

# Plant community persistence strategy is elevation-specific

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## Abstract

**Aims:** Persistence plays a key role in both plant population and community dynamics as it allows withstanding temporarily habitat conditions unsuitable for growth and reproduction. Plants can exploit three different strategies to persist *in situ* (building soil seed banks, increasing adult longevity and/or clonal reproduction), the dominance of which in a community might vary along environmental gradients. Yet, their relative role in plant persistence has never been investigated.

**Location:** The Bavarian Alps, Germany.

**Methods:** We collected data on seed soil persistence, adult longevity and clonality for 290 species occurring in 18 grasslands located along an elevational gradient of 1,000 metres and examined their contribution to persistence in a community. Linear models were used to estimate the relationship between elevation and these persistence strategies.

**Results:** We found that dominance of a certain persistence strategy varied depending on environmental variability. Specifically, persistence in lowlands was mainly achieved by persistent and dense soil seed banks along with extended clonal growth (larger spread distances and higher number of offspring). Contrastingly, the main persistence strategy in the alpine communities was increased adult longevity.

**Conclusions:** The changes in relative contribution of each strategy to community persistence along the elevational gradient are interrelated suggesting a trade-off among them. We conclude that this trade-off plays an important role in species co-existence and community assembly, and might be useful to understand vegetation dynamics under ongoing climate change and improve restoration efforts of upland ecosystems.

## KEYWORDS

adult longevity, Alps, Clonality, Community, elevational gradient, grassland, persistence, soil seed bank

## 1 | INTRODUCTION

Persistence plays a decisive role in both plant population and community dynamics. It allows plants to withstand or survive temporarily short- or long-term habitat conditions unsuitable for growth and reproduction, especially in habitats subjected to high climatic

variability, habitat fluctuations and high levels of disturbance, competition and predation (Grime, 2002; García & Zamora, 2003; Ozinga et al., 2007). Moreover, in times of ever-increasing anthropogenic stress, persistence is critical for a plant's potential to adapt to global changes (Ooi, 2012; Corlett & Westcott, 2013). Species that are not able to persist at a local or regional scale are particularly vulnerable

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to extinction, whereas persistent species can easily recover even after direct destruction of above-ground vegetation (Saatkamp et al., 2018). Thus, the knowledge on plant persistence traits of natural communities is not only of interest for plant population biology, but also provides useful tools for conservation and restoration efforts (Bakker et al., 1996; Poschlod et al., 1998; Schweingruber & Poschlod, 2005).

Plants can exploit three alternative strategies to persist *in situ*: (a) produce seeds that can persist long term in the soil ("soil seed bank"); (b) grow old to be able to occupy their present site as long as possible in order to have a larger number of chances for successful seed regeneration ("adult longevity"); and/or (c) reproduce vegetatively ("clonality"; García & Zamora, 2003; Schweingruber & Poschlod, 2005; Saatkamp et al., 2014; Laiolo & Obeso, 2017). Given finite reserves of energy, the allocation of resources to vegetative growth directly leads to a reduction of regeneration by seed, resulting in a trade-off between seed persistence in soil and clonality along with extended life span (Molisch, 1938; Ehrlén & van Groenendael, 1998; Obeso, 2002; Honda, 2008; Laiolo & Obeso, 2017). Therefore, the dominance of a certain persistence strategy is expected to be habitat-specific depending on whether regeneration by seed is limited or not (Forbis, 2003; García & Zamora, 2003; Laiolo & Obeso, 2017). Thus, we suggest that the shift from "regeneration" by persistent seed banks to persistence by adult longevity and/or clonality occurs gradually along gradients of decreasing favourability for sexual reproduction. In general, clonality and long individual life span are especially significant in environments with low levels of disturbance, high competition or abiotically stressful environments (e.g. nutrient-poor and/or cold habitats), where regeneration by seed is hampered by resource limitation (Callaghan et al., 1992; García & Zamora, 2003; Rusch et al., 2010). Contrastingly, soil seed banks contribute to plant persistence under conditions of frequent disturbance, low competition or low abiotic stress promoting regeneration by seed (García & Zamora, 2003; Anderson et al., 2012; Saatkamp et al., 2014).

Contribution of single strategies (seed bank, extended life span or clonality) to plant persistence *in situ* in relation to ecological gradients has been the focus of many studies. For example, the role of the seed bank as a persistence strategy has been found to decrease with increasing elevation, due to increasing low-temperature stress (e.g. high frequency and severity of frost events, short growing and reproductive period), which strongly reduces seed inputs into soil (Funes et al., 2003; Ma et al., 2010). In a similar system, Nobis and Schweingruber (2013) revealed a general increase in adult age towards higher elevations that can be explained by higher allocation of available resources to vegetative growth (Rosbakh & Poschlod, 2018). Similarly, decreasing allocation to regeneration along gradients of abiotic stress was found to favour clonal reproduction at the dry, cold or very wet ends of the gradients (Song et al., 2002; Ye et al., 2014).

Although many of these studies have looked at changes across gradients, a literature review indicates that only a few of them

have evaluated persistence traits along an entire gradient (e.g. Molau & Larsson, 2000). Specifically, soil seed bank research has been done almost exclusively either in lowlands (Bekker et al., 1998) or in alpine habitats (Arroyo et al., 1999; Cummins & Miller, 2002) and observations at intermediate altitudes are lacking. Furthermore, previous research is usually limited to one of the persistence traits; either seed banks (Ma et al., 2010), extended life span (Nobis & Schweingruber, 2013), or clonality (Ye et al., 2014), in single (e.g. seed bank; Cummins and Miller (2002)) or a very few species (e.g. adult longevity; Rosbakh & Poschlod, 2018). Moreover, these studies are scattered over regions with different climatic conditions, successional stages and land use types and intensities making any generalisations about trade-offs among persistence strategies impossible. Finally, observations of persistence trait variability along environmental gradients have mainly been made at the population and species level (e.g. maximal individual longevity in and Nobis and Schweingruber, 2013, respectively), and rarely at community level.

Here, we study the relative role of soil seed bank, clonality and adult longevity in local persistence in 18 grassland communities located along an elevational gradient in the Bavarian Alps, Germany. This is an ideal study system to address the sensitivity of persistence traits to environmental variability, because at higher elevations the conditions for regeneration by seed become less favourable (e.g. short vegetation period, high frequency and severity of frost events; Billings & Mooney, 1968; Körner, 1999), whereas the low-stress environment in lowlands selects for generative regeneration (Cummins & Miller, 2002; Molau & Larsson, 2000). In this context, our *a priori* hypothesis was that the importance of clonality and extended life span as persistence strategies will increase with increasing elevation, whereas the contribution of soil seed banks to persistence will increase towards lower elevations, where regeneration by seed is more frequent. We expected the contribution of each trait to community persistence to be gradual along the environmental gradient, because the decrease in one should be compensated by increasing the relative importance of other traits.

## 2 | METHODS

### 2.1 | Study system

The field work was conducted in the Bavarian Alps (northern part of the Calcareous Alps; Appendix S1) from 2009 to 2017. The study region has a typical alpine relief, with steep mountain peaks composed of Triassic lime and dolomite rocks (Marke et al., 2013). The climate is typically montane with a strong decrease in mean annual air temperatures along the elevational gradient with a lapse rate of ca. 0.6°C/100 m of elevation. Mean annual precipitation in the region varies, ranging from approximately 1,500 mm to 2,600 mm (Marke et al., 2013).

For the purpose of this study, we established 18 sites in species-rich grasslands on calcareous nutrient-poor soils (the



most widespread non-forest vegetation type in the study area) along an elevation gradient from 935 m to 2,032 m above sea level (a.s.l.). At lower elevations, grasses (e.g. *Arrhenatherum elatius*, *Dactylis glomerata*, *Holcus lanatus*) and tall herbs (e.g. *Centaurea jacea*, *Crepis biennis*, *Leucanthemum ircutianum*) dominated in the grasslands being replaced by sedges (e.g. *Carex firma*, *Carex sempervirens*), dwarf shrubs (e.g. *Dryas octopetala*, *Vaccinium myrtillus*) and short-stature herbs (e.g. *Bistorta vivipara*, *Crepis aurea*, *Homogyne alpina*) as altitude increases. All the grasslands were intensively grazed by domestic cattle or used for hay-making until the mid of the 20th century. Today, the grasslands below the tree-line are used or managed by cattle grazing at a low intensity, whereas the alpine grasslands (above ca. 1,700 m a.s.l.) are occasionally grazed by sheep or wild ungulates.

## 2.2 | Environmental characteristics of the study sites

We characterised each site in terms of its vegetation composition, temperature conditions, water supply, water conditions and disturbance (grazing). The vegetation at the sites was surveyed during the peak of the growing season, which was elevation-specific, in the year of soil seed bank collection (Appendix S2). We recorded the presence/absence of all vascular species within each of 10 plots per site, in which soil seed bank samples were collected (see subsection 2.3.1 *Soil seed bank* below). Site temperature conditions included mean annual air temperature (MAT), length of vegetation period (number of days with mean temperatures over +5°C) and thermic conditions during vegetation period. Air temperature data were obtained from 20 weather stations located close to the study sites at elevations from 360 m to 1,919 m a.s.l. MAT at each station was calculated over the period 2000–2008; from these data, lapse rates between elevation and MAT in the study region were calculated (0.63°C/100 m of elevation) to define the MAT at all the collection sites. The same temperature data were used to calculate the length of vegetation period. Thermic conditions during the vegetation period were estimated with the help of the Landolt indicator value for temperature (Landolt *T*), a proxy for mean soil and surface temperatures after snow melt (Landolt et al., 2010; Scherrer & Körner, 2011).

Site water supply included mean annual precipitation (MAP), soil depth and the Landolt indicator value for soil moisture (Landolt *F*). The MAP was obtained from the same weather stations (average for the period 2000–2008) as for the temperature data and indicates total amount of precipitation the sites receive during the whole year. Soil depth was used as a proxy for soil water capacity (e.g. shallower soils keep water for shorter times as compared to deeper soils) and was estimated by repeatedly sticking an iron rod of 0.6 mm diameter into the soil (30 random measurements per site). Landolt *F* indicates soil water availability to plants during the vegetation period.

Soil nutrients included total soil nitrogen (N), plant available phosphorus (P) and potassium (K) and Landolt indicator value for soil

nutrients (Landolt *N*). The soil N, P and K were collected in the year of soil seed bank and vegetation sampling, and analysed as described in Rosbakh and Poschlod (2018).

Finally, grazing intensity (ordinal scale), the main disturbance factor in the study sites, was recorded at all study sites and included three levels: (a) no agricultural usage in the present and occasional grazing by sheep and wild ungulates; (b) occasional extensive grazing by cows; and (c) mountain dairy farm with permanently grazing cows (except for site HO5 which was extensively grazed by sheep).

## 2.3 | Persistence strategy data

### 2.3.1 | Soil seed bank

Depending on elevation, soil seed bank sampling took place right after snowmelt from the first week of April to the second half of May in 2010–2017. At each site, we selected randomly ten 2 m × 2 m plots (replicates) with homogenous vegetation. At each plot, 10 random soil samples were collected by coring the soil to 10 cm depth with a soil auger of 4 cm in diameter, divided into two 5-cm layers (0–5 and 5–10 cm). We focused on the first 10 cm of the soil profile, in order to account for possible site-specific differences in sampled volume of soil (e.g. soils in depressions and lowlands tend to be deeper). The soil of each layer was bulked together. Altogether, there were 100 samples from each site and 1,800 samples from all sites.

Immediately after collection, soil samples were transported to the lab, where they were stored at +4°C for a maximum of five days before the next step. The soil samples were sieved through a 0.2 mm sieve, spread evenly and thinly on plastic trays (width 40 cm) filled with potting soil (Heerdt et al., 1996) and cultivated in an outdoor house under field conditions in the Botanical Garden of the Regensburg University (Bavaria, Germany). All the samples were cultivated for two growing seasons, to allow all viable seeds to germinate. Trays were watered regularly. Emerging seedlings were identified and removed or replanted for later identification regularly to reduce possible negative effects on non-germinated seeds. After the initial flush of germination during the first cultivation year had ended, the soil samples were carefully turned over with a fork, to facilitate germination of ungerminated seeds. After the cold stratification during the winter between two growing seasons, the soil samples were turned over one more time. Cultivation was stopped when no more seedlings emerged for several consecutive weeks. Five containers with only potting soil were used to control for contamination of airborne seeds or seeds present in the potting soil.

Based on these data, we assigned the ability of a species to persist in a site in the form of soil seed bank as a binary variable (1, able to build up a seed bank; 0, otherwise) if it had at least one germinable seed in collected soil samples. The soil seed bank presence/absence was calculated for all species detected both in the vegetation and

soil samples. In addition, for each study site we estimated seed bank density (seeds/m<sup>2</sup>) as a quantitative measure for persistence in soil by adding up the numbers of seedlings of all single species germinated from the corresponding soil samples.

### 2.3.2 | Adult longevity

Adult longevity was expressed in two ways: as a binary trait, where “1” are perennial plants and “0” annual ones, and maximum life span (“perenniality”). The information on annual/perennial species was collected from the CLO-PLA, a database of clonal and bud bank traits of the Central European flora (Klimešová et al., 2017). Maximum life span is a numeric variable (years) and is based on herbochronology, a technique adapted from dendrochronology using growth rings in the secondary xylem of the root collars (Schweingruber & Poschlod, 2005). Briefly, the annual rings are counted in thin, stained sections of main roots or rhizomes of herbaceous species collected from their typical habitats. The maximum life span data were obtained from “Flora Indicativa” (Landolt et al., 2010); data on 23 species missing in that source were collected by S. Rosbakh (unpublished) using the same method.

### 2.3.3 | Clonality

Similar to adult longevity, clonality was expressed as a binary trait (“capacity for clonal growth”, “1” is plants that live longer than one year, multiply vegetatively and flower several times in their lifetime and “0”, otherwise; Klimešová et al., 2017) and as a clonality index. This index expresses the annual rate of clonal spread (lateral spreading distance; <1 cm, 1–25 cm, 25+ cm) and multiplication (number of clonal offspring; <1, 1, 2–10, 10+) and can be used as a semi-quantitative measure for species clonality; species with lower index values tend to spread laterally for short distances and/or produce low numbers of clonal offspring. Briefly, number of clonal offspring was assigned to four different categories (0–3), representing 0, 1, 2–10 and >10 offspring produced per year, respectively. Lateral spread was assigned to three different categories (0–2), representing 0.01, 0.25 and >0.25 m/year, respectively. The clonal index equals the sum of the category values for number of clonal offspring (0–3) and lateral spread (0–2; Johansson et al., 2011). Furthermore, we collected data on distance of lateral spread and number of clonal offspring for each species, to provide a better explanation for clonality index variation along the elevational gradient (see below). The data on capacity for clonal growth and clonality index were retrieved from the CLO-PLA database.

## 2.4 | Statistical analysis

### 2.4.1 | Environmental characteristics of the study sites

Community-weighted mean (CWM) Landolt indicator values for temperature, soil moisture and soil nutrients using the species

abundances in each of the 18 grasslands and corresponding indicator values available in “Flora Indicativa” (Landolt et al., 2010) were calculated with the help of package *FD* (Laliberté et al., 2014). Data on soil nitrogen, phosphorus and potassium are presented as the mean values of six replicates per site.

The correlation between elevation and site environmental characteristics, as well as among all environmental factors, were analysed using the Kendall rank correlation coefficient (Kendall  $\tau$ ).

### 2.5 | Persistence strategy data

As the first step, we compiled a data set including vegetation, soil seed bank (both a binary variable for ability to build a seed bank and seed bank density), adult longevity and clonality data. In the data set, for each species occurring in a study site we assigned a corresponding trait value. It was not feasible to measure adult longevity and clonality at all sites; therefore, these traits were considered to be “fixed”, i.e. we used the single mean trait value for individual species used for all sites where the species was found (Lepš et al., 2011). We are aware of the fact that the results of our study may have limited predictive power as both traits are known to be subject to intraspecific variability (for clonality see Klimešová et al., 2010; for plant life span see Rosbakh and Poschlod, 2018).

Because the soil seed bank strategy is subject to extremely high site-specific variability (Thompson et al., 1997; Ma et al., 2010; Abedi et al., 2014; Saatkamp et al., 2014) and published data on it were available for a small number of species, we used soil seed persistence data (both seed bank presence/absence and density) obtained from each study site. To determine the relative importance of different strategies in community level persistence along the elevational gradient, we performed linear models with community mean values calculated based on species presence/absence data for soil seed bank, adult longevity and clonality traits as explanatory variables and elevation of the collection sites as the predictor in all models. To account for possible non-linear relationships between persistence strategies, we also included elevation as a quadratic term into the linear models (Persistence trait  $\sim$  Elevation + Elevation<sup>2</sup>). The quadratic term was retained only for models in which it was statistically significant. To improve normality of the data on soil seed bank density, we included in the corresponding model only data from the range between the 5th and 95th percentile. The explanatory variables in all models were scaled prior to the analysis, to enable comparison of the effect sizes between the various strategies. The model requirements and assumptions were met in all cases.

To estimate and visualise the co-variation of the studied persistence strategies, we conducted a principal component analysis (PCA on the community-trait matrix (Table 1)). All statistical calculations were done with the help of the R software (R Core Development Team, 2021, R Foundation for Statistical Computing, Vienna, AT).

**TABLE 1** Relative role of soil seed bank, adult longevity and clonality in persistence strategy in the study communities located along the elevational gradient

Site	Elevation, m a.s.l.	Soil seed bank		Adult longevity		Clonality			Number of offspring
		Proportion of species with soil seed banks	Density, seeds/m <sup>2</sup>	Proportion of perennial species	Average max life span, years	Proportion of clonal species	Clonality index	Lateral spread distance, cm/year	
M2	935	0.7	452	0.9	10	0.62	2.4	8.4	2.0
HO2	1,045	0.56	825	0.95	7	0.76	3.0	9.3	2.1
H3	1,105	0.55	552	0.97	13	0.73	2.9	8.2	2.0
WM2-2	1,140	0.64	1,000	0.91	8	0.71	2.8	9.7	1.9
M1	1,168	0.65	727	0.93	13	0.65	2.5	8.1	1.8
M3	1,393	0.5	1,067	0.96	14	0.73	2.7	8.2	2.1
M4	1,405	0.48	606	0.97	13	0.73	2.7	7.3	1.9
HO4	1,552	0.33	453	1	19	0.7	2.3	6.4	1.4
WM1-4	1,773	0.36	422	0.98	17	0.75	2.4	5.5	1.7
HO4-5	1,774	0.29	892	0.98	23	0.54	1.9	5.7	1.2
H6	1,800	0.29	123	0.98	16	0.74	2.4	6.2	1.5
W6	1,803	0.27	238	0.97	12	0.67	2.2	4.3	1.4
WM2-5	1,813	0.19	454	0.98	14	0.7	2.4	5.9	1.6
HO5	1,825	0.37	676	0.98	17	0.61	2.1	6.0	1.5
H7	1,984	0.21	465	0.98	21	0.65	2.1	5.6	1.5
H10	2,000	0.28	201	0.98	21	0.68	2.3	4.8	1.4
W7	2,020	0.31	484	0.97	19	0.62	2.1	5.5	1.6
WM1-5	2,032	0.46	538	0.98	26	0.65	2.1	4.3	1.5

Note: Values are arithmetic trait means calculated on species presence/absence data.

### 3 | RESULTS

#### 3.1 | Environmental characteristics of the study sites

Detailed site environmental characteristics are presented in Appendix S2.

The elevational gradient encompassed strong variation in temperature conditions, water supply, soil nutrients and disturbance in the form of grazing (Appendix S3). MAT, length of vegetation period and the Landolt T CWM values strongly decreased significantly (Kendall  $t = -0.98$ ,  $-0.96$  and  $-0.69$ , respectively) with increasing elevation suggesting a strong correlation between temperature conditions and elevation. Furthermore, we detected a moderate significant negative relationship ( $t = -0.34$ ; drier soils at high elevations) between elevation and soil moisture availability calculated as Landolt F CWM values indicating presence of a soil moisture gradient among the study sites. Moreover, the amount of soil nutrients (Landolt N CWM) in upland sites was significantly lower than in their lowland counterparts ( $t = -0.44$ ); this relationship was interpreted as the soil fertility gradient, the third ecological gradient behind the elevation. Finally, grazing intensity was found to be negatively significantly correlated with elevation ( $t = -0.646$ ) with lowland sites experiencing higher levels of disturbance by grazers.

Mean annual precipitation, soil depth, total soil nitrogen, plant available soil phosphorus and potassium were not correlated with elevation.

#### 3.2 | Vegetation data

In the 18 study sites, we recorded 290 species, belonging to 45 families. The most dominant families were Asteraceae (45 species), Poaceae (30 species), Cyperaceae (21 species) and Caryophyllaceae (16 species). Graminoids dominated in the vegetation of all sites surveyed.

#### 3.3 | Soil seed bank

In total, 247,995 seedlings germinated in the collected soil samples, belonging to 162 species and 35 families. The most dominant families in the soil seed bank were Poaceae (23 species), Asteraceae (22 species), Cyperaceae (16 species) and Scrophulariaceae (11 species). At the lowest site (935 m a.s.l.), 70% of all species occurring in the grassland community were found to be able to build up a soil seed bank, whereas at the alpine sites (1,984–2,032 m a.s.l.) this value ranged between 21% and 46% (Table 1). The linear model revealed that elevation had a strong ( $R^2 = 0.72$ ,  $F = 43.2$ ,  $df = 17$ ) significantly negative effect on soil seed bank presence/absence (Table 1; Figure 1a).

Soil seed bank density in the study sites varied considerably from 26 seeds/m<sup>2</sup> at site H6 to 2,200 seeds/m<sup>2</sup> at site WM 1-5 with an

average of 501 seeds/m<sup>2</sup> (Table 1). Despite a comparatively high seed bank density in the two upland sites WM1-5 and HO5 (2,200 and 1,500 seeds/m<sup>2</sup>, respectively) and generally high within-site variability the linear model indicated that soil seed bank density at the community level significantly decreased with increasing elevation (Table 2; Figure 1b). The power of this relationship was moderate ( $R^2 = 0.25$ ,  $F = 5.3$ ,  $df = 17$ ).

#### 3.4 | Adult longevity

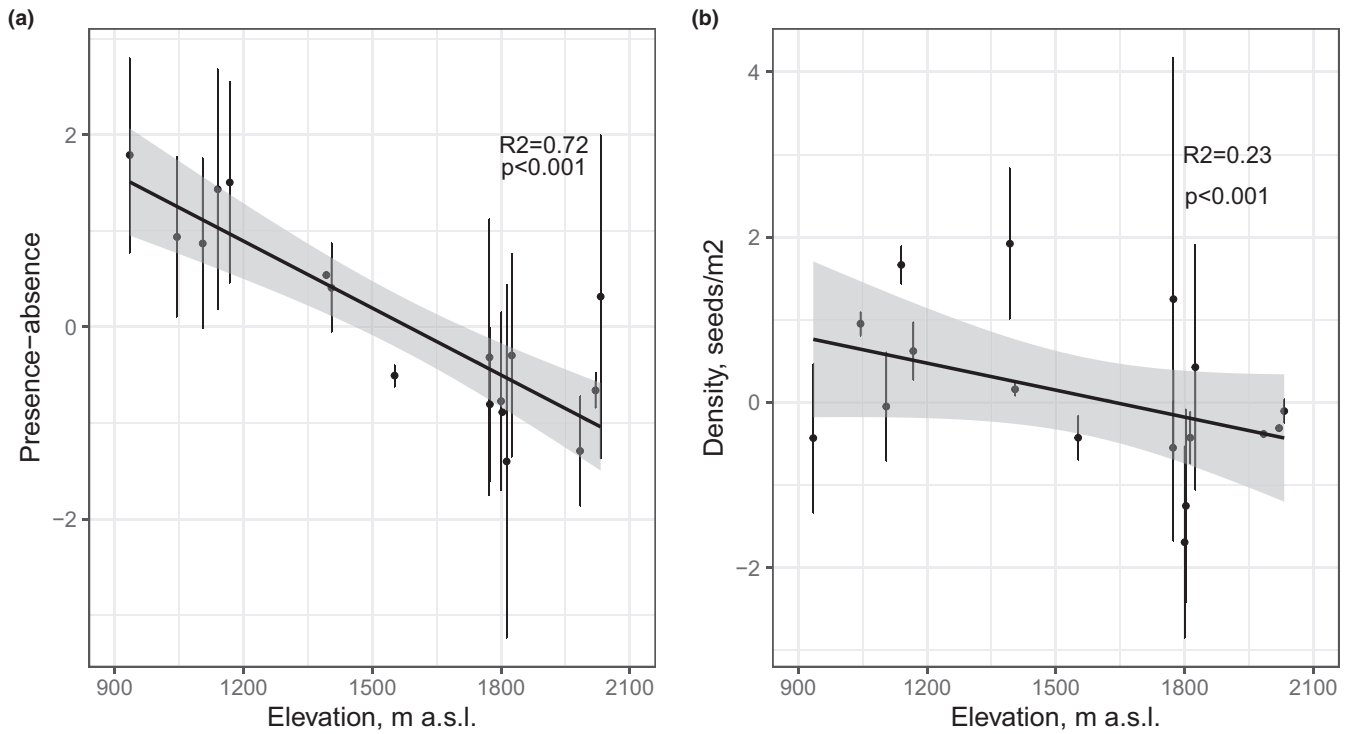
Although annual species were detected in almost all sites, they represent a very small fraction of the species in the study system: annuality was found to be a characteristic of only 18 out of 290 species (6%) occurring in the vegetation in all sites. The proportion of annual species in the studied communities was generally low and varied from 0 at site HO4 at 1,552 m a. s. l. to 10% at site M2 at 935 m a. s. l. with an average of 3% of total species number. The linear model revealed that elevation had a strong ( $R^2 = 0.66$ ,  $F = 14.6$ ,  $df = 17$ ) positive effect on perenniality; species with this trait were found to be more frequent in uplands (Table 2; Figure 2a). The nature of this relationship was found to be non-linear, with a considerably stronger decrease in annual species proportion in the communities within the elevation range 900–1,600 m a. s. l. and constant numbers at sites located above 1,600 m a.s.l.

Maximum plant life span of species occurring at the study sites ranged from 1 (several annual species such as *Rhinanthus glacialis* and *Senecio vulgaris*) to 132 years (*Rhododendron hirsutum*) with an average over all species of 13.3 years. Grasslands at low elevations in our gradient were dominated by comparatively short-lived perennials, whereas those at high elevations were dominated by long-lived perennials (Table 1). The linear model revealed that the communities at the highest sites included significantly more species with longer life span (Table 2; Figure 2b); the average adult longevity at the lowest sites, around 1,000 m a. s. l., was between 7 and 13 years, whereas at the highest site, WM1-5 at 2,032 m a. s. l., this value was 26 years, i.e. more than two times longer (Table 2; Figure 2b). The positive effect of elevation on community-averaged maximum life span was very strong ( $R^2 = 0.61$ ,  $F = 27.9$ ,  $df = 17$ ).

#### 3.5 | Clonality

Among 290 species for which data on clonality were available, almost 70% (193 species) were able to reproduce clonally. The high number of clonal species in the study system was reflected in the community data: the proportion of clonal species at a study site varied from 0.54 at site HO4-5 (1,774 m a.s.l.) to 0.76 at site HO2 (1,045 m a.s.l.) with an average over all communities of 0.68 (Table 1). The linear model did not detect any significant relationship ( $p$ -value = 0.24,  $R^2 = 0.09$ ,  $F = 1.5$ ,  $df = 17$ ) between the proportion of clonal species in the studied grasslands and the elevational gradient (Table 2; Figure 3a).

Soil seed bank



**FIGURE 1** Changes in soil seed bank persistence expressed as (a) species’ ability to build up soil seed bank (1, able to build up a seed bank; 0, otherwise) and (b) soil seed bank density in 18 grasslands located along the elevational gradient in the Bavarian Alps. Single data points and vertical lines are mean arithmetic mean values and standard errors, respectively, calculated for each study community based on species presence/absence data. The regression lines show significant ( $p$ -value  $< 0.05$ ) correlations between the characteristics of interest and elevation (see Table 2 for model output). The shaded areas denote the 95% confidence interval. Explanatory variables were scaled to mean variance prior to the analysis

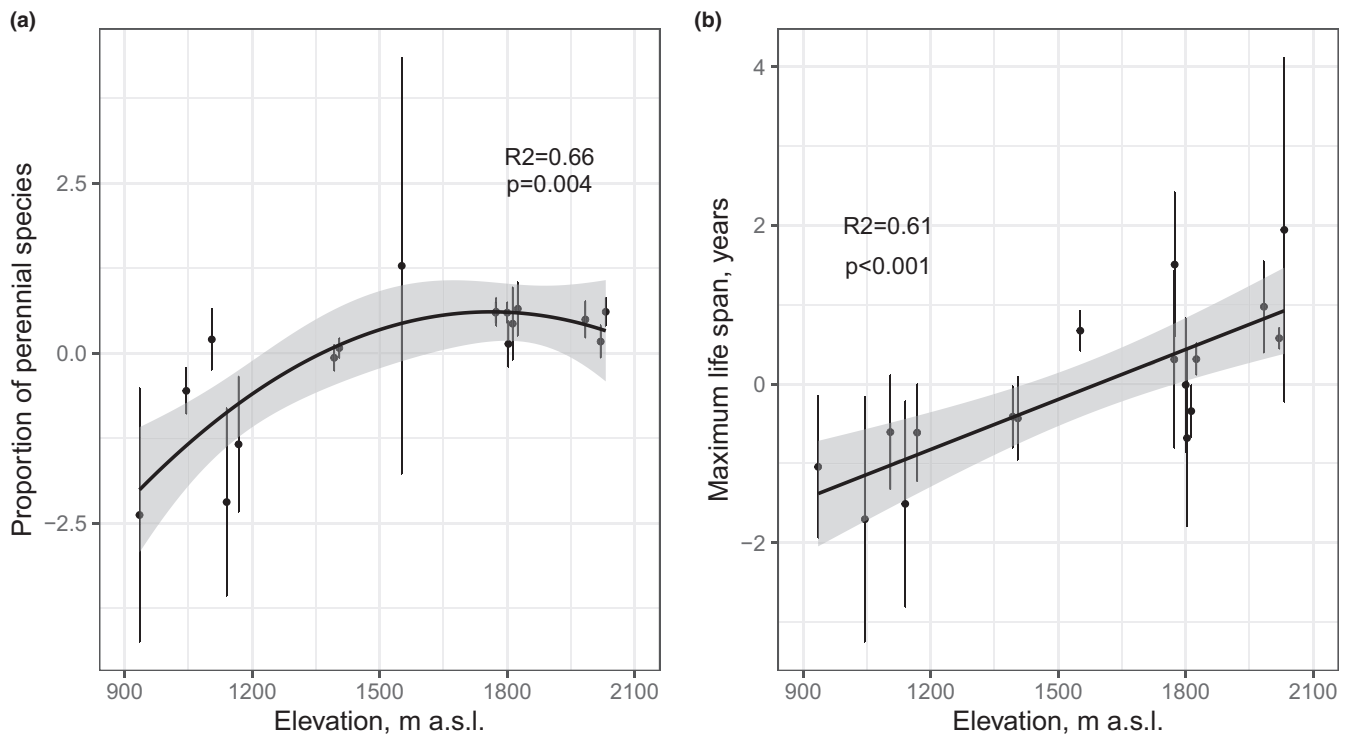
**TABLE 2** Effects of elevation on soil seed bank (presence/absence and density), adult longevity (perenniality and maximum life span) and clonality (ability for clonal growth, clonality index, lateral spread distance and number of offspring) as based on linear models

Persistence strategy	Characteristic	Variable	Estimate	SE±	p-value	R <sup>2</sup>
Soil seed bank	Presence/absence	Intercept	2.56	0.43	<0.001	0.73
		Elevation	-0.17	0.26	<0.001	
	Density	Intercept	2.04	0.91	0.04	0.25
		Elevation	-0.13	0.06	0.04	
Adult longevity	Perenniality	Intercept	9.56	2.78	0.004	0.66
		Elevation	1.1	0.4	0.01	
		Elevation <sup>2</sup>	-0.0003	0.0001	0.03	
	Maximum life span	Intercept	-2.79	0.56	0.002	0.61
		Elevation	0.18	0.34	<0.001	
Clonality	Ability for clonal growth	Intercept	0.57	0.64	0.38	0.09
		Elevation	-0.5	0.4	0.24	
	Clonality index	Intercept	3.05	0.69	<0.001	0.55
		Elevation	-0.19	0.4	<0.001	
	Lateral spread distance	Intercept	3.06	0.33	<0.001	0.83
		Elevation	-0.18	0.02	<0.001	
	Number of offspring	Intercept	2.60	0.45	<0.001	0.66
		Elevation	0.15	0.27	<0.001	

Note: Explanatory variables were scaled to mean variance prior to the analysis. Bold entries are statistically significant ( $p < 0.05$ ). “Elevation” represents the rate of change in corresponding traits per 100 m of elevation.



## Adult longevity



**FIGURE 2** Changes in adult longevity expressed as (a) perennality (1, perennial species; 0, annuals) and (b) maximum life span (in years) in 18 grasslands located along the elevational gradient in the Bavarian Alps. Single data points and vertical lines are mean arithmetic mean values and standard errors, respectively, calculated for each study community based on species presence/absence data. The regression lines show significant ( $p$ -value  $< 0.05$ ) correlations between the characteristics of interest and elevation (see Table 2 for model output). The shaded areas denote the 95% confidence interval. Explanatory variables were scaled to mean variance prior to the analysis

The data set was dominated by species with clonality index values of zero (99 species) followed by four (72 species) and three (58 species) with six being the least frequent value (six species). The average community clonality index varied between 1.9 (site HO4-5 at 1,774 m a.s.l.) and 3.0 (H3 at 1,105 m a.s.l.), with an average of 2.4 across all communities. The linear regression revealed a strong ( $R^2 = 0.55$ ,  $F = 19.6$ ,  $df = 17$ ) negative effect of increasing elevation on the clonality index (Table 2; Figure 3b). The decrease of the clonality index along the elevational gradient was due to a significant decrease in both lateral spread and number of offspring (Figure 4). In both cases the elevation had a very strong effect on these two traits ( $R^2 = 0.83$  and  $R^2 = 0.66$ ,  $F = 80.1$ ,  $F = 31.5$ ,  $df = 17$ , respectively).

The variability in persistence strategies in the 18 communities studied could be summarised by two principal components (PCs) with eigenvalues  $>1.5$ , which together accounted for 80.9% of the total variance (Figure 5: Table 3). The third PC accounted for an additional 11.7% of the total variation. PC1 explained 56.4% of the variance and loaded most heavily and positively on clonality index and soil seed bank presence/absence, followed by soil seed bank density and ability for clonal growth. At the same time, PC1 loaded negatively on adult longevity and perennality. The second PC accounted for an additional 24.5% of the variance and loaded most heavily on the ability for clonal growth, perennality and clonality

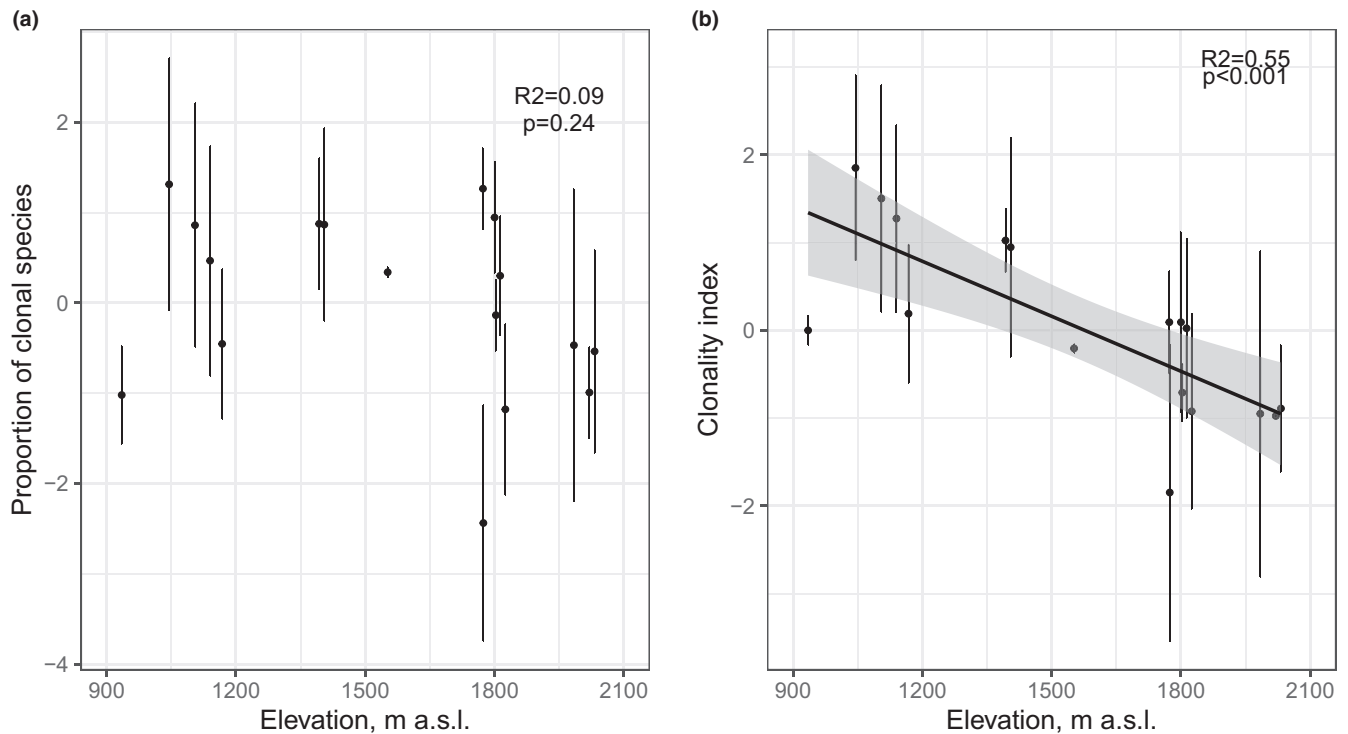
index (positive values). PC2 also loaded heavily and negatively on both soil seed bank presence/absence and density.

## 4 | DISCUSSION

Our results clearly indicate that the studied communities have multiple alternative persistence strategies involving persistence by soil seed banks, adult longevity and/or clonal growth to cope with changing environmental conditions (thermic conditions, water supply, soil fertility and disturbance). Yet, the dominance of a certain persistence strategy was found to be elevation-specific. In agreement with our hypothesis, the importance of persistence by soil seed banks gradually decreased with increasing elevation. This finding is in concert with the observations made along elevational gradients elsewhere (Ortega et al., 1997; Welling et al., 2004; Ma et al., 2010). The low percentage of species building up soil seed banks in the focal communities at high elevations can be explained by two reasons. First, high levels of low-temperature stress (short growth period with overall low temperatures coupled with frequent and severe frost events) limit pollination, fertilization and seed maturation (Lundemo & Totland, 2007; Steinacher & Wagner, 2013; Rosbakh & Poschlod, 2016) resulting in low seed quality and quantity (Welling et al., 2004; Rosbakh et al., 2018). Second, if, nevertheless, seeds



## Clonality



**FIGURE 3** Changes in clonality expressed as (a) capacity for clonal growth (1, clonal species; 0, otherwise) and (b) clonality index in 18 grasslands located along the elevational gradient in the Bavarian Alps. Single data points and vertical lines are mean arithmetic mean values and standard errors, respectively, calculated for each study community based on species presence/absence data. The regression lines show significant ( $p$ -value  $< 0.05$ ) correlations between the characteristics of interest and elevation (see Table 2 for model output). The shaded areas denote the 95% confidence interval. Explanatory variables were scaled to mean variance prior to the analysis

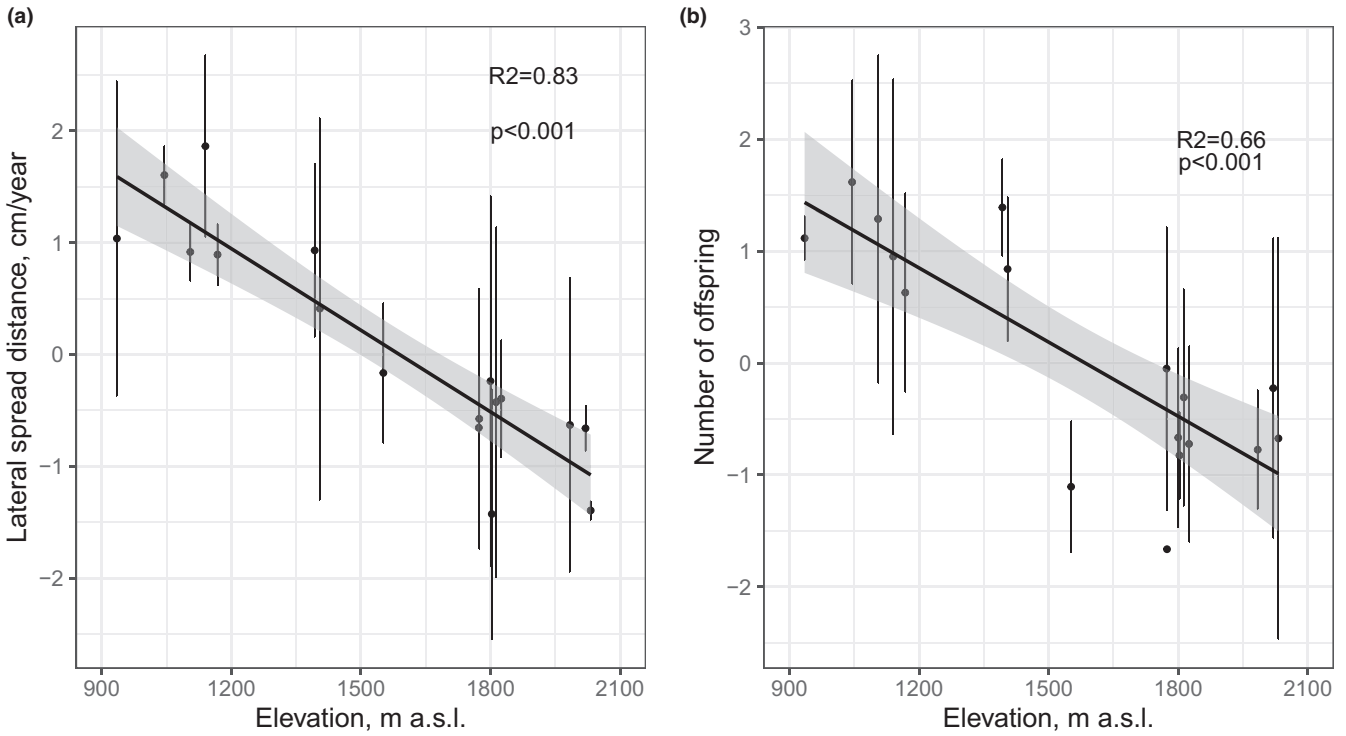
are produced, for example in an exceptionally warm summer, the stressful alpine environments constrain seedling recruitment at high elevations (Molau & Larsson, 2000; Forbis, 2003). Additionally, comparatively lower amounts of soil nutrients along with drier soils can amplify these negative effects of low-temperature stress on regeneration by seed. Therefore, because of the unpredictable seed input into the soil, which decreases with increasing elevation, this should result in a turn-over from species with a persistence strategy of replacing individuals by seeds germinating from the seed bank to species specialised in *in situ* maintenance of established individual plants by emphasizing the adult plant stage getting older to increase the chance of successful reproduction during their lifetime (García & Zamora, 2003; Ozinga et al., 2007; Laiolo & Obeso, 2017).

Ecological theory predicts that, because of the trade-off between regeneration by seed and vegetative growth, the limited reproductive output along with slow growth rates in stressful environments will increase plants' somatic investments that positively affect plant longevity (Obeso, 2002; Laiolo & Obeso, 2017). The revealed increase in adult longevity in the grassland communities along the elevational gradient is in line with these theoretical considerations and previous empirical studies (Rees, 1993; García & Zamora, 2003; Honda, 2008). Furthermore, the results also confirm our hypothesis that persistence by adult longevity is the most frequent persistence strategy at higher elevations (Molisch, 1938;

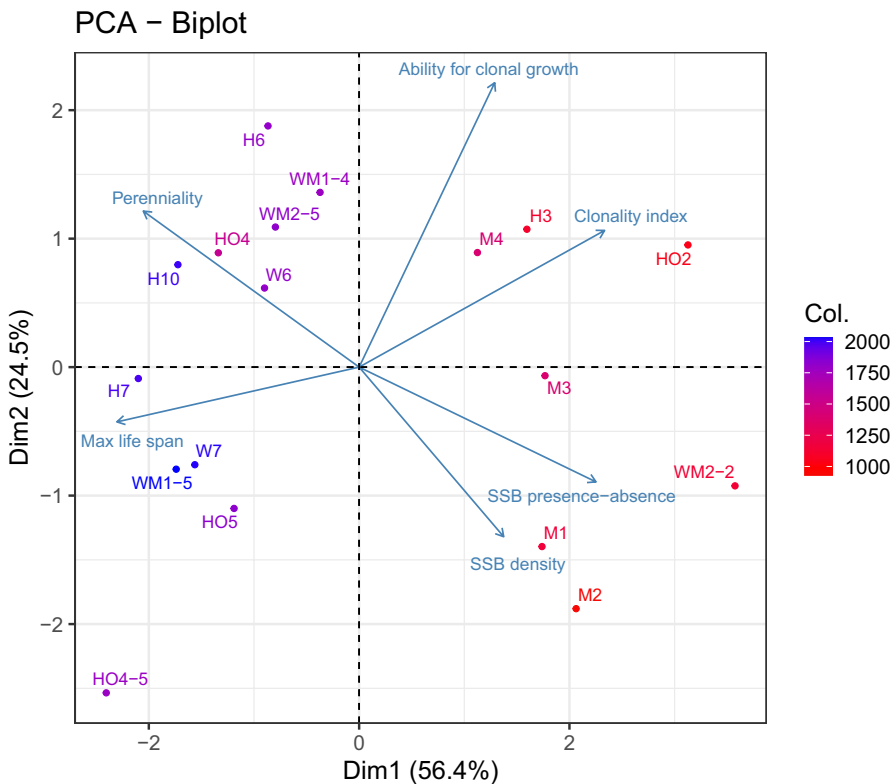
Schweingruber & Poschlod, 2005; Nobis & Schweingruber, 2013). The remarkable gradual character of replacement of annual and comparatively short-lived species by long-lived species in the grasslands located along the gradient suggests that increasing adult longevity could compensate for the decreasing role of seed reproduction and consequently soil seed banks in the same communities (Pakeman & Eastwood, 2013; Saatkamp et al., 2014; Chen et al., 2020).

Elevational gradients encompass a complex combination of environmental gradients related to climate (temperature, precipitation), soil conditions (soil texture and nutrients), disturbance regimes (substrate stability, past and present land use type) and many other environmental properties (Klimeš, 2003; Körner, 2007). Therefore, not only increasing low-temperature stress in the form of a shorter growth period and higher frequency and severity of freezing events along the elevational gradient could result in the patterns reported here. Particularly the lowland sites are subject to stronger anthropogenic pressure at present as they are more intensely used for grazing compared to their upland counterparts. Additionally, some land use legacy might also influence the communities as lowland sites were historically more intensely used for agricultural purposes. Therefore, the higher number of species with persistent seed banks and/or their high density, along with higher frequencies of annual and short-lived species at lowland elevations could be additionally explained by the higher disturbance levels (Wellstein & Kuss, 2011; Saatkamp et al., 2014).

Components of clonality index



**FIGURE 4** Changes in lateral spread distance (a) and number of offspring (b), two components of the clonality index (a semi-quantitative measure of species clonality) along the elevational gradient in the Bavarian Alps. Single data points and vertical lines are mean arithmetic mean values and standard errors, respectively, calculated for each study community based on species presence/absence data. The regression lines show significant ( $p$ -value < 0.05) correlations between the characteristics of interest and elevation (see Table 2 for model output). The shaded areas denote the 95% confidence interval. Explanatory variables were scaled to mean variance prior to the analysis



**FIGURE 5** Two-dimensional illustration of the principal components analysis (PCA) ordination of the persistence strategies of 18 studied communities. See Table 3 for associated eigenvalues and PC loadings. Arrows indicate the direction of loading of each persistence strategy. Dots represent study communities (See Table 1 and Appendix S1 for details)

**TABLE 3** Summary of principal components analysis on a community-trait matrix of study persistence traits

	PC1	PC2	PC3
Eigenvalue	3.4	1.5	0.7
Proportion of variance (%)	56.4	24.5	11.7
Cumulative proportion (%)	56.4	80.9	92.6
Soil seed bank presence/ absence	0.85	-0.34	-0.07
Soil seed bank density	0.52	-0.50	0.68
Perenniality	-0.78	0.46	0.38
Maximum life span	-0.87	-0.16	0.23
Ability for clonal growth	0.49	0.84	0.14
Clonality index	0.88	0.40	0.15

Note: For each axis, the eigenvalues and proportion of variance explained are provided, in addition to loadings for the first three principal components for each trait.

Clonality is regarded as an alternative strategy for local species persistence, especially in stressful environments less favourable for seed production and seedling establishment (Callaghan et al., 1992; Grime, 2002; García & Zamora, 2003; Ozinga et al., 2007). As an alternative, clonal species have an increased vegetative reproduction under unfavourable conditions, because of reduced seed production and/or high-risk seed germination and seedling establishment (Stöcklin & Bäumler, 1996). Despite increasing environmental unfavourability along the elevational gradient, the proportion of clonal species in all grasslands studied was equally high. Thus, our hypothesis of increasing importance of clonality as persistence strategy at high elevations was not supported by the data on capacity for clonal growth. These findings are in agreement with studies in similar systems (e.g. Rusch et al., 2010; Wellstein & Kuss, 2011) and the widely reported observation of a high proportion of clonal species in grassland vegetation over temperate Europe in general (Klimeš, 1997; Klimešová & Herben, 2015). The high frequency of clonal species in all study communities can be explained by two different reasons. Firstly, at high elevations, the communities are predominantly made up of clonal perennials, the life span of which is at least one order of magnitude longer than that of non-clonal perennials (Steinger, Körner & Schmid, 1996; de Witte & Stöcklin, 2010). Alternatively, it may also be the result of the dominance of short-statured plants in uplands, because clonal growth is apparently a typical persistence strategy in plants of relatively small size, a typical trait of alpine species (Aarssen, 2008; Rusch et al., 2010). Secondly, the reason for the surprisingly high contribution of clonal species to lowland communities may be the more intense management by current cattle grazing and higher anthropogenic influence in the past resulting in comparatively higher levels of disturbance regimes. As indicated by research in similar systems, in stable mown or grazed grasslands with limited safe sites for regeneration by seeds, investing in clonal reproduction favours species more (Bossuyt & Honnay, 2008; Wellstein & Kuss, 2011).

In contrast to our expectations, the relative importance of clonality, expressed as the semi-quantitative clonality index, as part of a persistence strategy declined with increasing elevations, due to decreasing proportions of species with larger lateral spread distances and larger numbers of offspring in the corresponding communities, respectively. The lower clonality levels at high elevations contradict the theory that low reproductive output of plants occurring in stressful environments should increase plants' somatic investment, thereby supporting clonal growth (Molisch, 1938; Van Groenendael et al., 1998; Obeso, 2002; Ozinga et al., 2007; Honda, 2008; Laiolo & Obeso, 2017). Probably, there are two non-exclusive reasons for this pattern, differences in: (a) site productivity; and (b) disturbance levels among the study sites. As for the former, the more productive lowland sites in our study system are occupied by taller plants that tend to produce longer spacers, due to allometric effects of size (Aarssen, 2008; Klimešová et al., 2015). As environmental favourability for growth decreases with increasing elevation (e.g. vegetation periods shorten, soils become drier and more nutrient-poor) such species are being replaced with smaller, short-statured plants with reduced lateral spread distances (i.e. "phalanx" clonal growth type; Stöcklin, 1992). As for the latter, the above-mentioned comparatively higher disturbance levels of anthropogenic origin could select species with high lateral spread from the regional species pool (Klimeš, 2003; Klimešová et al., 2015). Although there is no published evidence for that, we suggest that these two reasons explain the decline in community-average values for number of offspring per plant detected here: communities in more productive and/or disturbed habitats tend to be made up of species having more offspring as compared to those in less productive and/or disturbed habitats.

## 5 | CONCLUSIONS

The overall conclusion is that plants can exploit three different strategies to persist *in situ* (building soil seed banks, increasing adult longevity and/or clonal reproduction), the dominance of which in a community can vary depending on environmental variability, in our case along elevational gradients. This finding has three important implications for vegetation ecology in general and nature conservation and restoration ecology in particular. Firstly, it confirms earlier suggestions that persistence traits play an important role in species' stable co-existence and community assembly (Chesson, 2000; Grime, 2006; Moora et al., 2009; Klimešová & Herben, 2015). As for the former, the diverse persistence strategies detected within the study sites could partially explain the comparatively high species richness (e.g. up to 42 species/m<sup>2</sup> in the alpine vegetation belt; Bundesamt für Umwelt, 2009) in the calcareous grasslands on nutrient-poor soils, our study system. Further, the presence of these three persistence strategies representing independent mechanisms buffering population growth (Chesson, 2000) could explain the long-term stability of the studied grasslands, especially the upland ones, against temporal environmental fluctuations (Steinger et al., 1996;

de Witte & Stöcklin, 2010). As for the latter, the gradual change in the dominant persistence strategy along the elevational gradient suggests a strong filtering effect (Figure 5) on these traits, confirming previous suggestions that plant persistence traits may play a crucial role in plant community assembly along environmental gradients (e.g. Rusch et al., 2010 and Klimešová and Herben, 2015).

Secondly, continuing global warming might potentially lead to shifts in community composition and structure in the long term, due to the tight association between persistence strategy and elevation. Given that seed production is largely limited by temperature in cold environments (e.g. Pigott & Huntley, 1981; Jump & Woodward, 2003), a warmed climate may continuously favour species relying on soil seed banks and clonality as persistence strategies, resulting in their higher frequency and abundance and the reduced role of non-clonal, long-lived species with no or scarce soil seed banks in the corresponding communities.

Thirdly, restoration of severely disturbed or even degraded grasslands at high elevations by topsoil translocation from intact patches, a common practice in restoration (e.g. Török et al., 2011), seems to be limited as both species number and seed density in the soil are comparatively low. Thus, seed sowing, hay transfer or plant translocation can be used there as effective restoration techniques (Urbanska & Chambers, 2002).

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#### AUTHOR CONTRIBUTIONS

PP and SR conceived the paper; SR collected the data and performed the statistical analysis. SR and PP wrote the paper. Both authors contributed substantially to the paper and gave approval for publication.

#### DATA AVAILABILITY STATEMENT

The original soil seed bank data used in this paper are available in Appendix S4. The data on maximum life span and clonality are available in the "Flora Indiativa" and "CLO-PLA" databases, respectively.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Location of the study sites in the Bavarian Alps, Germany.

**Appendix S2.** Environmental characteristics of the study sites.

**Appendix S3.** Correlation matrix for environmental factors measured in the study sites along the elevational gradient.

**Appendix S4.** Soil seed bank data used for the analysis.

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