

Plant diversity effects on plant longevity and their relationships to population stability in experimental grasslands

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Abstract

1. Identifying to what degree inherent characteristics of plant species and their variation in response to their environment regulate the temporal stability of plant populations is important to understand patterns of species coexistence and the stability of ecosystems. Longevity is a key characteristic of plant life history and an important component of demographic storage, but age is usually unknown for herbaceous species.
2. In a 12-year-old biodiversity experiment (Jena Experiment) comprising 80 grassland communities with six levels of plant species richness (1, 2, 4, 8, 16 and 60 species) and four levels of functional groups richness (1, 2, 3 and 4 functional groups), we studied populations of 38 dicotyledonous forb species ($N = 1,683$ plant individuals). The sampled individuals represented three plant functional groups (legumes, small herbs and tall herbs) and two different growth forms (species with long-lived primary roots and clonal species with rhizomes/stolons). We assessed the age of plant individuals by means of growth ring analysis and related the age of plant populations to their temporal stability in terms of peak biomass production.
3. On average, plant species richness did not affect the mean age of the populations or the maximum age of individuals found in a population. Age of herbs with taproots increased and age of herbs with clonal growth decreased with increasing species richness, cancelling out each other when growth forms were analysed together. Mean population age was lowest for small herbs and highest for tall herbs, while legumes had an intermediate population age. Herbs with a taproot were on average older than herbs with a rhizome. Across all species-richness levels, populations with older individuals were more stable in terms of biomass production over time.
4. *Synthesis.* Our study shows for the first time across multiple species that the longevity of forbs is affected by the diversity of the surrounding plant community,

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and that plant longevity as an important component of demographic storage increases the temporal stability of populations of grassland forb species.

KEYWORDS

biodiversity, growth ring analysis, Jena Experiment, plant longevity, population age, population stability

1 | INTRODUCTION

Biodiversity is a major force driving ecosystem functions often studied as above-ground biomass production (Cardinale et al., 2011; Gross et al., 2014). Community biomass production is often positively influenced (Cardinale et al., 2011; Hector et al., 1999; Tilman et al., 2014) and temporally stabilized (de Mazancourt et al., 2013; Hector et al., 2010; McCann, 2000) by biodiversity.

Longevity as a measure of temporal persistence of an individual might be a key component of temporal stability of populations and communities. The ecological consequences of ageing and longevity of plants have been discussed for a long time (Gatsuk et al., 1980; Thomas, 2013). For plants with their multiple meristems and modular structure, demographic senescence, that is, the increasing risk of death or gradual decline in fecundity with increasing age after reaching sexual maturity (Kirkwood, 1977), is not easily predictable. Empirical evidence has shown various survivorship curves (Harper, 1967), and the chance to survive may even rise with age (Baudisch et al., 2013; Lauenroth & Adler, 2008). More recent studies have shown that age may positively and negatively influence the vital rates, that is, survival, growth and fecundity, of plant individuals in herbaceous species (Baden et al., 2021; Baudisch et al., 2013; Roach, 2012). Moreover, plant age has been shown to significantly control biomass allocation in plants, and may thereby affect competitive interactions (Doležal et al., 2020). Therefore, the perception that age is indeed important for plants becomes more accepted and is reflected in an increased number of studies (Büntgen et al., 2015; Caswell & Salguero-Gómez, 2013; Klimešová et al., 2016; Salguero-Gómez et al., 2013; Tuomi et al., 2013).

Numerous experimental studies have provided compelling empirical evidence that species diversity increases the temporal stability of above-ground community biomass production (e.g. de Mazancourt et al., 2013; Roscher, Weigelt, et al., 2011; Tilman, 1996). Contrastingly, the temporal stability of population biomass production (i.e. the biomass production of individual species in a community) on average decreases with higher species diversity (Hector et al., 2010; Roscher, Weigelt, et al., 2011). Although biomass production does not directly translate into population sizes in terms of numbers of individuals, a high population biomass corresponds to a higher number of individuals (Chen et al., 2008; Marquard et al., 2009). This allows the assumption that the temporal stability of population biomass production is higher, if a population shows little variation in the number of individuals it consists of. It is important to know as the stability of populations has several ecological

consequences; populations with a lower temporal stability are more likely to experience times of low abundance and are therefore more prone to local extinction.

There are various mechanisms, which may stabilize the coexistence of multiple species and thereby maintain the species diversity of plant communities (Chesson, 2000). One important stabilizing mechanism ensuring the survival of populations during adverse environmental conditions is demographic storage (Chesson, 2003; Warner & Chesson, 1985). Demographic storage relies on durable life stages, which may allow the plant to survive unfavourable environmental conditions and become founder individuals in growing populations. Such durable life stages are seeds in the seed bank and long-lived adult individuals. Long-lived species have more time to establish, to accumulate resources and to reproduce multiple times (Salguero-Gómez et al., 2015), but longevity also increases the risk for being affected by accumulating pathogens (Dudycha & Roach, 2003) or being exposed to unfavourable environmental conditions. Short-lived species may be able to respond faster to environmental conditions through stronger fluctuations in their populations, but they are more dependent on the regular re-establishment from seeds (Ehrlén & Groenendaal, 1998).

Although it has been suggested that slower growing and therefore long-lived species have a higher temporal stability (Chesson, 2000), the relationship between plant longevity and the temporal stability of their populations has never been examined so far. It might seem obvious that populations with long-lived individuals also show a higher temporal stability in biomass production. However, it is also conceivable that species with short-lived individuals, which reliably re-establish new individuals from seeds, might show higher temporal stability than a species with long-lived individuals but rare recruitment.

While numerous biodiversity experiments have shown that increasing plant diversity alters community biomass production, only few studies have investigated diversity effects on vital rates of individual populations (reviewed in Barry et al., 2019). Different plant species show the full spectrum of possible responses ranging from negative to neutral to positive effects of plant diversity on the biomass of plant individuals and their populations (Marquard et al., 2009; Thein et al., 2008). This may be partly explained by altered competitive interactions between plant species themselves, but also by differences in environmental conditions and trophic interactions, such as herbivory or pathogen attack. In mesic grasslands, species-rich communities have a taller canopy and greater density (Lorentzen et al., 2008; Marquard et al., 2009) reducing light availability in lower strata and increasing competition for light,

especially for small-statured species (Roscher, Kutsch, et al., 2011). Plants growing in more diverse plant communities have been shown to become taller, weigh less and are less likely to flower (Lipowsky et al., 2015; Schmidtke et al., 2010). Based on these exemplary results indicating that plant diversity affects vital rates, and the fact that the relative importance of growth, survival and reproduction to fitness varies between and within species across environments (Laughlin et al., 2020), we expected that plant diversity might affect plant longevity and finally the temporal stability of their populations.

For numerous herbaceous species, age data derived from single individuals exist (Landolt et al., 2010), but studies at the population level under field conditions are generally scarce. One possibility to get reliable data on plant age for multiple individuals in ecological studies of herbaceous communities is growth ring analysis (Roeder et al., 2017; Schweingruber & Poschlod, 2005). This method is usually applied in dendrochronology, but it is also possible to count growth rings of herbaceous plant in the secondary root xylem to determine the age of individuals. Von Arx and Dietz (2006) have experimentally proven that growth rings in dicotyledonous herbaceous species are indeed formed on annual basis and that the annual rhythm is not modified by competition (e.g. varying plant densities) or disturbance (such as mowing), which is an important prerequisite to apply this method in grassland communities.

In the present study, we used the 12-year-old communities of a grassland biodiversity experiment, the Jena Experiment, to study the populations of 38 dicotyledonous forb species. The sampled species were assigned to three functional groups (10 legumes, 11 small herbs

and 17 tall herbs) and represent different growth forms (18 species with a long-lived primary root and 20 clonal species with rhizomes/stolons). The biodiversity experiment had 80 plant communities of varying species richness (1, 2, 4, 8, 16 and 60 species). We sampled individuals of each available sown forb species in all communities (=1,683 plant individuals in total) and applied growth ring analysis to determine plant age. We studied following question (Figure 1):

1. Do forb species representing different plant functional groups (legumes, small herbs, tall herbs) and growth forms (species with long-lived primary roots and little clonal growth, or rhizomes/stolons and extensive clonal growth) differ in the observed age of their plant individuals?
2. Does plant community diversity affect the observed age of plant individuals? Do the effects of plant diversity on age differ among species assigned to different functional groups or representing different growth forms?
3. Is the observed age of plant individuals positively related to the temporal stability of their populations?

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the Jena Experiment (Roscher et al., 2004). This is a large long-term biodiversity experiment

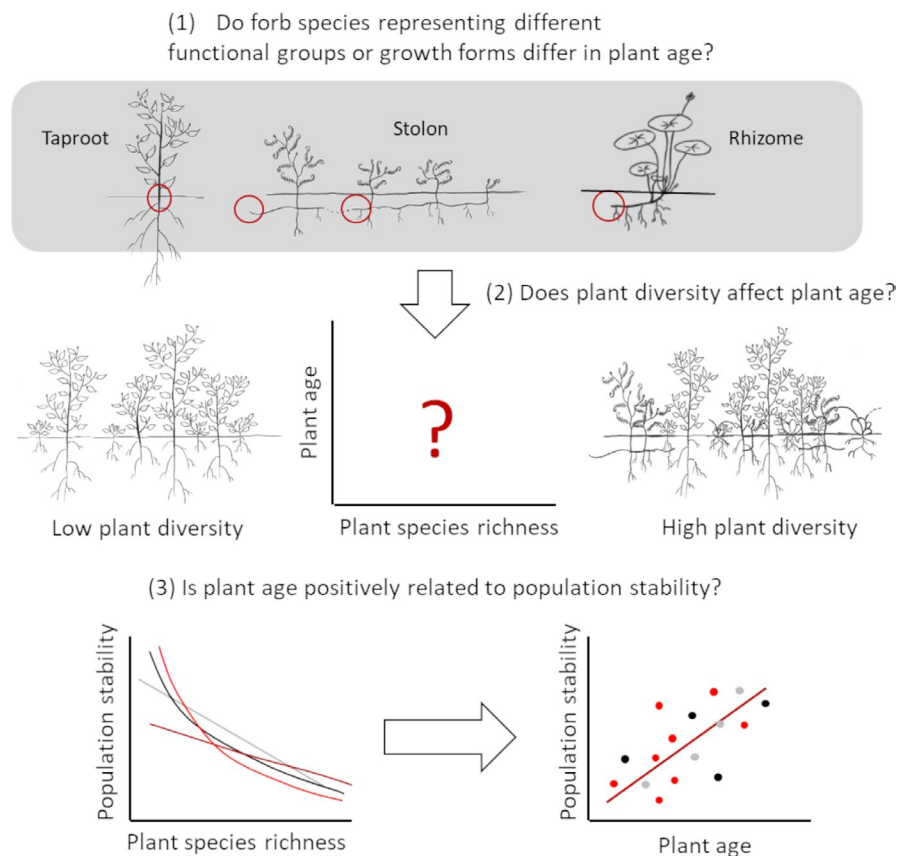


FIGURE 1 Schematic illustration summarizing the study questions and visualizing the growth forms of the studied species with their oldest part (marked by a red circle)

situated in the floodplain of the river Saale near to the city of Jena (Thuringia, Germany; 130 m a.s.l.; 50°55'N, 11°35'E). The region around Jena has a mean annual temperature of 9.9°C and mean annual precipitation of 610 mm (1980–2010, Hoffmann et al., 2014). The soil of the experimental site is a Eutric Fluvisol nearly free of stones. Due the fluvial dynamics of the Saale River, soil texture ranges from sandy loam close to the river to silty clay with increasing distance from the river. The target community to create a species pool for the biodiversity experiment was Central European mesophilic grassland of the Arrhenatherion type (Ellenberg, 1988). Sixty species typical for these grasslands were selected and assigned to four functional groups: grasses (16 species), small herbs (12 species), tall herbs (20 species) and legumes (12 species). The Jena Experiment controls plant species richness (1, 2, 4, 8 and 16 species) and functional group number (1, 2, 3 and 4 functional groups) in a near orthogonal design with the restriction that it is not possible to have more functional groups than species in a community. Each species-richness level has 16 replicates with the exception of the 16-species mixtures, which had 14 replicates because enough species were not available in the species pool to have 16-species mixtures with only legumes or small herbs. The experimental communities were created by random draws from the respective functional group pools. In addition, there are four plots established with the complete 60 species pool. Plots were arranged in four blocks parallel to the river to account for the gradient in soil characteristics. The experimental communities were established by an initial sowing in May 2002 with a total of 1,000 viable seed per m² distributed equally among species in the mixtures. Some poorly established species were resown a single time in autumn 2002 (for details, see Roscher et al., 2004). The plots had an initial size of 20 × 20 m (=400 m²), but plot size was reduced to 6 × 6 m (=36 m²) in 2010. Furthermore, two poorly established monocultures (*Bellis perennis* L. and *Cynosurus cristatus* L.) were abandoned. The biodiversity experiment has been managed as it is typical for extensive hay meadows, that is, the plots are mown two times a year, in early June and in early September and the mown plant material is removed. Plots have not received any fertilizer. To maintain the original species composition, the plots were weeded two or three times a year (April, July and October).

2.2 | Data collection

2.2.1 | Sampling and sample processing for growth ring analysis

Plant individuals including the root crown are required for growth ring analysis. Due to clonal growth of some species, it is not always possible to identify individuals in a strict sense. Especially species that show an extensive clonal growth tend to fragment and the primary root either decays at an early stage or is undiscoverable. In such cases, usually a rhizome or stolon as an 'apparent individual' was harvested. For species with limited clonal growth, individuals could be harvested and the taproot was found in most cases. In species

without clonal growth, a plant individual originating from a single seed is a 'genet', while the 'apparent individuals' are units of a plant, which are able to grow independently if separated from the genet. They are called 'ramet' (Harper, 1977). These differences in growth are important for the age determination, because from 'ramets' (rhizomatous and stoloniferous species) only the age of the oldest preserved tissue at the proximal end of a rhizome or stolon can be derived, while from genets the age of the individuals (since germination) can be determined. Furthermore, growth forms can be of ecological importance, as plants with different growth forms may have different ageing strategies (Thomas, 2013). Thus, species were grouped by growth form as (a) species with long-lived taproots ('taproot species'), and (b) clonal species with rhizomes or above- or below-ground stolons ('clonal species'). Species assignment was based on a priori knowledge from databases (CLO-PLA, Klimešová & de Bello, 2009; and Bioflor, Kühn et al., 2004) and supplemented by our own data on which part of the plants was harvested most often (see Table S1 for species assignment to growth forms). An exception was the assignment of *Medicago × varia* Martyn to the species with clonal growth, although it forms persistent taproots, because it was impossible to harvest the primary root under field conditions (Roeder et al., 2017).

Sampling was conducted between 20 August and 6 September 2013. The sampling in late summer ensures that the growth ring of the current year is fully developed. To limit the disturbance of the experimental plots, sampling was restricted to a 1-m² subplot in each plot. In this subplot, five or six individuals (or rhizomes or stolons respectively) of all available perennial dicotyledonous plant species belonging to the sown species combinations were excavated, but in several cases fewer individuals per species were available, and it was not possible to harvest five individuals per species. More samples (20 individuals per plot) were taken for *Plantago lanceolata* L., *P. media* L. and *Knautia arvensis* (L.) Coult. for specific studies (see Roeder et al., 2019). To reduce bias by different sample sizes, six samples per plot were randomly selected for these species for statistical analyses. Two perennial forb species belonging to the Jena Experiment pool were excluded: species from the genus *Ranunculus* (*R. acris* L., *R. repens* L.), which are known to not form growth rings. Two further species (*Anthriscus sylvestris* (L.) Hoffm. and *Campanula patula* L.) could not be sampled, because they were not present in the sample subplots. Another species, *Primula veris* L., does not form growth rings as well, but instead it forms morphological markers. The rhizome thickens every spring, when new leaves and subsequently leaf scars are formed. For all species forming growth rings, the discernibility of the rings varied among and within species. This variation was accounted for by rating the discernibility of each individual. On average, all species had a sufficient discernibility to be included in analyses (Roeder et al., 2017). From the total number of 1,774 samples, 151 samples had undiscernible growth rings and were excluded. The samples represented 38 plant species (10 legumes, 11 small herbs and 17 tall herbs according to the functional group classification of the Jena Experiment; see Table S1 for species occurrences at different diversity levels).

To get an accurate estimate of the age of the individuals, we strived to harvest the oldest part (Figure 1). The oldest part in a plant with a

long-lived taproot this is the root crown, while in a plant with clonal growth, the oldest part is the most proximal part of the rhizome or above- or below-ground stolon respectively. From each sample, a 5-cm long piece of the sample including the oldest part was preserved in 70% alcohol. In the laboratory, the samples were cut using a microtome (Microtome type GSL1; Gärtner & Schweingruber, 2013). Absolute alcohol was used to keep the sample moist, to harden the tissue and to make the sample float onto the blade. Microtome sections were put on a slide into a drop of a glycerol-water mixture (1:1) and covered with a cover glass. The age of the plants was determined by counting growth rings (Schweingruber & Poschlod, 2005) under the microscope (Keyence VHX_2000D, Higashi-Nakajima, Japan). If necessary polarized light was used to facilitate the growth ring visibility. For a more detailed method description, see Schweingruber and Poschlod (2005) and Roeder et al. (2017).

2.2.2 | Temporal stability of individual populations and plant community variables

Above-ground biomass was harvested two times per year, once in spring (in late May) and once in summer (late August). Plants were clipped at 3 cm above soil surface, and samples were sorted to live biomass of individual species sown on a particular plot, total live biomass of weeds (species not sown on a particular plot) and detached dead material. Three or four samples of 20 × 50 cm size were taken on each plot between 2003 and 2010. Two samples were harvested after the reduction of plot size from 2010 onwards. All samples were dried at 70°C for 48 hr and weighed. Population biomass of each species sown on particular plot was calculated as mean from the replicated samples per plot for each harvest. For further details, see Weigelt et al. (2016). For comparability with a previous study of temporal stability in the Jena Experiment (Roscher, Weigelt, et al., 2011), we used peak biomass (spring harvest) from 2003 to 2013 for our study.

Temporal stability (S) of population biomass (S_{pop}) for each sown species on each plot was calculated as the reciprocal of the coefficient of variation (CV) by using the ratio of the mean population biomass (μ) to the standard deviation of population biomass (σ ; Tilman, 1999):

$$S_{pop} = \mu / \sigma. \quad (1)$$

Furthermore, we derived the following characteristics of the plant communities to assess their effects on plant longevity. Plant community biomass of sown species was calculated from yearly harvests, as described above, as mean values across the last 5 years to account for variation between years (2009–2013). Similarly, realized evenness (Simpson evenness) was assessed from yearly cover estimates on an area of 3 × 3 m shortly before biomass harvest in spring autumn and averaged across seasons and the last 5 years (Weisser et al., 2017). Finally, we derived realized species richness as the total number of sown plant species found in the cover estimates for each plot in the study year 2013.

2.3 | Statistical analysis

The following variables were derived for each population: Growth ring counts of all samples per species and plot were averaged to derive the mean age for each population. Additionally, the maximum age was determined by identifying the oldest individual per population. Finally, age variation was determined as CV (ratio of the standard deviation divided by the mean of all samples per population × 100). While maximum age could provide information on plant longevity under different growth conditions in communities of different plant diversity, mean age and age variation may indicate variation in age-specific demography (Roach, 2003). To reduce bias due to different numbers of samples per population, only populations with a sample size between four and six samples were included in statistical analyses (=195 populations) (Roeder & Roscher, 2021).

The software R 3.3.1 (R Development Core Team, <http://www.R-project.org>) including the library 'lme4' (Bates et al., 2015) was used for statistical analysis with linear mixed-effects models. First, data on mean age, maximum age and age variation populations were analysed to assess how plant diversity (species richness), morphological growth form and functional group identity influenced these variables. To account for the block design of the experiment and the sampling of different species on the same plots, block and plot nested in block were used as random effects in the models. Species identity was used as further independent random effect to consider the sampling of multiple species in each functional group or each growth form. Fixed effects were plant species richness (as a log-linear term), species grouping (growth form with two factor levels: taproot species and clonal species; or functional group with three factor levels: legume, small herb and tall herb) and the interaction of species grouping with plant species richness. Afterwards, we started from a constant null model with the described random effects, and the fixed effects were entered stepwise in the order as described above. The same model structure was used to test for effects of realized species richness (as log-linear term), evenness or community biomass on mean age, maximum age or age variation (replacing sown species richness with one of these variables). Realized species richness was tested, because it deviates from sown species richness in the long-term biodiversity experiment (Weisser et al., 2017). Evenness and community biomass were tested to assess whether other community characteristics than species richness affect variables related to population age.

Second, it was tested whether plant populations with a higher mean or maximum age or age variation also have a higher temporal stability in terms of their population biomass. To assess the significance of plant age for the temporal stability of plant populations, the structure of random effects was the same as described above. To account for the underlying species-richness gradient, the following fixed effects were fitted sequentially: sown species richness (as a factor with six levels), population age (either as mean or maximum age, or age variation), the interaction term between species richness and population age, growth form and the interaction term between population age and growth form. In alternative

models, growth form was replaced by functional group identity. To secure the results that population stability decreases with increasing species richness in the set of studied populations for growth ring analysis, we also fitted a model with population stability as response variable and sown species richness (as log-linear term) as explanatory variable. To assess relationships between population age, population stability and traits related to leaf economy, which have previously been shown in independent analyses (Klimešová et al., 2016; Májeková et al., 2014), we used data on SLA and leaf dry matter content (LDMC) measured in 40 mixtures (10 replicates of each 2-, 4-, 8- and 16-species mixtures) of the Jena Experiment in 2011 (Bachmann et al., 2018). Leaf traits were averaged for each species × mixture combination across five sampling dates (April, May, June, July and September) to account for trait variation along the plant diversity gradient and across seasons. Using the same structure of random effects as explained above, we fitted SLA (or LDMC), growth form (or functional group identity) and the interaction between both terms to test for effects on mean or maximum age and age variation or population stability respectively.

The models were fitted with the maximum likelihood method (ML), model fit was compared using likelihood ratio tests (χ^2 ratio). For all models that showed a significant effect of functional group identity, Tukey's HSD test for multiple comparisons was used to identify which groups were different from each other. For this analysis, the function 'glht' from the package MULTCOMP (Hothorn et al., 2008) was applied to models fitted with restricted maximum likelihood (REML). In all analyses, mean and maximum age as well as the temporal stability of population biomass was log-transformed to meet the requirements of the model. Homogeneity of variances was checked graphically and with Levene's test.

3 | RESULTS

3.1 | Do functional groups or growth forms differ in longevity?

Species assigned to different functional groups varied in the mean age of their populations (Figure 2A), and the maximum age of individuals collected for each population (Figure 2B, Table 1). Mean age of tall herbs was highest with $3.5 (\pm 0.15 \text{ SE})$ years ($N = 73$), legumes had intermediate values with a mean age of $2.8 (\pm 0.24)$ years ($N = 38$) and small herbs were youngest and on average only $2.5 (\pm 0.10)$ years old ($N = 84$). Similarly, maximum age of tall herbs (5.5 ± 0.30 years) was higher than that in small herbs (3.7 ± 0.17 years), while legumes had intermediate values (4.3 ± 0.36 years). Age variation of individuals sampled for a population was not different among functional groups (Figure 2C; Figure S1).

Mean and maximum age also differed between species with different growth forms; both were higher in species with a persisting taproot (Figure 3A,B; Table 1). Populations of species with a persistent taproot had a mean age of 3.5 ± 0.12 years ($N = 96$), while populations of species with clonal growth were on average 2.4 ± 0.11 years

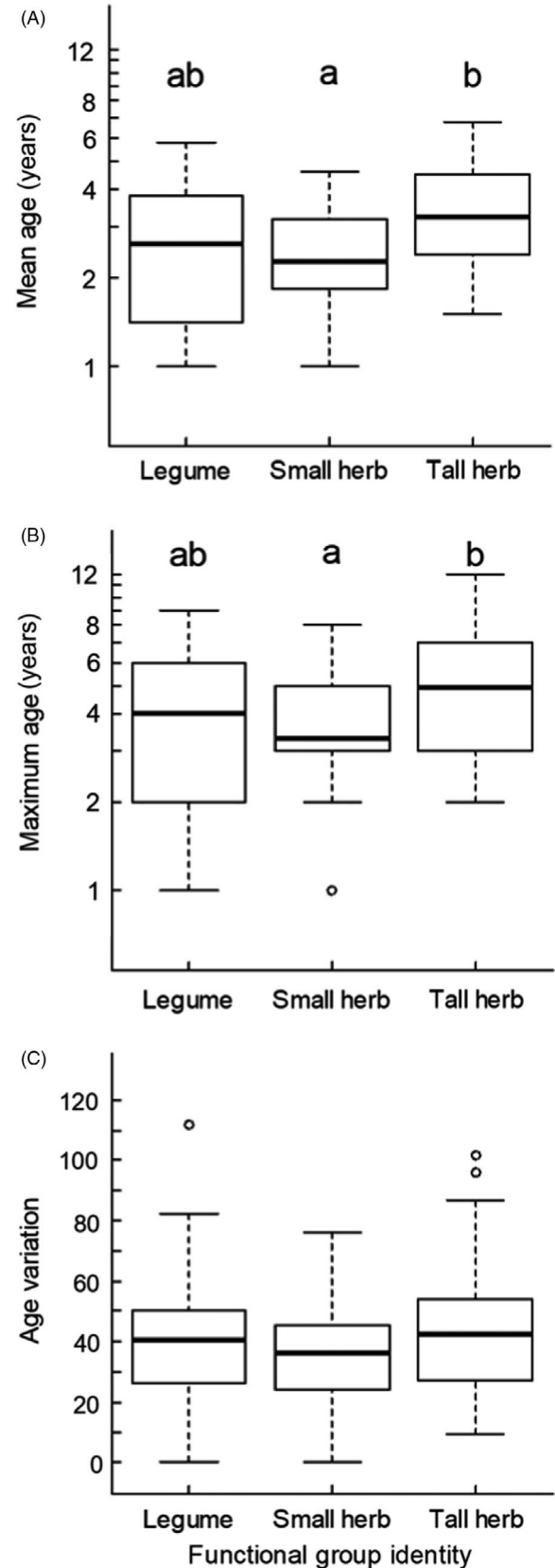


FIGURE 2 Mean age of populations (A), maximum age of individuals found in a population (B) and age variation (C) of the three functional groups as box plots. Letters above the bars indicate significant differences among groups according to the results of Tukey's HSD test

TABLE 1 Summary of mixed-effects model analysis testing for effects of species richness on mean population age, maximum age of individuals found in a population and age variation, dependent on functional group identity and growth form respectively

	df	Mean age		Maximum age		Age variation	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Functional group identity							
Species richness	1	1.805	0.179	0.011	0.916	1.685	0.194
Functional group ID	2	6.320	0.042	7.911	0.019	3.976	0.137
Species richness × Functional group ID	2	3.261	0.196	2.885	0.236	0.012	0.994
Growth form							
Species richness	1	1.805	0.179	0.011	0.916	1.685	0.194
Growth form	1	7.240	0.007	8.827	0.003	3.945	0.047
Species richness × Growth form	1	10.237	0.001	6.571	0.010	0.006	0.939

Note: Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood ratio tests (χ^2) that were applied to assess model improvement and the statistical significance of the fixed effects (*p* values). Significant effects (*p* < 0.05) are marked in bold. Mean and maximum age as well as species richness was log-transformed.

old (*N* = 99). Maximum age of samples collected in populations of species with a persistent taproot was 5.5 ± 0.23 years, and for samples collected in populations of species with clonal growth it was 3.6 ± 0.19 years. Age variation of individuals per population was also higher in species with a persistent taproot than in those with clonal growth (Figure 3C; Figure S2).

3.2 | Does diversity affect longevity, and does the influence of diversity on age differs between functional groups and growth forms?

Across all species, plant species richness did not affect the mean age of the populations (Table 1). On average, mean age was $2.9 (\pm 0.09)$ years (*N* = 195). Maximum age of individuals found in a population also did not change with increasing plant species richness and was on average $4.5 (\pm 0.16)$ years (Table 1). The effects of species richness on mean or maximum age of populations did not vary among functional groups (Table 1; Figure 4A,B; no significant interaction Species richness × Functional group ID). However, the effects of species richness on mean age of populations or the maximum age of individuals found in a population varied between growth forms; species with a persistent taproot were on average older in communities of higher species richness than in communities with lower species richness (slope over species richness = 0.0735), while species with clonal growth were younger at higher species richness (slope over species richness = -0.0548; Table 1; Figure 4C). Similarly, the observed maximum age increased slightly with increasing species richness in species with a persistent taproot (slope over species richness = 0.0472), and decreased in species with clonal growth (slope over species richness = -0.0870; Figure 4D). Age variation of individuals sampled per population did not change with species richness of the plant communities.

Diversity effects on plant longevity (i.e. mean age, maximum age and age variation) did not change, when realized species richness was used instead of sown species richness (Table S2; Figure S3A,B). Overall, evenness did not affect plant longevity, except for growth form-dependent effects on maximum age of the sampled individuals per population. Maximum age of species with a persistent taproot decreased with increasing evenness (slope over evenness = -0.2984), while it increased in species with clonal growth (slope over evenness = 0.2543; Table S2; Figure S3C,D). On average, community biomass had a negative effect on mean age of populations (irrespective of functional group identity). With respect to growth form, mean and maximum age of species with a persistent taproot tended to increase with community biomass, while species with clonal growth showed the opposite response (Table S2; Figure S3E,F). Age variation of individuals sampled per population decreased with increasing community biomass (Table S2).

3.3 | Is there a positive relationship between longevity and temporal stability of plant populations?

Increasing species richness of the plant communities decreased temporal stability (*S*) of plant populations (Table 2). Temporal stability of populations increased with mean age and maximum age of the individuals sampled per population (Figure 5; Table 2) across all levels of sown species richness (Figure 5; Table 2; Table S3). The relationship between population stability and plant longevity was not different among functional groups or growth forms (Table 2; no significant interactions). Temporal stability of populations was not related to age variation of the sampled individuals per population (analysis not shown). Maximum age of plants sampled per population showed a negative relationship with SLA sampled in a subset of these populations (*N* = 106), while the relationships were not significant for mean

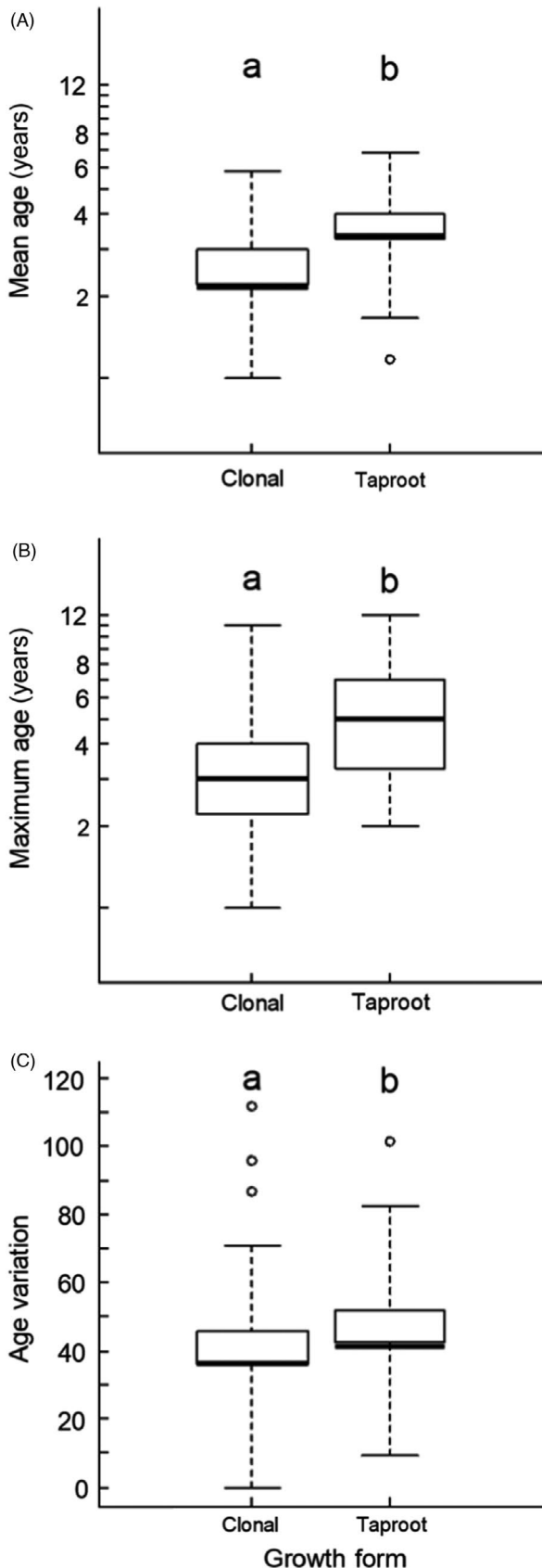


FIGURE 3 Mean age of populations (A), maximum age of individuals found in a population (B) and age variation (C) of the two different growth forms as box plots. Letters above the bars indicate significant differences among groups

age (Figure S4; Table S4). Plant longevity varied independently from LDMC (Table S4). Temporal stability of populations of the subset, where leaf traits were available, was not related to SLA ($\chi^2 = 1.903$, $p = 0.168$) or LDMC ($\chi^2 = 0.235$, $p = 0.628$).

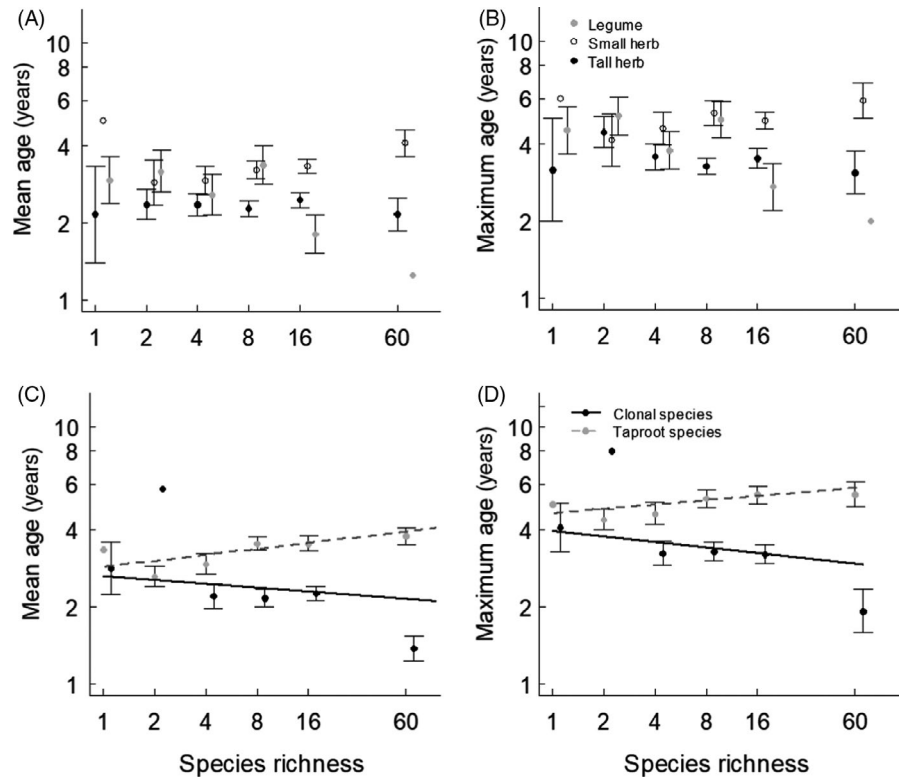
4 | DISCUSSION

It is increasingly acknowledged that demographic processes are important to understand the patterns of species coexistence, the stability of ecosystems and ecosystem functioning (Barry et al., 2019). Although recent studies have shown that age affects major vital rates of plants, that is, survival, fecundity and growth, little is known how the abiotic and biotic environment affects the longevity of herbaceous plants. So far, it has not been studied across multiple species whether plant community diversity affects age-related variables of their populations. In our study conducted in a large grassland biodiversity experiment, we could show that plant longevity is indeed influenced by the diversity of the surrounding plant communities. Age of species with taproots increased with higher species richness, while the age of species with clonal growth decreased. We also found that populations with a higher mean and maximum age of their individuals are temporally more stable.

4.1 | Do functional groups differ in longevity?

Overall, we found that the age of most samples varied between 1 and 4 years and only very few individuals were as old as the biodiversity experiment, suggesting a full turnover of the populations. These results are in line with findings from mapping of permanent plots in North American mixed grass prairies showing that most herbaceous perennials die young (Lauenroth & Adler, 2008). With respect to the functional group classification of the Jena Experiment (Roscher et al., 2004), the functional group with the highest mean age of their populations was tall herbs. They were significantly older than populations of small herbs, while legumes had intermediate values and were not significantly different from either tall or small herbs. The distribution of both growth forms was fairly balanced among functional groups (Table S1). A bias due to a prevalence of a particular growth form in a functional group could therefore not be the cause for the differences in mean age among functional groups. The major difference among species assigned to the functional groups of 'small herbs' and 'tall herbs' in the Jena Experiment was growth height. On average, small herbs are <20 cm in height, while growth height of tall herbs is mostly more than 30 cm at peak canopy development (Roscher et al., 2018). Marbà et al. (2007) tested for allometric scaling in plants, as it is well known for animals, that is, the size dependency of 'birth' and mortality rates, across species spanning from phytoplankton to trees. The size differences among grassland species in our study are much smaller, but following the idea of Marbà et al. (2007), it could be expected that the two groups of non-legume herbs follow different life-history strategies, and that tall herbs show

FIGURE 4 Mean age of populations (A, C) and maximum age of individuals found in a population (B, D) plotted against sown species richness. Species are either grouped by functional groups (A, B) or by growth form (C, D). Shown are means per species-richness level (± 1 SE) for each functional group and growth form respectively. Regression lines indicate significant relationships according to the results of linear mixed-effects models with log-transformation for sown species richness and population age (Table 1)



a different age structure than small herbs. Our analyses showed that mean population age as well as the maximum age of individuals found in a population was higher in tall herbs than in small herbs. Therefore, the difference is not only due to greater longevity in tall herbs but probably to higher recruitment rates in small herbs. This is also supported by the observation that species classified as small herbs have a larger seed bank and more seedlings than tall herbs in monoculture plots of the Jena Experiment (Dietrich et al., 2020). Furthermore, it has been suggested that plant longevity is related to traits of the plant economics spectrum, such as SLA (Klimešová et al., 2016). In situ measurements have shown that SLA decreases from small herbs to legumes to tall herbs in the Jena Experiment (Roscher et al., 2018). This observation provides further evidence for demographic differences between slow- and fast-growing plants (Klimešová et al., 2016), because mean and maximum age decreased in our study from tall herbs to legumes to small herbs.

4.2 | Do growth forms differ in longevity?

In the Jena Experiment, populations of species with persistent taproots were older than populations of species with clonal growth. Furthermore, we found that age variation within populations was smaller in clonal species than in species with taproots and generally shifted to younger ages (Figure S2a). These differences between growth forms can be explained by the growth form itself. Species with persistent taproots usually have no or limited clonal growth. Therefore, the genet is sampled, and the sample contains all tissues formed since germination. In species with extensive clonal growth,

the individuals tend to disintegrate older tissues decay, and it is nearly impossible to harvest an entire individual. The sampled 'apparent individuals' are actually fragments and contain only tissues as old as the independence from the mother plant. For some species (e.g. *Ajuga reptans* L., *Bellis perennis* L., *Prunella vulgaris* L., *Trifolium repens* L. and *Veronica chamaedrys* L.), it was obvious that tissues older than 2 or 3 years had decayed, as no older tissues could be found. The sampled individuals were clearly fragments of genets and ended with decayed tissues. The example of *Lathyrus pratensis* L. further supports this assumption; for some individuals of this species, we could find the primary root and could compare the values. While the roots had a mean age of 2.8 years, below-ground stolons had a mean age of only 1.4 years. Therefore, it is likely that genets of species with rhizomes were older than we could verify with growth ring analysis. Although the study of age in species with clonal growth is restricted by the caveat that it is not possible to determine the age of the genet, data are still ecologically relevant, because environmental conditions in plant communities of different diversity could influence the age of species with clonal growth just as well as in species with taproots, and we took all samples in a standardized procedure along the diversity gradient.

4.3 | Does diversity affect longevity, and does the influence of diversity on age differs between functional groups and growth forms?

Overall, there was no effect of increasing species richness on mean or maximum age of plant populations or age variation within

TABLE 2 Summary of mixed-effects model analysis testing for relationships between the temporal stability of population biomass and population age dependent on sown species richness, functional group identity and growth form respectively

	Temporal stability		
	df	χ^2	p
Species richness	1	10.239	0.001
Mean age			
Functional group identity			
Species richness	5	10.778	0.056
Mean age	1	7.893	0.005
Species richness × Mean age	5	4.210	0.520
Functional group ID	2	2.198	0.333
Mean age × Functional group ID	2	0.150	0.928
Growth form			
Species richness	5	10.778	0.056
Mean age	1	7.893	0.005
Species richness × Mean age	5	4.210	0.520
Growth form	1	0.175	0.676
Mean age × Growth form	1	0.001	0.977
Maximum age			
Functional group identity			
Species richness	5	10.778	0.056
Maximum age	1	5.802	0.016
Species richness × Maximum age	5	6.119	0.295
Functional group ID	2	1.704	0.427
Maximum age × Functional group ID	2	0.358	0.836
Growth form			
Species richness	5	10.778	0.056
Maximum age	1	5.802	0.016
Species richness × Maximum age	5	6.119	0.295
Growth form	1	0.052	0.820
Maximum age × Growth form	1	0.238	0.626

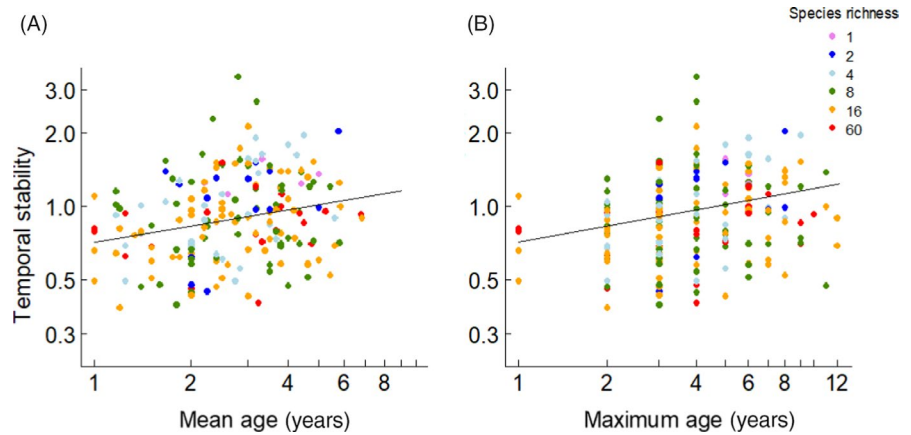
Note: Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood ratio tests (χ^2) that were applied to assess model improvement and the statistical significance of the fixed effects (p values). Significant effects ($p < 0.05$) are marked in bold. Mean and maximum age as well as temporal stability was log-transformed.

populations. Growth forms, however, responded differently—in populations of species with clonal growth, mean and maximum age decreased; and in populations of species with taproots, age slightly increased with higher species richness of the plant communities (Figure 4). Moreover, in taproot species, the strength of positive species-richness effects was more pronounced for mean

age (greater positive slope) than for maximum age. On the contrary, in clonal species, the strength of negative species-richness effects was less pronounced for mean age (smaller negative slope) than for maximum age.

Increasing species richness alters the environment for a species in many aspects. One important factor that changes is competition, as intraspecific competition is gradually replaced by interspecific competition (Chesson, 2000). Plant–soil feedbacks are more pronounced and more negative at low diversity, where pathogens are more likely to accumulate (Dudenhöffer et al., 2018; Hendriks et al., 2013). Species with clonal growth may be on average younger and achieve a lower maximum age at higher diversity, because there they possibly discard older tissues earlier and allocate resources preferably to new growth to escape interspecific competition (Hutchings & Wijesinghe, 1997; Klimešová et al., 2015; Schmid & Harper, 1985). In a previous study, *Trifolium fragiferum* L. showed less fragmentation and heavier shoots in denser vegetation (Huber & Wiggermann, 1997). In our study, we found that higher community biomass was related to a shorter life span in species with clonal growth (decrease of observed maximum age). A higher community biomass, as it is usually found at higher species richness (Marquard et al., 2009), may indicate an environment with higher competition, especially for light and space. In our experiment, evenness declined with increasing species richness (Weisser et al., 2017). Together with our findings that clonal species were older at higher evenness, these results suggest that diversity effects on age may be driven by interspecific competition by dominant species at higher species richness. Discarding tissues earlier can also be a response to higher pathogen pressure (Klimešová et al., 2015), but this explanation is more likely to happen at lower plant diversity. Several clonal plants in our study are stoloniferous species, that is, a fast renewal of tissues also allows for faster occupation of new patches. This corresponds to the findings of Ehrlén and van Groenendael (1998), who suggested that species with good colonization ability have a low survival, while species with extended survival have a limited ability to colonize new patches. The latter group corresponds to our group of species with taproot. These species do not have the chance to reach new patches, therefore their survival under adverse conditions relies on stored reserves (Chapin et al., 1990). In species with taproots, age distribution showed that most sampled individuals were between 2 and 4 years old, while fewer individuals of this year's cohort (1 year old) or older than 4 years were found (Figure S2b). Although this age distribution was observed across all species-richness levels and age distribution within populations was not different along the species-richness gradient, the strength of positive species-richness effects was less pronounced for maximum age than for mean age. On the one hand, these results are probably due to a higher likelihood for younger life stages at lower species richness, when recruitment from seeds and early survival may be facilitated in the less dense vegetation. On the other hand, more negative plant–soil feedback (Bennett & Klironomos, 2019) may limit the longevity of taproot species at

FIGURE 5 Relationship between temporal stability and (A) mean age of populations, and (B) maximum age of individuals found in a population. Symbols show populations sampled at different sown species-richness levels. Regression lines indicate significant relationships according to the results of linear mixed-effects models with log-transformation for population age and temporal stability ($p < 0.05$; Table 2)



low diversity. In contrast, at higher species richness, seedlings establish less easily (Roscher et al., 2009), and individuals are possibly limited in survival because fewer reserves may be stored under higher competition for light in more diverse plant communities. For a single species, *Trifolium pallescens* Schreb., a similar pattern was found. In the most competitive environment, fewer young plants were found, and the old plants were younger compared to the least competitive environment (Kuen & Erschbamer, 2002).

4.4 | Is there a positive relation between longevity and temporal stability of plant populations?

Results from several biodiversity experiments, including the Jena Experiment, have shown that the temporal stability of populations decreases with increasing species richness (e.g. Hector et al., 2010; Roscher, Weigelt, et al., 2011), and our own data (biomass data up to year 2013 for populations studied for growth ring analysis) confirm the previous results. So far, the reasons for varying temporal stability of plant populations with changing plant community diversity are not well-understood. Specifically, the link between temporal stability and age has not been addressed using real-life age data, although it is generally thought that extended longevity of plants increases population persistence (Morris et al., 2008; de Witte & Stöcklin, 2010). Our findings linking temporal stability and different variables related to age of the populations indeed confirmed that there is a positive relationship between the mean and the maximum age of the populations and their temporal stability across all species-richness levels and irrespective of species assignment to functional groups or growth forms.

Previous studies relating temporal stability and plant traits found that species with high LDMC had greater population stability (Májeková et al., 2014; Polley et al., 2013). Leaf dry matter content is an important component of the plant economics spectrum (Reich, 2014). This spectrum describes trade-offs between fast-growing species with high resource acquisition and slow-growing species with conservative resource acquisition. Fast species have leaves with a low LDMC, high SLA and higher rates of photosynthesis, while slow species have leaves with the opposite

characteristics. Klimešová et al. (2016) related data on plant age (Nobis & Schweingruber, 2013) and SLA taken from databases, and found that both variables were negatively correlated across various habitat types. Based on these previous results, we expected that population temporal stability and age are positively related to LDMC and negatively to SLA. For the subset of populations, where data on leaf traits and age were available, we did not find any significant relationships between population stability and leaf traits though. One possible reason for this difference between studies is the restriction of our analyses to forb species, while previous studies on the relationship between population stability and traits in grasslands included grasses, or the study systems were even dominated by grass-like species (grasses, sedges). Leaf dry matter content differs among functional groups, and it usually greater in grasses than in forbs (Bachmann et al., 2018). Thus, it is possible that the smaller between-species variation and larger within-species variation in LDMC as affected by plant diversity in our study reduced the chance to find a significant relationship between population stability and leaf traits. Regarding the relationships between age and leaf traits in our subset of populations, we could confirm that the maximum age of individuals found in a population was negatively related with SLA, while this was neither the case for mean age nor for LDMC. Adult age of plant species analysed in Klimešová et al. (2016) represent the typical age of mature, full-grown plants (Nobis & Schweingruber, 2013), which is likely more related to our estimate of maximum age per population than mean age. Thus, the relationship between plant longevity and SLA is also valid at the local scale. Taken together, our results from the biodiversity experiment suggest that plants with a greater longevity have more stable populations, while fast-growing species have lower longevity of their individuals and temporally less stable populations.

5 | CONCLUSIONS

Local coexistence and ecosystem functioning are determined by trade-offs between and within populations in terms of their growth, survival and fecundity (Barry et al., 2019), which may be influenced

by plant age. In this study, we could show for the first time that the age of populations is affected by the diversity of plant communities and that populations with older individuals show a higher temporal stability. Our study provided new insights into the temporal dimension of plant communities and calls to greater attention on plant demography to understand the effects of plant diversity on ecosystem functioning.

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AUTHORS' CONTRIBUTIONS

C.R., M.F. and A.R. made the conceptual design of the study; A.R., C.R. and A.E. collected the data; F.H.S. helped substantially with growth ring analysis; A.R. led the analysis and interpretation of the data with support of C.R. and wrote the manuscript; A.E., N.E., M.F. and C.R. contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Age data are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.rfj6q579f> (Roeder & Roscher, 2021). Leaf trait data are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.4k03n> (Bachmann et al., 2017). Biomass time-series data are available from PANGAEA <https://doi.org/10.1594/PANGAEA.866358> (Weigelt et al., 2016). Data on species-specific vegetation cover are available from PANGAEA, <https://doi.org/10.1594/PANGAEA.865275> (Temperton et al., 2016).

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SUPPORTING INFORMATION

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

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