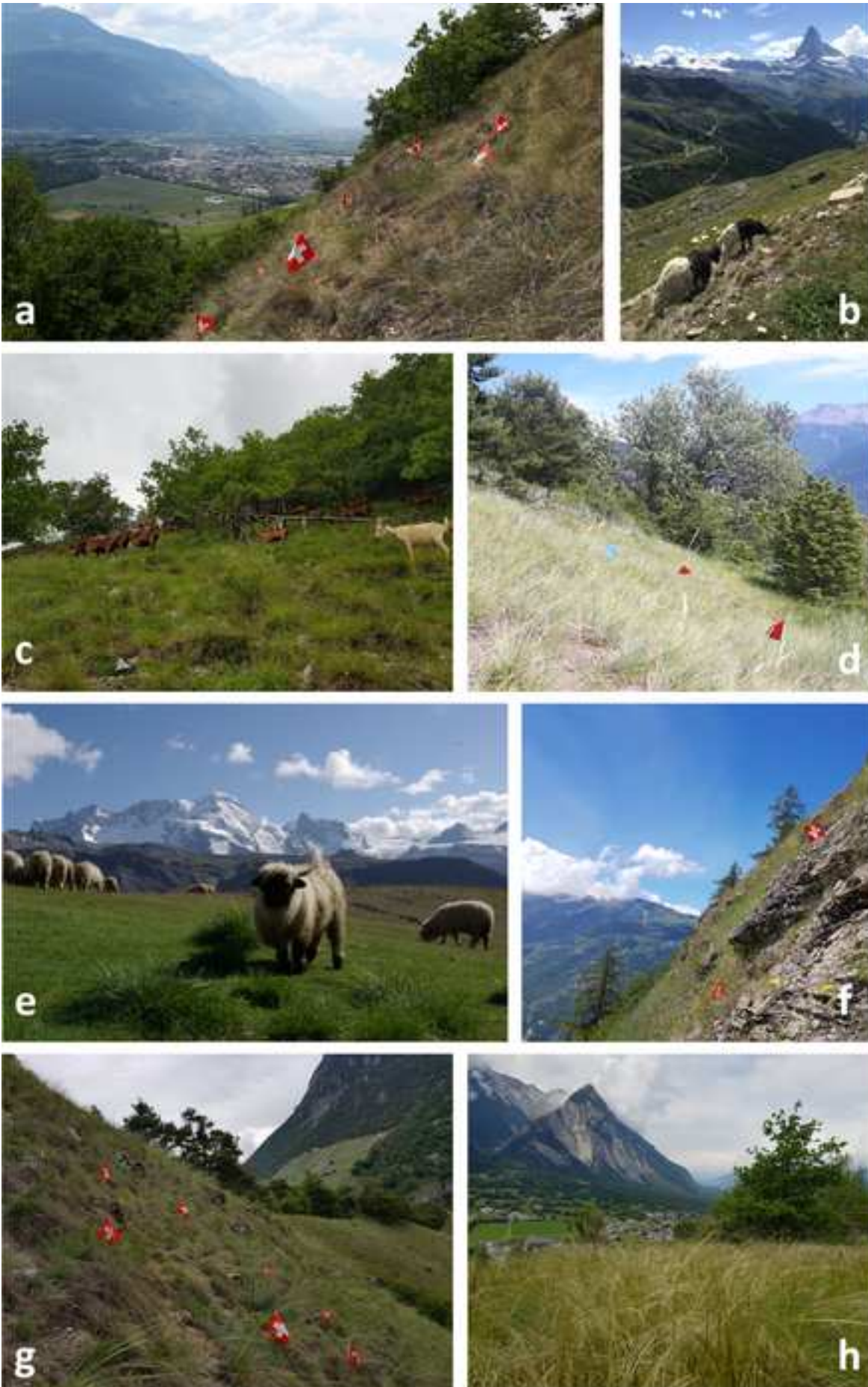
Fig. 1: Location of the 148 steppe plots (black dots) at 40 sites of national importance in Switzerland.

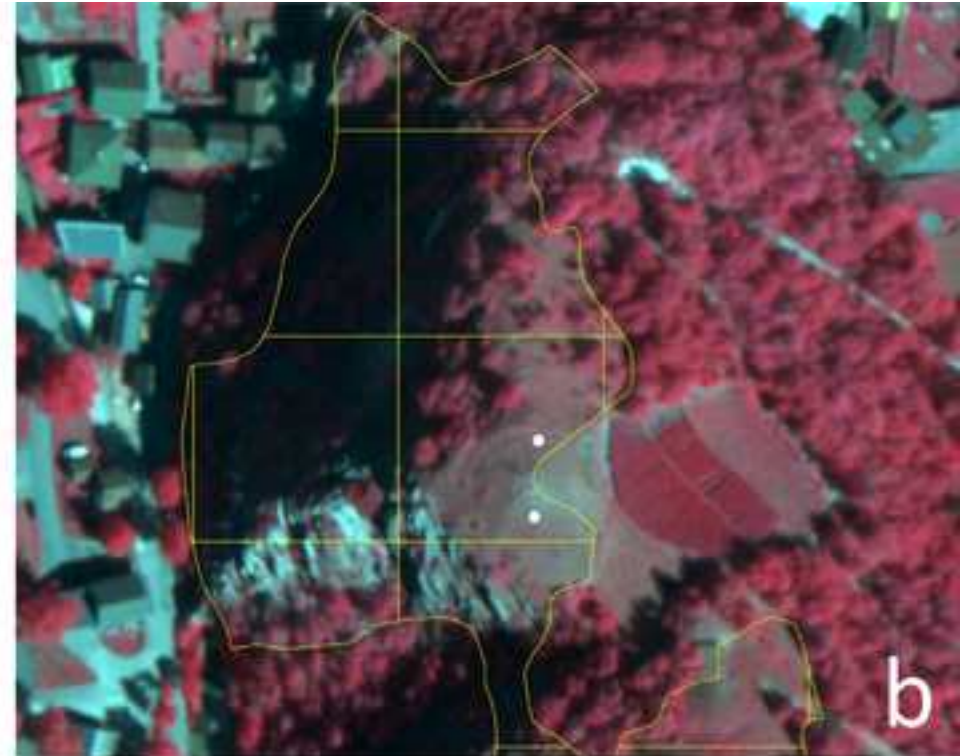
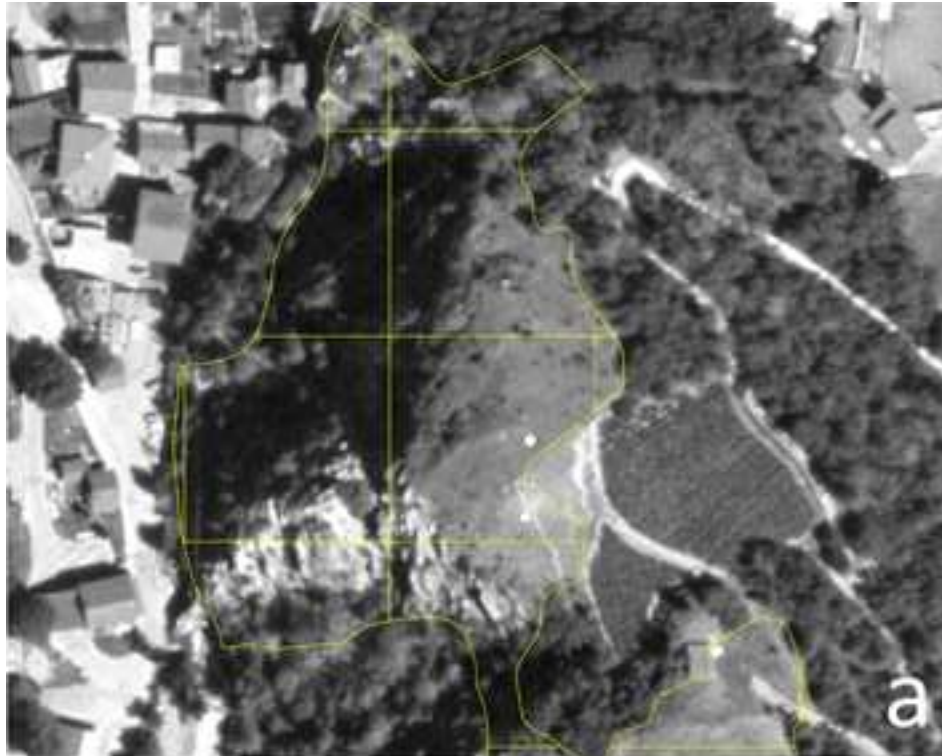
Fig. 2: Impressions of dry grassland sites of national importance showing steppe vegetation types in the canton of Valais in the close proximity of a) Savièse, b) Zermatt, c) Erschmatt, d) Ausserberg, e) Zermatt, f) Mase, g) Vex and h) Erschmatt.

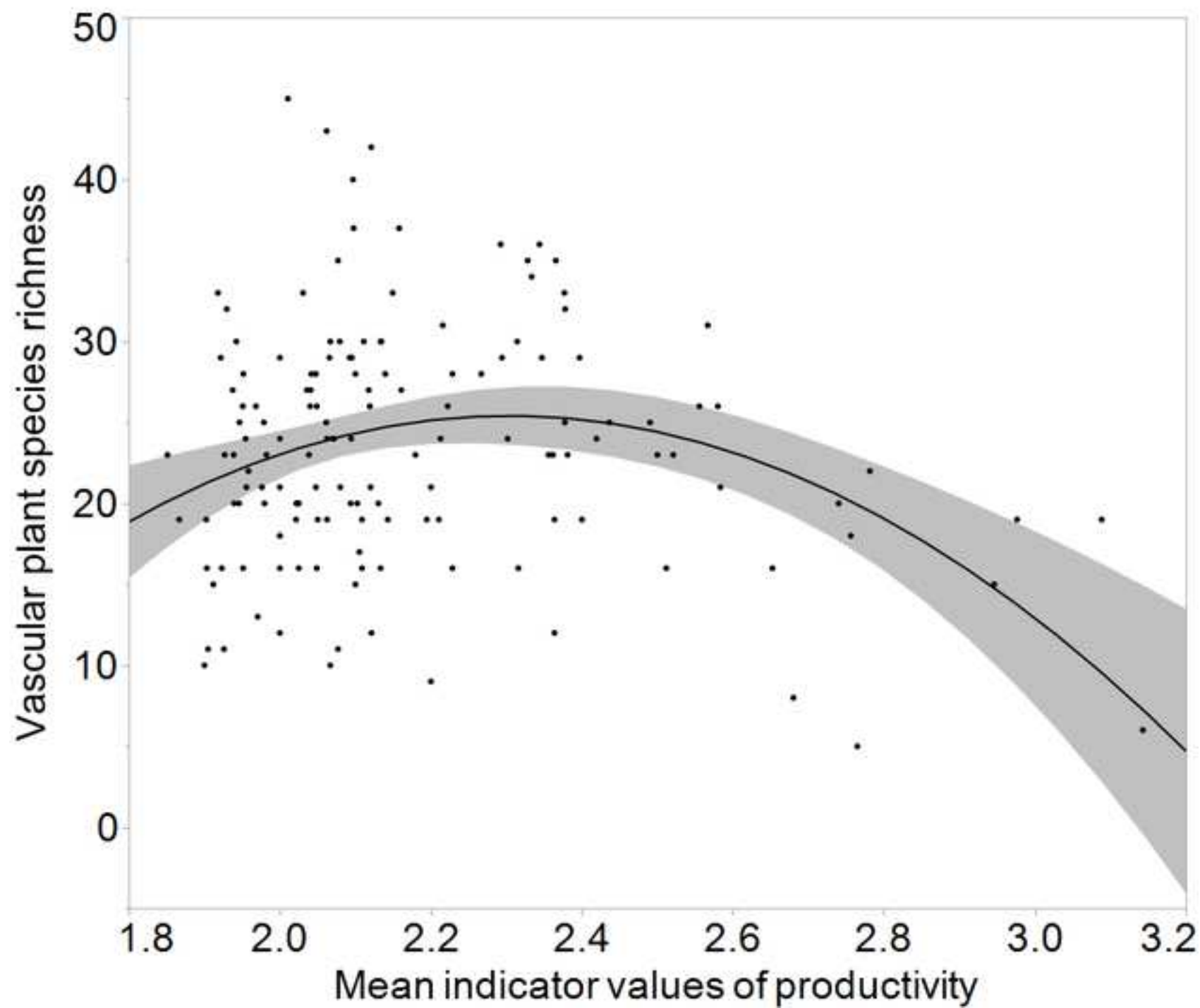
Fig. 3: Digital aerial pictures of a dry grassland site of national importance showing wood encroachment in the upper part of the site from a) 1999 to b) 2010. The white dots indicate plots which remained unaffected from the wood encroachment (©swisstopo; JA100118).

Fig. 4: Relationship between vascular plant species richness and mean indicator value for productivity (= indicator value for nutrients; 148 plots; untransformed raw data). The trend line indicates a significant quadratic relationship ($R^2 = 0.11$, $P < 0.001$) with 95% confidence interval in grey.











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Supporting File

Supplementary table S1 - Species list.xlsx

