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ORIGINAL ARTICLE

Dominant shrub species are a strong predictor of plant species diversity along subalpine pasture-shrub transects

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Abstract
Abandonment of pastures and successional shrub expansion are widespread in European mountain regions. Moderate shrub encroachment is perceived beneficial for plant diversity by adding new species without outcompeting existing ones, yet systematic evidence is missing. We surveyed vegetation along 24 transects from open pasture into shrubland across the Swiss Alps using a new protocol distinguishing different spatial scales, shrub cover of each plot (2 × 2 m) and larger-scale zonal cover along the transect. Data were analysed using generalized linear models of shrub cover, shrub species and environmental conditions, such as geology, aspect or soil. Most shrub communities were dominated by *Alnus viridis* (62% of transects) and *Pinus mugo* (25%), and the rest by other shrub species (13%). These dominant shrub species explained vegetation response to shrub cover well, without need of environmental variables in the model. Compared to open pasture, *A. viridis* resulted in an immediate linear decline in plant species richness and a marginal increase in beta-diversity (maximally + 10% at 35% cover). Dense *A. viridis* hosted 62% less species than open pasture. In *P. mugo,* species richness remained stable until 40% shrub cover and dropped thereafter; beta-diversity peaked at 35% cover. Hence, scattered *P. mugo* increases beta-diversity without impairing species richness. In transects dominated by other shrubs, species richness and beta-diversity peaked at 40–60% shrub cover (+ 23% both). *A. viridis* reduced species richness in a larger area around the shrubs than *P. mugo*. Therefore, effects of shrub encroachment on plant diversity cannot be generalized and depend on dominant shrub species.

Keywords Biodiversity · Vegetation · Mountain · Succession · Shrub encroachment · Conservation

Introduction

Grasslands cover large areas in mountains worldwide (Dong et al. 2011). Many of them are created and modified over millenia by human activities, especially by forest clearance, mowing and grazing livestock in transhumance systems (Holtmeier 2009; Lauber et al. 2013). In the European Alps, forest established after the retrieval of glaciers around 10,000 years ago, but was already modified by humans from around 6500 before present (Schwörer et al. 2015). Since then, vegetation has adapted to the regular disturbance exerted by selective defoliation and trampling of ruminants (Pauler et al. 2020). Depending on environmental conditions and management, diverse pasture communities have developed, thereby forming a cultural landscape (Ellenberg 1988). The establishment of pastoralism increased species richness but also reduced wood cover (Schwörer et al. 2015). In the Alps, this has lowered the treeline by up to 350 m: Open land was created in the subalpine zone, where in contrast to the alpine zone, trees would dominate naturally (Carnelli et al. 2004). Alpine and subalpine pastures range amongst the most biodiverse habitats worldwide (Wilson et al. 2012) and provide important services to society (Tasser et al. 2020).

Farming of mountain grassland has undergone considerable changes in recent decades (Lauber et al. 2013). Besides land use intensification on fertile land, land abandonment of remote areas is common (Queiroz et al. 2014; Tasser and

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Tappeiner 2002) and both these changes were found to have negative effects on plant species diversity (Peter et al. 2009; Strebel and Bühler 2015). Steep slopes not suitable for modern machinery, areas not developed with roads and zones of shallow soils tend to be given up (Gellrich and Zimmermann 2007). Abandonment is enforced by the shortage of labour due to increased employment outside the agricultural sector and by altered livestock production due to a shift from goats to sheep or from dairy to suckler beef cows (Liechti and Biber 2016). As a consequence, summer-grazed pastures in Switzerland have diminished by 295 km^2 (equivalent to 5.4% of the total) between 1985 and 2009, primarily in the subalpine zone (BFS 2013).

The reduction or removal of grazing pressure in pasture ecosystems changes vegetation composition. Grazing-resistant plant species lose their competitive advantage and decline relative to species which grow taller and invest more resources into persistent above-ground structures such as woody plants, tall herbs and grasses (Díaz et al. 2007). Not surprisingly, the above-mentioned changes in mountain farming are reflected in land cover. Between 1993 and 2006, shrubland in the Swiss Alps increased by more than 120 km^2 (20%) and this type of vegetation represents one of the fastest expanding habitats in Switzerland (Brändli 2010). The Swiss National Forest Inventory (Brändli 2010) defines shrubland as vegetation, in which woody plants below 3 m height (excluding dwarf shrubs) cover more than two thirds of the area. Eighty percent of the shrublands in Switzerland are located in the subalpine zone. They are commonly neighboured by late-successional coniferous forests at their lower and by dwarf-shrub communities at their upper boundaries. Shrublands grow on sites which are at an early stage of reforestation after a recent land use change or where natural conditions, such as avalanches and soil lability, limit tree height and the establishment of tall trees. Typically, shrublands are dominated by a few woody species, which are optimally adapted to the prevailing environmental conditions. In the Swiss Alps, 70% of shrublands are formed by *Alnus viridis* DC., 20% by *Pinus mugo* TURRA subsp. *mugo* and 10% by *Salix* species, *Corylus avellana* L. and other woody species (Brändli 2010). Sediment records suggest that especially *A. viridis* was rare in pre-neolithic vegetation but became more abundant alongside the establishment of pastoralism (Schwörer et al. 2014). Because of the substantial expansion of shrubland in the Alps it is important to understand its effects on plant species diversity and how they depend on the environmental site conditions and shrub species.

Pasture-shrub transects are characterised by a gradual shift from one habitat (open pasture) to another (closed shrub). As suggested by Duelli (1992) our first hypothesis H1 was that maximum species richness appears in the intermediate transition zone. However, studies testing H1 are contradictory and show evidence for a decline (Pajunen et al. 2012; Ratajczak et al. 2012; Teleki et al. 2020), a linear increase (Howard et al. 2012; Knapp et al. 2008) as well as hump-shaped response of plant species richness to shrub cover (Anthelme et al. 2001, 2003, 2007; Kesting et al. 2015; Pornaro et al. 2013; Soliveres et al. 2014). Reported responses of faunal diversity to shrub encroachment are equally varying (Blaum et al. 2007; García-Tejero et al. 2013; Hilpold et al. 2018; Kaphengst and Ward 2008; Laiolo et al. 2004). No consistent theory has been developed regarding which response model applies under which conditions. For example, Soliveres et al. (2014) found a hump-shaped response of floral diversity in drylands and a linear negative response on wetter sites. In contrast, Pornaro et al. (2013) concluded that the response on subalpine sites was governed by mean temperature. Howard et al. (2012) demonstrated that shrubs generally had positive effects on plant diversity in semi-arid ecosystems. Based on this evidence, our second hypothesis H2 was that yet-to-be-identified environmental conditions determine the response of plant diversity to shrub encroachment in the Swiss Alps.

In addition to environmental conditions, plant species identity may play an important role in recruitment speed and vegetation change. For example, Cairns and Moen (2004) have postulated that the speed of wood establishment under grazing may peak at low, intermediate or high grazing pressure depending on the relative palatability of herbaceous and arboreal vegetation. Loranger et al. (2017) found that tree species establishment interacted with grassland vegetation and that senescent herbs facilitate carbohydrate reserves in seedlings of evergreen trees. Modelling studies indicate that also the initial conditions may affect shrub encroachment (Komac et al. 2013). Hence, an analysis of vegetation dynamics at the pasture-shrub interface needs to take into account multiple contrasting sites.

Sampling vegetation across successional stages poses a number of challenges. Besides the difficulty of physical access and movement of the observer, sampling needs to account for heterogeneity and the different species-area relationship of open grassland and shrub forest (Rejmének and Rosén 1992). This is because the average size of individual plants changes by orders of magnitude from herbs to shrubs and because shrubs establish in patches (Wild and Winkler 2008). Moreover, processes such as plant competition, nutrient turnover or dispersal operate at different scales and hence, shrub cover may affect vegetation dynamics at local as well as larger scale. Since the N_2-fixing shrub *A. viridis* is known to affect the environment beyond its own canopy zone (Bühlmann et al. 2016), our third hypothesis H3 was that various shrub species may differ in the spatial scale of their effects. An appropriate sampling method along transects of shrub cover, therefore, needed to take into account different spatial scales.

The objectives of our study in the subalpine zone of the Swiss Alps were to test the three hypotheses developed above by (1) quantifying the impact of shrub encroachment on the plant species diversity across different environmental conditions (climate, topography and soil), (2) disentangling the effects of environmental conditions from those of dominant shrub species and (3) developing and testing an efficient and objective sampling method that accounts for different spatial scales of shrub effects.

Materials and methods

Selection of pasture-shrub transects

Potential transects from open pasture to closed shrubland within the subalpine zone (1300 m a.s.l. to 2400 m a.s.l.) of the Swiss Alps were identified by first selecting all cells of the Swiss land cover map (BFS 2013) that were classified as pastures (NOAS04 classes 42–49) and were directly adjacent to shrubland (NOAS04 class 57, excluding dwarf shrubs). Each selected cell was visually inspected using aerial imagery (Swissimage 25 cm, Federal Office of Topography Swisstopo). We excluded cells with abrupt changes from pasture to shrubland due to fences, water courses, roads, topography or other features, leaving a total of 117 possible locations with a gradual change in shrub cover. The candidate locations were stratified according to geology (Calcareous and Flysch, Siliceous and Dolomite) and aspect (South, North, East/West). Many of the locations were spatially clumped, for example, in remote valleys with high abandonment. We therefore calculated the centred, standardized mean of the distances from each location to every other location and multiplied it by one of four quality grades (0, 1.5, 3, 6) based on transect length and the smoothness of shrub cover change. The resulting values were used as weights in the random sampling of eight transects in each of the six groups, which were verified on-site. Finally, 24 transects were selected that were reasonably accessible and had not been cleared in the time since the Swissimage had been captured (Fig. 1).

Survey layout

In the field, the pasture-shrub transect was marked by a central line. Along this line, five cover zones (hereafter labelled zonal cover, c_z) with an estimated shrub cover of 0, 25, 50, 75 and 100% were marked by a pole (Fig. 2). The distances between poles varied depending on how quickly the shrub cover changed along the transect. Perpendicular to the

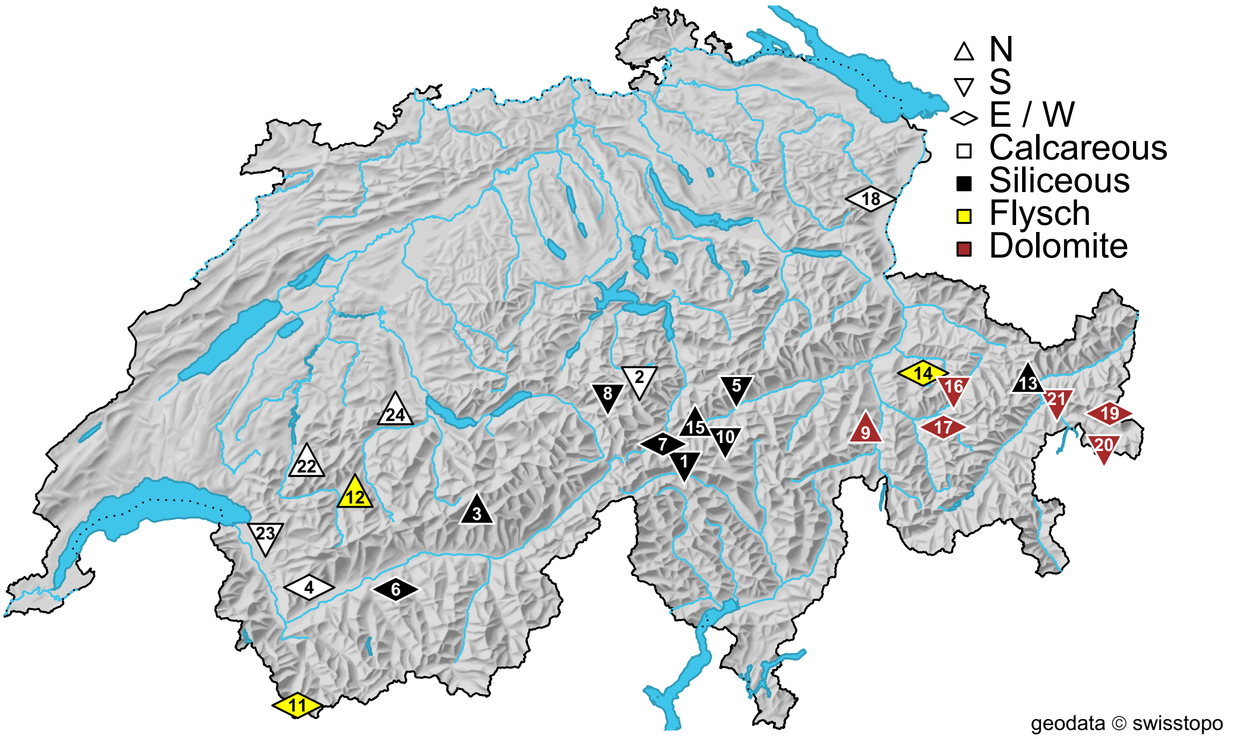

Fig. 1 Geographic location of sampled pasture-shrub transects in the Swiss Alps. Symbols indicate terrain aspect (upper triangles: North-West to North-East; lower triangles: South-East to South-West; rhombi: South-West to North-West and North-East to South-East). Colours indicate different substrates

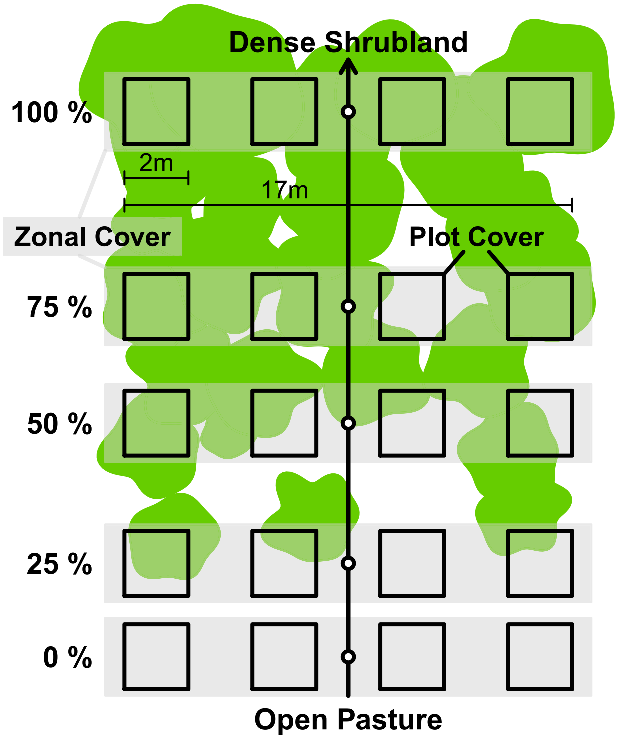

Fig. 2 Schematic representation of the sampling approach along a transect from open pasture to dense shrubland. The arrow represents the centre line along the transect. Small circles along the arrow indicate poles in five zones with estimated zonal cover of 0, 25, 50, 75 and 100%. Quadrates show four sampling plots of 2 × 2 m at fixed distances along lines perpendicular to the pasture-shrub transect. A value of plot cover was assessed for each sampling plot

central line, square plots of 2 × 2 m were established at fixed distances of 2.5 and 7.5 m from each pole in both directions, minimizing subjectivity of plot placement. This resulted in four plots (at fixed distance of 3 m apart) in each of the five cover zones and a total of 20 plots at each location. Within each plot, shrub cover was visually estimated on a continuous scale (hereafter labelled plot cover, c_p), in contrast to the discrete values of c_z. At low to medium cover values, c_p was not necessarily similar to c_z, because of the size of shrub patches. For example, a 2 × 2 m plot randomly placed in the 50% cover zone may have a c_p anywhere between 0 and 100% depending on the presence of shrub patches. Both values, c_p and c_z, are important and have different implications with respect to light and nutrient availability, as well as accessibility by grazing animals.

In each plot, all higher vascular plants were recorded and classified to the species level based on Lauber and Wagner (2007). Percentage cover p_k of each species k was visually estimated, separately for the herb layer (0–50 cm vegetation height, including woody species) and the shrub layer (woody species above 50 cm). Herbaceous structures (stems, leaves and flowers) above 50 cm were not accounted for in the shrub layer. In addition, topsoil (0–10 cm) was sampled from each plot and analysed for plant-available phosphorus (P) content, as an indicator of soil nutrient status, using ammonium acetate EDTA (Demaria et al. 2005) and pH in a soil–water suspension.

For each transect, additional environmental variables were quantified. Elevation and steepness were based on the digital terrain model of the Federal Office of Topography at 25 m resolution. Mean annual temperature and precipitation were extracted from climate data of the Federal Office of Meteorology and Climatology.

Data analysis

During data analysis, it became evident that pasture-shrub transects were dominated by a very limited number of woody species, mainly *A. virdis* and *P. mugo*. Therefore, *Picea abies* (L.) H. Karst., *Rhamnus alpina* L. and *Salix appendiculata* Vill. were aggregated into a third group labelled 'Others'. In order to assess species association to shrub cover, IndVal values were calculated for each of the 15 combinations q of the five cover zones within the three dominant shrub species according to Dufrêne and Legendre (1997). The IndVal$_{\mathrm{kq}}$ of a plant species k in combination q is defined as the ratio of the mean p_k across plots in q and the mean p_k over all combinations multiplied by the ratio of the number of plots in q where species k is present and the total number of plots in q. With this approach, rare species present in a few plots of a combination only, are not mistaken as a species closely associated to that combination.

Plant species composition was represented by six vegetation-related indices: (1) Species richness R_{i} was calculated as the number of all species of each plot i. (2) Evenness was calculated based on the Shannon diversity index as $E_i = -(\sum_{k=1}^{R} p_k \ln p_k)/\ln R_{\mathrm{i}}$. (3) Beta-diversity was calculated as the average Jaccard distance (Jaccard 1901) of species composition in a plot to the three other plots in the same cover zone. (4) Nutrient, (5) light and (6) water requirement indices were calculated by averaging indicator values of all species k according to Landolt and Bäumler (2010) weighted by their cover percentage p_k. Species richness, evenness and beta-diversity were calculated for the combined shrub and herb layers. Nutrient, light and water requirement indices were restricted to the herb layer only, in order to avoid confounding with shrub cover against which they were analysed.

Vegetation indices were analysed considering dominant shrub species, environmental variables, plot and zonal cover as well as their interactions. The complexity of the sampling structure of the data was accounted for by including transects and cover zones as random effects into a linear mixed-effects model. Diagnostic checks indicated that species richness and indicator values followed a normal likelihood, whereas evenness and beta-diversity were bounded between 0 and 1 and best modelled using a beta likelihood. Specifically, vegetation index y_{ijg} in plot $i = 1, \ldots, 480$ in cover zone $j = 1, \ldots, 120$ of transect $g = 1, \ldots, 24$ was $\mathrm{y}_{\mathrm{ijg}} \sim \mathrm{N}(\mu_{\mathrm{ijg}}, \sigma)$ for species richness and requirement indices and $\mathrm{y}_{\mathrm{ijg}} \sim \mathrm{B}(\mu_{\mathrm{ijg}}, \varphi)$ for evenness and beta-diversity, where

$$f(\mu_{ijg}) = \beta_0 + \beta_1 s_g + \beta_2 c_j + \beta_3 c_j^2 + \beta_4 d_c + \beta_5 c_j s_g + \beta_6 c_j^2 s_g + \beta_7 d_c s_g + \beta_8 v_g + \beta_9 c_j v_g + \beta_{10} c_j^2 v_g + b_{1j} + b_{2g} + b_{3g} c_j + b_{4g} c_j^2 \tag{1}$$

and

$$b_{1j} \sim \mathrm{N}(0, \sigma_1),\ (b_{2g}, b_{3g}, b_{4g})^{\mathrm{T}} \sim \mathrm{N}(0, \Sigma) \tag{2}$$

Link function *f()* was specified as identity for the normal likelihood and logit for the beta regression models. The independent variable s_g was the dominant shrub species in transect g. Variables c_j and c_j^2 were shrub cover and its square, standardized and centred in zone j. Including c_j^2 allowed for the inclusion of a potential hump-shaped relationship. Models were run with either plot cover c_p and its square c_p^2, or zonal cover c_z and its square c_z^2. Variable d_c was the standardized difference between the two shrub cover variables c_p and c_z. The reason for using cover difference d_c was that c_p and c_z were strongly collinear and including them individually would hinder stable model fitting. Variable v_g was an environmental covariate at the transect level, e.g. steepness. Initially, several covariates were included analogously, but only one is shown in Eq. 1. Environmental covariates (v_g) were reduced with stepwise likelihood-ratio tests based on significance $P > 0.05$ (Table 3b) and compared to the models with dominant shrub species as predictors based on the Akaike information criterion (AIC), log-likelihood and R^2. The terms β_0–β_{10} were coefficients for the fixed effects and their interactions. Coefficients b_{1j} were random intercepts for cover zones within transects accounting for the pseudo replication arising from the four dependent plots within each cover zone. Term b_{2g} were random intercepts for transects, b_{3g} and b_{4g} were random slopes for zonal cover and its square allowing for individual response curves at each transect. The Σ was a general 3 × 3 positive-definite variance–covariance matrix.

All models were fitted to the data with maximum likelihood using packages lme (Pinheiro and Bates 2000) and glmmADMB (Fournier et al. 2012) in R 3.6.3 (R Core Team 2020). Marginal and conditional R^2 were calculated according to Nakagawa and Schielzeth (2012). Estimates and predictions are presented for the model with the lowest AIC. Predictions for individual transects were obtained based on the estimated random coefficients b_2, b_3 and b_4 for each transect g. Overall trends were predicted based on fixed effects coefficients and the global mean of d_c.

The data used to fit the linear models are available at https://doi.org/10.5281/zenodo.3886472. More detailed vegetation data is available upon request to the authors.

Results

Characteristics of pasture-shrub transects

The selected transects were evenly distributed across the Swiss Alps and ranged from 1300 to 2200 m a.s.l. with a mean elevation of 1786 ± 253 m (Table 1). All transects were on slopes ranging from moderate (19%) to very steep (> 70%). Annual precipitation ranged from 830 mm in the inner-alpine Engadine valley (transect 19 in Fig. 1) to 2070 mm in the wet Northern Alps (transect 18). In all 480 plots, a total of 483 plant species were identified in the herb layer and 23 woody species in the shrub layer. Plant species richness per plot (2 m × 2 m) averaged 25.4 and ranged from 4 to 52, while plant species richness per transect (20 plots) averaged 98.9 and ranged from 54 to 146. On average, each plot contained 0.9 shrub species. *A. viridis* was the dominant shrub species in 15 of the 24 sampled transects, followed by *P. mugo* (6 transects). *P. abies*, *R. alpina* and *S. appendiculata* each dominated one transect. *P. abies* is not a shrub species in the strict sense, but this transect was still included in NOAS04 class 57 of the Swiss land cover map because of the small size of the trees. The three transects of other species were mainly located at the Western border of the Swiss Alps, whereas transects dominated by *P. mugo* were situated more towards the East. No such pattern was obvious for transects dominated by *A. viridis*.

Transects significantly differed in elevation, with *P. mugo* dominating high (2020 ± 280 m), *A. viridis* intermediate (1761 ± 160 m asl.) and other shrub species low elevations (1440 ± 108 m; Fig. 3). Correspondingly, mean annual temperature for transects dominated by *P. mugo* (0.8 ± 2 °C) was significantly lower ($P < 0.05$) than that of transects dominated by other shrub species (4.3 ± 0.6 °C). Transects dominated by the three dominant shrub species *A. viridis*, *P. mugo* and others did not differ significantly in steepness, annual precipitation, soil phosphorus or soil pH. For steepness and precipitation, the lack of significance may also be due to the large variability between transects and relatively small sample sizes. Because all transects were located in the transition zone between pasture and dense shrubland, they did not differ in their distance to old stands, on the one hand, or grazed areas, on the other.

Table 1 Environmental descriptors for the 24 transects surveyed across the Swiss Alps

Nr	Aspect	Geology	Dominant shrub species	Elevation (m a.s.l.)	Steepness (%)	Precipitation (mm y^{-1})	Mean annual temperature (°C)
1	S	Siliceous	*Alnus viridis*	1798	59	1722	− 2
2	N	Calcareous	*Alnus viridis*	1297	51	1703	3
3	N	Siliceous	*Alnus viridis*	1657	60	1099	4
4	E/W	Calcareous	*Alnus viridis*	1875	48	1509	2
5	S	Siliceous	*Alnus viridis*	1820	67	1597	2
6	E/W	Siliceous	*Alnus viridis*	1812	56	967	2
7	E/W	Siliceous	*Alnus viridis*	1677	56	1495	2
8	S	Siliceous	*Alnus viridis*	1783	73	1934	2
9	N	Dolomite	*Alnus viridis*	1953	65	1283	2
10	S	Siliceous	*Alnus viridis*	1707	61	1677	2
11	E/W	Flysch	*Alnus viridis*	1961	43	1353	2
12	N	Flysch	*Alnus viridis*	1758	36	1562	3
13	N	Siliceous	*Alnus viridis*	1840	57	953	0
14	E/W	Flysch	*Alnus viridis*	1829	56	1276	3
15	N	Siliceous	*Alnus viridis*	1653	54	1312	3
16	S	Dolomite	*Pinus mugo*	1981	32	1081	0
17	E/W	Dolomite	*Pinus mugo*	2180	74	982	1
18	E/W	Calcareous	*Pinus mugo*	1472	51	2070	5
19	E/W	Dolomite	*Pinus mugo*	2185	19	837	− 1
20	S	Dolomite	*Pinus mugo*	2192	32	889	0
21	S	Dolomite	*Pinus mugo*	2109	48	1137	0
22	N	Calcareous	*Picea abies*[1]	1396	34	1552	5
23	S	Calcareous	*Rhamnus alpina*[1]	1562	30	1738	4
24	N	Calcareous	*Salix appendiculata*[1]	1360	46	1694	4

Transects were selected in strata of aspect and geology with distance-specific weights to avoid clustering

[1] Pooled to shrub species ‚Other‘

Explanatory power of environmental conditions and dominant shrub species

In order to test hypothesis H2, we compared models describing the response of species richness in dependence of environmental conditions or dominant shrub species. The three most important models are shown in Table 2. Model 1, containing the full set of eight environmental variables (Table 2), had the highest R^2 of all evaluated models but was penalized for the high number of parameters and resulted in a high AIC (lower is better, i.e. more parsimonious). Reducing model 1 by successive likelihood-ratio tests led to model 2, with only steepness and geology. However, the models based on environmental variables were less parsimonious than model 3, which considered effects of the three dominant shrub species. The conditional R^2_c of models 3 and 1 were similar, although model 3 contained only the shrub species instead of the eight environmental variables and therefore resulted in a much lower AIC. Therefore, dominant shrub species is a strong predictor of the response of species richness to shrub cover.

Explanatory power of zonal and plot cover and their difference

The sampling protocol was able to catch the small-scale patchiness within intermediate cover zones (Fig. 4). In the 0% cover zone, plot cover (c_p) was always 0% because there were no scattered shrubs in this zone. In the 25, 50 and 75% cover zones, half of the values of observed c_p (the gray boxes in Fig. 4) spanned 48%, on average. In the 100% cover zone, observed c_p was less variable but a few very low values were observed (shrub gaps). In addition, c_z was generally slightly overestimated in comparison to c_p.

In order to test hypothesis H3, we evaluated models for plant species richness run with either c_z or c_p and the cover difference d_c as predictors (Table 3). Using c_z (model 3) resulted in a higher conditional R^2_c and lower AIC compared

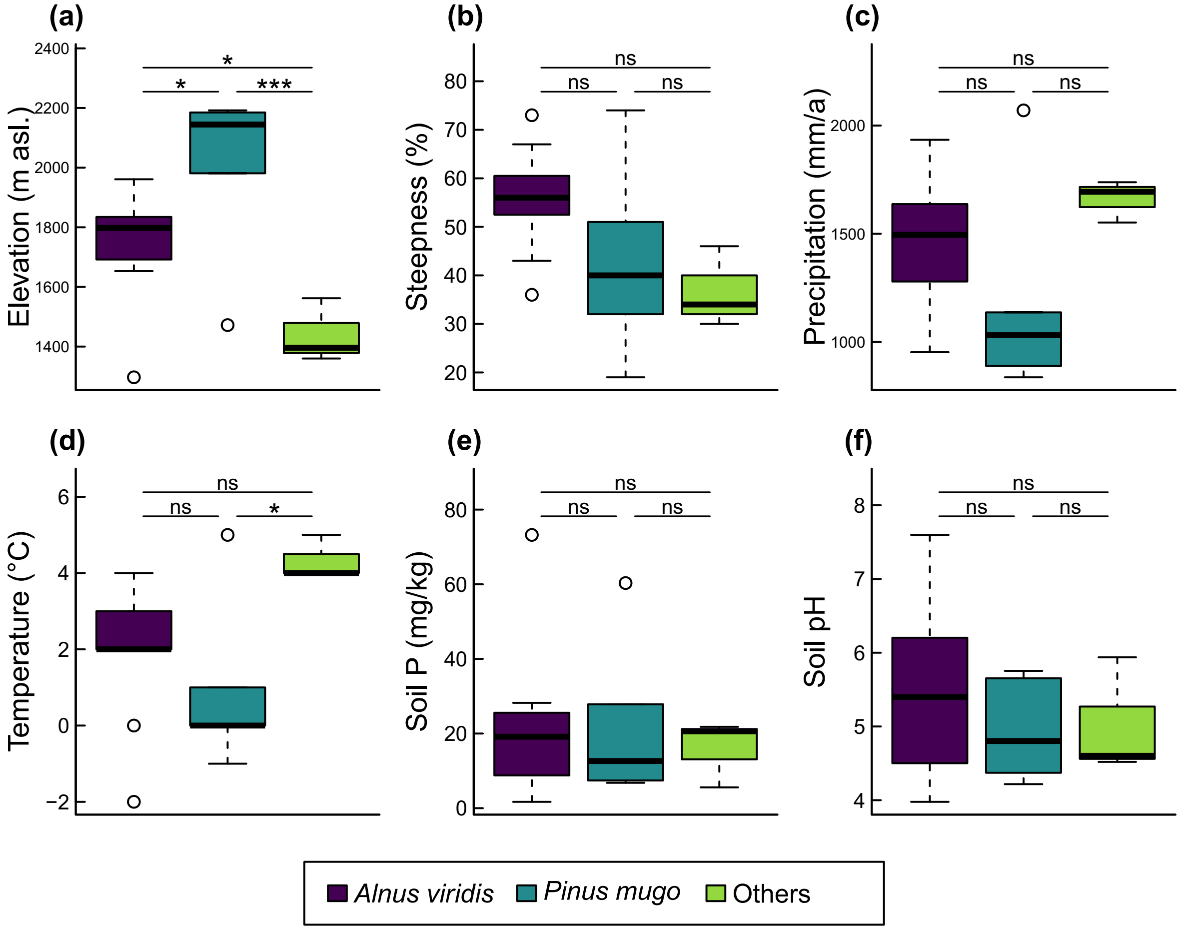

Fig. 3 Differences in environmental variables among transect dominated by *Alnus viridis*, *Pinus mugo* and other shrub species. Elevation and steepness are based on the digital terrain model of the Federal Office of Topography Swisstopo. Mean annual temperature and precipitation based on climate data of the Federal Office of Meteorology and Climatology MeteoSwiss. Soil P values were determined by ammonium acetate EDTA and pH in a soil–water suspension. Boxes show 25th–75th quartile ranges (IQR); line: median; whiskers: max. 1.5 · IQR; points: outliers. Lines and asterisks above the boxplot indicate results of pairwise Tukey test at ***$P < 0.001$, *$P < 0.05$, *ns* not significant

to using c_p (model 4). Removing the cover difference (model 5) reduced R^2_c and increased the AIC.

Effects of shrub cover and shrub species on plant species richness

Predictions based on the most parsimonious model 3 indicate that a high c_z was usually associated with low plant species richness (Fig. 5). On average, species richness at 100% shrub cover was 48.9% of that in open pasture (0% shrub cover). This reduction was observed in every transect except transect 23, in which an average of 20.8 species were recorded at 0% cover and 21.6 species at 100% cover. This transect was dominated by *R. alpina* and characterized by a comparatively low elevation, high precipitation and high mean annual temperature. In 20 of the 24 transects, highest species richness, averaged over the four plots of a cover zone, was observed at 0 or 25% shrub cover. In the remaining four transects the maximum species richness was observed at 50% (transects 2, 16 and 22) and 75% shrub cover (transect 23). Moreover, mean species richness was among the highest in these transects.

Plant species richness was not directly associated with dominant shrub species. The mean number of species per plot in transects dominated by *P. mugo* was only 2.8 species higher than in transects dominated by *A. viridis* (estimated coefficient of the difference = 2.8; not significant; Table 4). Transects dominated by other shrub species contained 3.6 species more (not significant) than those dominated by *A. viridis*.

In contrast, the effects of shrub cover on species richness were strongly associated with dominant shrub species. In transects dominated by *A. viridis,* species richness strongly declined with increasing shrub cover. The decline

Table 2 Goodness of fit measures for models of plant species richness regressed on different environmental variables and dominant shrub species

ID	Model	R^2_m	R^2_c	AIC	LogLik
1	$c_z + c_z^2 + d_c + G + St + A + E + Pr + P + T + pH$	0.664	0.793	3093.4	– 1490.7
2	$c_z + c_z^2 + d_c + G + St$	0.595	0.792	3067.7	– 1505.8
3	$\mathbf{c_z + c_z^2 + d_c + S}$	**0.503**	**0.792**	**3061.6**	**– 1510.8**

The final model 3 is shown in bold. Not all intermediate models are shown. R^2_m variance explained by the fixed effects, R^2_c variance explained by both the fixed and the random effects, *AIC* Akaike information criterion, *LogLik* log likelihood, c_z zonal cover, c_z^2 squared zonal cover, d_c cover difference $c_z - c_p$, *G* geology (four classes: Calcareous, Dolomite, Flysch, Siliceous), *St* steepness, *A* aspect (three levels: North, South, East/West), *E* elevation, *Pr* annual precipitation, *P* soil phosphorous, *T* mean annual temperature, *pH* soil pH, *S* dominant shrub species (three classes: *A. viridis*, *P. mugo* and Others)

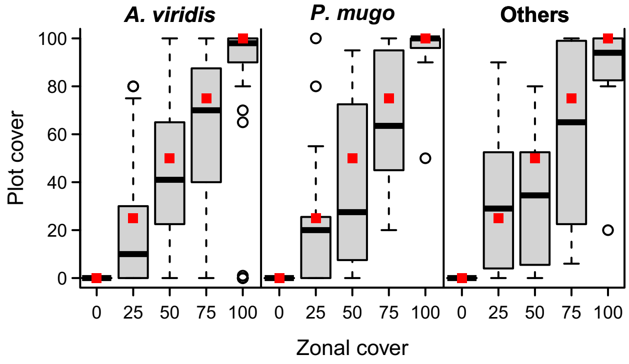

Fig. 4 Distribution of observed plot cover (boxplots) in cover zones (red squares) of the three dominant shrub species *Alnus viridis*, *Pinus mugo* and others. Boxes show 25th–75th quartile ranges (IQR); line: median; whiskers: max. 1.5 · IQR; points: outliers

Table 3 Goodness of fit measures for models of plant species richness regressed on zonal cover (c_z) or plot cover (c_p) an their difference (d_c)

ID	Model	R^2_m	R^2_c	AIC	LogLik
3	$\mathbf{c_z + c_z^2 + d_c + S}$	**0.503**	**0.792**	**3061.6**	**– 1510.8**
4	$c_p + c_p^2 + d_c + S$	0.483	0.788	3101.7	– 1530.9
5	$c_z + c_z^2 + S$	0.486	0.777	3089.8	– 1527.9

The final model 3 is shown in bold. R^2_m variance explained by the fixed effects, R^2_c variance explained by both the fixed and the random effects, *AIC* Akaike information criterion, *LogLik* log likelihood, c_z zonal cover, c_z^2 squared zonal cover, c_p plot cover, c_p^2 squared plot cover, $d_c = c_p - c_z$, *S* dominant shrub species (three classes: *A. viridis*, *P. mugo* and others)

was linear with a decrease of – 21.6 species ($P = 0.001$) across the entire range of the transect and with no effect of squared cover (coefficient of – 0.54; $P = 0.93$). For *A. viridis*-dominated transects, a maximum of 33.9 species per plot was estimated to occur in open pasture, which dropped to only 12.8 species (38% of maximum) in dense shrub. The response of plant species richness to the cover of *P. mugo* was concave. A linear slope of 9.3 ($P = 0.36$) and an effect of squared cover of – 24.6 ($P = 0.008$) resulted in a hump-shaped response with a maximum of 34.6 species per plot at 19% shrub cover. In open pasture, 33.9 species (97% of maximum) were estimated and 18.6 species (54% of maximum) were estimated for closed shrubs. Transects dominated by other shrub species also showed a concave response pattern with a peak at 42% shrub cover with an estimate of 36.9 species. With estimated coefficients of 32.5 ($P = 0.03$) for the linear term and – 38.6 ($P = 0.004$) for the squared term, the concave shape was more pronounced than for *P. mugo*. Estimates at 0 and 100% shrub cover were 30.1 and 23.9 species (81 and 65% of maximum), respectively. Even though only three transects were dominated by other shrub species, estimates were significantly different from the *A. viridis*-dominated transects.

The estimates of the cover difference d_c indicated that the two cover measures c_z and c_p acted additively on plant species richness. In transects dominated by *A. viridis* and *P. mugo*, cover difference ($d_c = c_p - c_z$) had a significant negative effect ($P < 0.001$) on plant species richness. Hence, in cases where $c_p > c_z$, species richness was lower. For example, if a plot located in the 50% cover zone (c_z) of *A. viridis* had a local shrub cover (c_p) of 70%, species richness was reduced by $-4.2 \cdot 0.2 = -0.84$ species. The estimated effect of cover difference was lower ($P = 0.03$) for *P. mugo* than for *A. viridis,* indicating that species richness in *P. mugo* transects was more locally influenced by c_p than in transects dominated by *A. viridis*. In case of 70% plot cover of *P. mugo* in the 50% cover zone, the reduction was $-(4.6 + 5.7) \cdot 0.2 = -2.0$ species. The marginal effect of d_c in transects dominated by other shrub species indicated that species richness was predominately determined by c_z.

Effects of shrub cover and shrub species on evenness and beta-diversity of plant species

The model of species evenness was simpler than that of species richness because c_z^2 was insignificant and omitted ($P > 0.05$). Compared to *A. viridis*-dominated gradients, evenness was similar in *P. mugo*-dominated gradients and significantly higher for those dominated by other shrub species ($P = 0.01$). Evenness of species abundance linearly decreased with increasing shrub cover ($P > 0.001$), that is, vegetation in dense shrub was dominated by fewer plant species. The decrease of evenness with shrub cover was

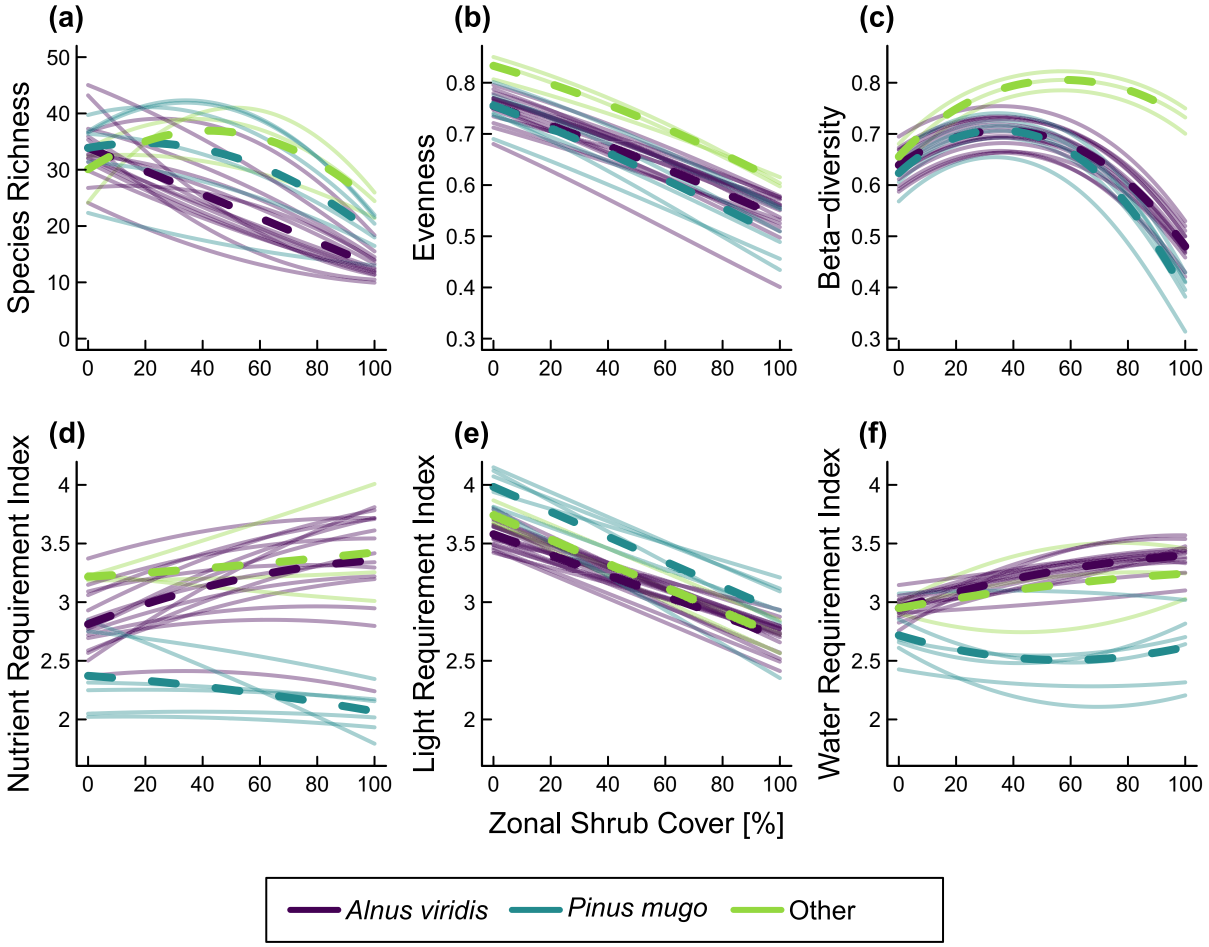

Fig. 5 Predictions of **a** plant species richness, **b** evenness, **c** beta-diversity, **d** nutrient requirement index, **e** light requirement index and **f** water requirement index regressed on zonal shrub cover. Bold dotted lines were predicted based on linear mixed-effects models with the fixed terms zonal cover and dominant shrub species. Thin, solid lines were predicted with zonal cover, dominant shrub species and random effect estimates of each transect

insignificantly stronger in *P. mugo* and other shrub species than in *A. viridis*.

Beta-diversity among plots within the same cover zone showed a hump-shaped response to shrub cover. Both, the effects of c_z and c_z^2 on beta-diversity were highly significant ($P < 0.001$). Beta-diversity peaked at 36% and 35% cover of *A. viridis* and *P. mugo* and values in open pasture were 90% and 88% of the maximum, respectively. At 100% shrub cover, beta-diversity decreased to 68% and 55% of the maximum, for *A. viridis* and *P. mugo*, respectively. That is, plots with dense stands of *P. mugo* were most similar in species composition. Indeed, vegetation underneath *P. mugo* was often dominated by *Lycopodium annotinum* L. or *Erica carnea* L. with cover percentages of ≥ 50%. Plots in transects dominated by other shrub species were significantly less similar than in the other two groups, independent of c_z. Beta-diversity in these transects peaked at 57% shrub cover and were 81% and 90% of the maximum in open pasture and closed shrub, respectively.

Effects of shrub cover and shrub species on nutrient, light and water requirement indices

Plant species in the herb layer of transects dominated by *P. mugo* had a significantly lower nutrient requirement index than those dominated by *A. viridis* ($P > 0.001$). Transects dominated by other shrub species and *A. viridis* did not differ significantly. The nutrient requirement index significantly increased (est = 0.93; $P < 0.001$) with the cover of *A. viridis*. An increasing cover of *P. mugo* and other shrub species did not change the nutrient requirement index of plants in the herb layer (est = -0.18; $P = 0.62$ and est = 0.15; $P = 0.76$, respectively).

Table 4 Estimated effects (Est.) and their significances (Sig.) of zonal shrub cover and dominant shrub species on (a) plant species richness, (b) species evenness, (c) beta-diversity, (d) nutrient requirement, (e) light requirement and (f) water requirement index as estimated by (generalized) linear mixed-effects models

	a) Richness		b) Evenness[1]		c) Beta-diversity[1]		d) Nutrient Index		e) Light Index		f) Water Index	
Variables	Est	Sig	Est	Sig	Est	Sig	Est	Sig	Est	Sig	Est	Sig
A. viridis (intercept)	23.4	***	0.64	***	0.25	**	3.08	***	3.14	***	3.17	***
P. mugo	2.83	ns	− 0.07	ns	− 0.22	ns	− 0.86	***	0.31	**	− 0.51	***
Other	3.63	ns	0.38	**	0.57	**	0.24	ns	0.09	ns	− 0.08	ns
c_z	− 20.5	**	− 0.97	***	1.69	***	0.93	***	− 0.88	***	0.73	***
c_z^2	− 0.54	ns			− 2.34	***	− 0.39	*			− 0.28	ns
d_c	− 4.23	***	− 0.94	***	− 0.6	***	0.16	**	− 0.26	***	0.14	***
c_z × *P. mugo*	29.8	*	− 0.15	ns	0.47	ns	− 1.11	*	− 0.19	ns	− 1.46	***
c_z × Other	53	**	− 0.2	ns	1.02	ns	− 0.78	ns	− 0.15	ns	− 0.3	ns
c_z^2 × *P. mugo*	− 24.1	*			− 0.78	ns	0.26	ns			0.91	**
c_z^2 × Other	− 38.1	**			− 0.03	ns	0.44	ns			0.14	ns
d_c × *P. mugo*	− 5.67	*	− 0.26	ns	0.37	**	− 0.07	ns	− 0.26	*	− 0.11	ns
d_c × Other	4.96	ns	− 0.31	ns	0.35	*	− 0.17	ns	− 0.17	ns	− 0.02	ns

Fixed effects were zonal cover (c_z), squared zonal cover (c_z^2), difference between zonal and plot cover (d_c) and dominant shrub species. Non-significant fixed effects were omitted from the models. To account for pseudo-replication, all models allowed for a random intercept for plots within the same cover class and transect. *A. viridis* was used as the baseline treatment and estimates of interaction terms are to be added to the main effects (e.g. the linear effect of c_z on richness is − 20.5 for *A. viridis* and 29.8–20.5 = 9.3 for *P. mugo*). c_z was standardized and centred and estimates of the intercept apply to 50% shrub cover. Significances are expressed as ns: $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

[1] Bounded between 0 and 1 and therefore fitted with β likelihood. Estimates are given on logit scale

The light requirement index of the herb layer in transects dominated by *P. mugo* was significantly higher than that of *A. viridis*-dominated transects ($P < 0.001$), transects dominated by other shrub species and by *A. viridis* did not differ. The light requirement index significantly decreased with the cover of *A. viridis* ($P < 0.001$). The cover of *P. mugo* and other shrub species tended to have a weaker effect on the light requirement index.

The water requirement index of plants in the herb layer was significantly higher for transects dominated by *A. viridis* and other species than by *P. mugo* ($P < 0.001$). There was a significant increase in water requirement of the herb-layer vegetation at higher cover of *A. viridis* and other shrub species ($P < 0.001$). Water requirement indices of vegetation were lowest at intermediate levels of *P. mugo*.

Species association to dominant shrub species and zonal shrub cover

The IndVal analysis clearly associated several typical plant species to each of the dominant shrub species (Fig. 6). At 100% shrub cover in *A. viridis*-dominated transects, it

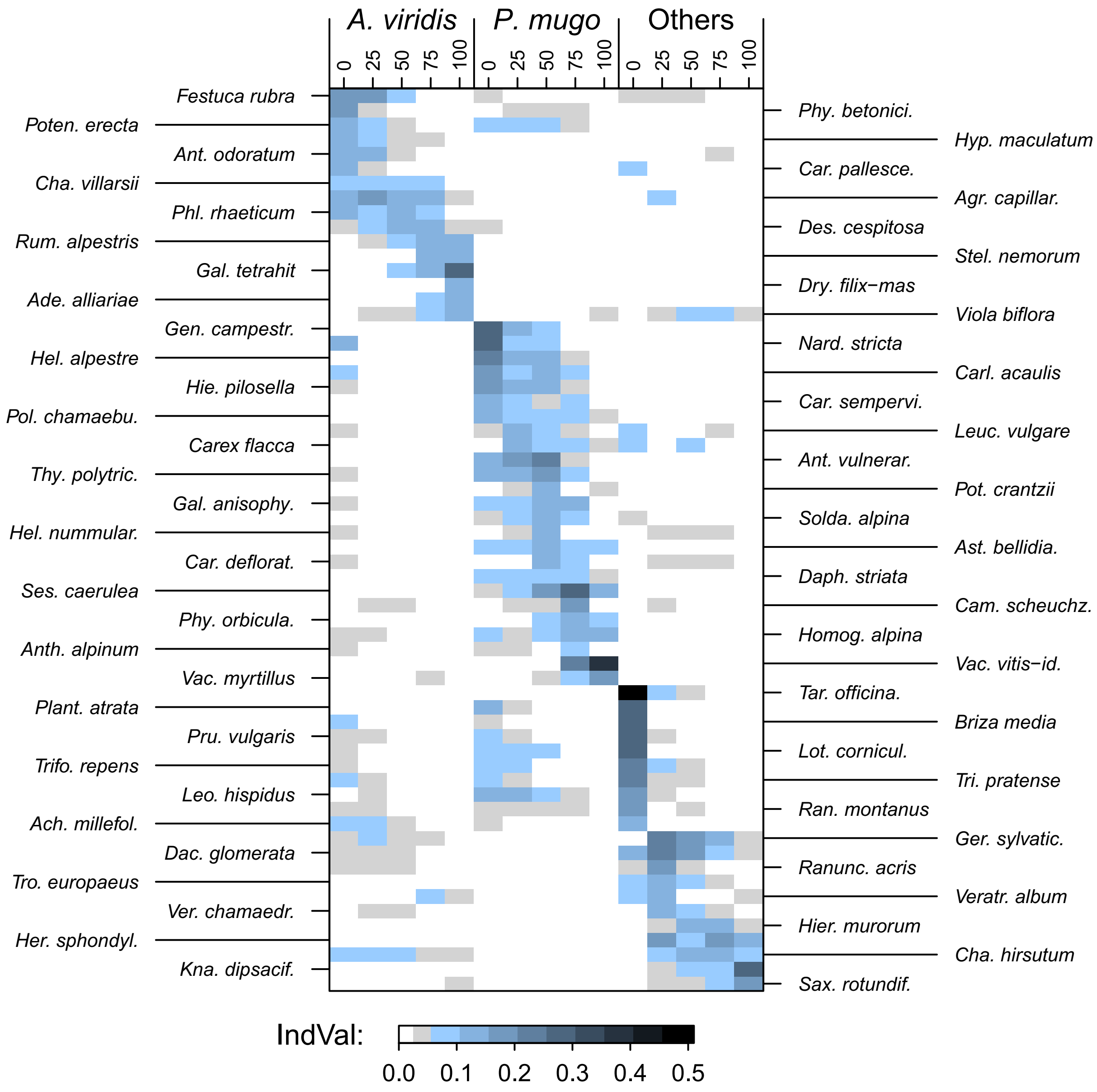

Fig. 6 Strength of association between plant species and combinations of dominant shrub species and zonal shrub cover, as quantified by IndVal values according to Dufrêne and Legendre (1997). IndVal values indicate how uniquely a species is associated to the cover zone of a given shrub species. Species ordered according to strongest association (several associations possible)

identified a very distinct plant species community with a high number of strongly associated species, such as the tall forb *Adenostyles alliariae* (Gouan) A. Kern. or the fern *Dryopteris filix-mas* (L.) Schott. The dwarf shrubs *Vaccinium vitis-idea* L. and *V. myrtillus* L. were strongly associated with dense stands of *P. mugo*. High cover of other shrub species favoured *Knautia dipsacifolia* Kreutzer and *Saxifraga rotundifolia* L.

At low shrub cover values (open pasture), species were non-specific and were present irrespective of the dominant shrub species, as demonstrated by the numerous additional ties to other cover zones outside the shrub species when vertically following the 0% cover zones in Fig. 5: For instance, species like *Nardus stricta* L., *Carlina acaulis* L., *Hieracium pilosella* L. and others were most strongly associated with open pastures (0% shrub cover) in *P. mugo*-dominated transects, but also had a significant association with the open pastures of *A. viridis* dominated transects. These associations with multiple dominant shrub species diminished as shrub cover levels increased. Hence, species at 100% shrub cover were distinctly associated with only one shrub species. Likewise, reading Fig. 5 horizontally shows that species growing in plots within 100% cover zones were also abundant in plots of other cover zones of the same dominant shrub species, but were rarely found in the herb layer of other dominant shrub species. In turn, species associated with low cover values have ties to other dominant shrub species, but only at cover values below 75%.

The change of species association along the pasture-shrub transect differed for the dominant shrub species. The lowest number of indicator species among the dominant shrub species was found for *A. viridis.* The change in species composition from open pastures to closed *A. viridis* was very sudden, with only a few indicator species found at intermediate levels. Transects of *P. mugo* showed a more gradual change of species composition with very few species associated with one specific proportion of shrub cover. The most distinct change in species composition from one cover zone to the next was observed in transects dominated by other shrub species. There was very little overlap between species at the 0% cover zone and species found between 25 and 100% shrub cover. In addition, these species had few similarities to *A. viridis*-dominated transects and none to those dominated by *P. mugo*.

Discussion

Drivers of botanical composition along pasture-shrub transects

Our investigation of 24 pasture-shrub transects in the subalpine zone of the Swiss Alps showed that the dominant shrub species is a parsimonious predictor of vegetation response along pasture-shrub transects. Environmental conditions such as elevation and geographic location also tended to affect the distribution of shrub species. For instance, *A. viridis* was typically dominating mid-elevation transects on siliceous substrate with northern aspect. However, *A. viridis*-dominated transects 2 and 4 had calcareous substrate and transects 1, 5, 8 and 10 had south-facing slopes, in line with Caviezel et al. (2017). Since each shrub species generally prefers certain environmental conditions, these conditions are already implicitly included in the factor shrub species. Thus, adding environmental variables in the model did not improve the prediction of vegetation response beyond the explanatory power of the three major shrub species. Hence, the data did not confirm our hypothesis H2 that environmental conditions are the primary determinant of the response of vegetation to shrub cover as suggested by earlier investigations in various biomes (Howard et al. 2012; Pornaro et al. 2017; Soliveres et al. 2014).

A further reason for the strong explanatory power of dominant shrub species may be that shrub species modify growth conditions by their presence. While such interactions have been well described for *P. mugo* (Wild and Winkler 2008), they are special for *A. viridis*, which is able to fix atmospheric N_2 by symbiotic bacteria of the species *Frankia alni* (1997). Leave and root litter of *A. viridis* are N-rich and their decomposition releases N into the environment and causes eutrophication (Bühlmann et al. 2016). Indeed, the IndVal analysis of our data revealed that dense stands of *A. viridis* were populated by a specialized community of very few species as described earlier by Anthelme et al. (2001, 2003, 2007). These species typically have a high nutrient requirement index suggesting a productive environment with high nutrient availability (Boscutti et al. 2014). Using the observed vegetation transects as a proxy for the temporal development of a given site, we argue that despite similar initial species composition, effects of the locally dominant shrub species supersede environmental influences over time.

As a consequence, in the majority of transects dominated by *A. viridis*, plant species richness steadily decreased with shrub cover. In contrast, many of the transects dominated by *P. mugo* and especially the few transects dominated by *Salix sp.*, *R. alpina* and *P. abies* showed the hump-shaped response of species richness to shrub cover often described in literature (Kesting et al. 2015; Pornaro et al. 2013; Soliveres et al. 2014). Moreover, the hump-shape differs between *P. mugo* and other shrub species. In *P. mugo* transects, plant species richness increases above the value in open pasture by only a single species, namely *P. mugo*. In dense stands of *P. mugo*, however, plant species richness is only half as large as in open pasture. Other shrub species seem to have other dynamics, but observations are too rare to draw conclusions. Hence, our initial hypothesis H1 of maximum richness in the intermediate transition zone is obviously not generally applicable, as it is evident for *A. viridis*.

Beta-diversity within cover zones shows a hump-shaped form independent of dominant shrub species, in line with hypothesis H1. In *A. viridis* and *P. mugo*, beta-diversity peaked in zones with scattered bushes, which offer more different habitat niches than open grassland (Villegas et al. 2010). However, while open pastures were only slightly more homogeneous in species composition (i.e. lower beta-diversity) than the maximum, dense shrub communities were much more homogeneous. One explanation for the homogeneity is that shrub stands are early successional communities which are dominated by a few plant species, namely the dominant shrub and a few associated species in the understorey. In addition, evenness of plant species composition decreased linearly in all transects, caused by the increasing dominance of a few shrub species.

Environmental factors may also have a crucial influence on vegetation but are difficult to quantify across large areas. One such factor is soil humidity. The water requirement index indicated that transects dominated by *A. viridis* as well as other shrub species were wetter than transects with *P. mugo*. Rainfall also tended to be smaller on sites dominated by *P. mugo*, but variability was really large. Since no comprehensive spatial information on soil water availability extists, it was difficult to investigate this aspect further.

Challenges of vegetation sampling in pasture-shrub transects

Sampling vegetation along pasture-shrub transects involves the assessment of plant communities with different structures (Pajunen et al. 2011). Pastures are usually short but dense communities dominated by numerous grasses and small herbaceous plants. Leaf area is concentrated near the soil surface. In contrast, shrub areas consist of two vegetation layers, a shrub layer formed by a limited number of woody species and an understory community of specialized grasses and herbs. Leaf area is thus concentrated at the shrub canopy as well as near the soil surface. Intermediate transition areas between open pastures and dense shrub stands are often heterogeneous because shrubs establish in patches (Duelli 1992), as can be seen from the large heterogeneity in vegetation.

In the subalpine zone, patch size of shrubs varies between a few square decimetres for young individuals to several tens of square meters for groups of individuals. The heterogeneity of the intermediate transition areas complicates placement of representative sampling plots and their subjective placement can bias the results. Moreover, not all shrub effects operate at similar spatial scales. We have overcome the difficulties of heterogeneity, representability and spatial scales by applying a novel sampling protocol. The method is related to Daubemire's transect sampling technique (Stohlgren et al. 1998) and involves two steps: (1) the establishment of cover zones along the transect and (2) the sampling of vegetation in multiple plots at fixed distances. Step 1 ensures representability of the samples for the respective cover zone; Step 2 takes into account heterogeneity and avoids the subjective choice of where to sample. Because of the large heterogeneity, the size of sampling plots needed to be relatively small (2 × 2 m). A larger plot size would have levelled variation within the four plots of a cover zone and blurred heterogeneity. Moreover, the small plot size allowed to survey one transect in approximately three days. Our data shows that the observed shrub cover in each sampling plot varied considerably within each cover zone, especially at intermediate values. This means that plant species were observed in the multitude of situations in which they occurred along the transects, be it open pastures, gaps without shrubs, half- or full-shaded spots.

A transparent assessment of the inherent heterogeneity in shrub-pasture transects at multiple spatial scales was possible by analysing the data in a mixed-effects model. It accounts for multiple samples within cover zones along transects and balances the variability within transects as well as within cover zones against variability between and along transects. These methods of sampling and statistical analysis enable unravelling the effects of two relevant levels of shrub cover: plot and zonal cover. The two cover measures differ in their ecological implications: Plot cover has a direct impact on light and nutrient availability for plants, germination success and grazing pressure. Zonal cover affects pollination, seed dispersal, the access of grazing animals in general and, especially in the case of *A. viridis*, the availability of mobile nutrients such as nitrogen. Indeed, plant species richness was more strongly affected by zonal cover in *A. viridis* than in *P. mugo*. Hence, our data confirmed hypothesis H3 and demonstrates that both cover types are important determinants of plant species composition depending on the dominant shrub species.

Practical implications for conservation

The analysis of vegetation indices suggested considerable differences among the three dominant shrub species studied. In *A. viridis*, species richness and evenness declined linearly with increasing cover, whereas beta-diversity peaked at around 35% and strongly declined in dense stands. A scattered occurrence of *A. viridis* with about 35% cover increases beta-diversity by 10%, but comes at the price of a species loss of 22%, likely due to the fact that N enrichment is not restricted to the shrub itself but expands to the surroundings (Bühlmann et al. 2016). Dense *A. viridis* resulted in 62% less species and a reduction of beta-diversity of 32%. In *P. mugo*, species richness was little affected up to a cover of 40% and beta-diversity peaked at around 35%. Hence, a scattered occurrence of *P. mugo* increases beta-diversity without impairing richness. The limited data on other species shows that both diversity measures peak at around 40 to 60% cover and suggests that a substantial cover of these species promotes species diversity by increasing species richness and beta-diversity (+ 23% for both).

Our study mainly demonstrates that generalizing effects of shrub encroachment on plant diversity is challenging and potentially misleading. Results of investigations carried out on a single shrub species should only be extrapolated when justifiable. For example, recommendations elaborated from data on dwarf-shrub communities (Koch et al. 2015) or for shrub communities in general (Gómez-Aparicio 2009) cannot be readily translated to communities of other shrub species. The basic message for management is that ‘shrub does not equal shrub’ and, hence, management decisions need to take into account shrub identity. Species-specific recommendations are necessary for efficient management of shrub-encroached areas. This is especially important, where shrubs expand beyond the habitat traditionally associated with their occurrence (Caviezel et al. 2017).

Traditionally, subalpine grasslands were created by a mix of grazing and wood cutting (Schwörer et al. 2014,2015) and it appears reasonable to maintain vegetation composition by the processes that created them (Vera 2000). The dominant shrub species in this study have different palatability to grazers (Cairns and Moen 2004). Leaves of *A. viridis* are relatively well consumed by ruminants (Leng 1997; Papachristou and Papanastasis 1994) and grazing at a sufficient stocking rate is a viable option to keep this species at low cover (Pittarello et al. 2016). In contrast, *P. mugo* is completely avoided by grazers, similar to *Pinus nigra* J. F. Arnold (Ledgard and Norton 2008) and as common for low-quality forage (Homburger et al. 2015; Pauler et al. 2020). Hence, mechanical interventions are necessary to manage encroachment of *P. mugo* in pastures. This highlights that the dominant shrub species not only determines the effects of encroachment on vegetation but also potential management strategies to maintain a diverse, semi-open landscape.

Conclusions

Our survey of 24 subalpine pasture-shrub transects in the Swiss Alps showed that the dominant shrub species is a strong predictor for the response of species diversity to shrub encroachment. *A. viridis*, the most frequent shrub species in the subalpine zone of the Swiss Alps, severely impairs plant species richness already at a low shrub cover and, in dense stands, also beta-diversity. For conservation of plant species diversity it is thus essential to maintain a low cover of this shrub species. Since *A. viridis* leaves are relatively palatable to ruminants, encroachment by *A. viridis* can potentially be controlled by adapted grazers. In contrast, a moderate cover of *P. mugo* and other shrub species is beneficial to plant species richness and beta-diversity. Since especially *P. mugo* is less attractive to grazers, a carefully designed combination of grazing and mechanical intervention is needed to maintain a semi-open arrangement of pasture and scattered shrubs.

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Author contributions MKS, AL, TZ, MK and JB conceived and designed the research; TZ, CR and MKS collected the data. MKS, TZ and CMP analysed the data. MKS and TZ wrote the manuscript with input from AL, MK and CMP.

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Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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