Climate and seed weight drive intraspecific variation in seed longevity in storage

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Running head

Intraspecific variation in seed longevity in storage

ABSTRACT

Premise: Conservation seed banks are essential for ex-situ plant conservation, but stored seeds slowly deteriorate and lose viability. Seed longevity in storage is determined by the initial seed viability and the rate of seed viability loss. The rate of seed viability loss in storage varies between species, and there is possibly also some variation between populations or even genotypes within species. However, the extent of this intraspecific variability and its drivers remain unclear.

Methods: We investigated both inter- and intraspecific variability in seed longevity and its predictors in 41 common grassland species and 188 seed accessions from across Europe. We exposed the seeds to artificial ageing conditions (60% RH, 45°C) and used probit analysis to obtain the rate of seed viability loss (σ) as a measure of seed longevity. We then related σ to both accession- and species-specific factors.

Key results: Seed longevity (σ) varied significantly among accessions within 58% of the species, and the probability of detecting such intraspecific differences increased with the number of accessions available for a given species. This suggests that within-species variation in seed longevity is widespread. Accession-specific predictors explained only 14.4% of the within-species variability. Specifically, seed longevity increased with the mean annual temperature at the accession origin and decreased with the accession-specific seed weight. Across species, seed longevity differed among plant families but was unrelated to seed weight or seed chemical composition.

Conclusions. Our findings highlight substantial within-species variation in seed longevity in storage, which, however, is difficult to predict.

KEYWORDS

artificial seed ageing, conservation seed bank, species comparison, intraspecific seed longevity, probit analysis, seed storage, variability, within-species variability

INTRODUCTION

Biodiversity conservation is one of the critical global challenges, and *ex situ* methods play an increasingly important role in this task (Cohen et al., 1991). One of the most common ex-situ methods for plant conservation is seed banks, dedicated facilities that store seeds of wild plant species, particularly the vulnerable ones (Peres, 2016). The stored seeds represent a snapshot of past populations and are valuable resources for species reintroductions or ecosystem restoration, and also for scientific research (Cochrane et al., 2007; Etterson et al., 2016; Wambugu et al., 2023). Thus, the ultimate task of conservation seed banks is to keep the seeds viable for decades or even centuries.

Seed survival in storage depends on the type of seeds and storage conditions. Some types of seeds, so-called recalcitrant seeds, do not survive desiccation, making long-term storage impossible. Other types of seeds, called orthodox, can survive desiccation, and they can be stored for a couple of months up to centuries, depending on the species (Hay & Probert, 2013). Conservation seed banks aim to maintain seed viability as long as possible by storing the seeds under low temperatures and humidity to slow down internal chemical processes such as lipid peroxidation and DNA damage (Nagel et al., 2015; Walters et al., 2005a). The seed longevity also depends on the quality and viability of the seeds (Hay & Probert, 2013; Niedzielski et al., 2009), and thus, guidelines for seed banking recommend storing accessions with high initial viability (ENSCONET, 2009; Millennium Seed Bank, 2022). Yet, even highly viable seeds stored under optimal conditions slowly deteriorate and eventually die. This mortality is faster when the seeds are stored in suboptimal conditions, for example when storing seeds for large-scale ecosystem restoration in ambient conditions at a farm (Merritt & Dixon, 2011). To optimise the long-term effectiveness of seed storage – be it for conservation, research or ecosystem restoration purposes – we need to understand which factors predict seed longevity in storage.

Studying seed longevity presents unique challenges, as it requires comparing old and fresh seeds of the same seed lot, which would need time travel. To circumvent this obstacle, researchers have developed artificial ageing protocols which simulate natural ageing by exposing the seeds to high temperatures and high relative humidity

(Delouche & Baskin, 2021). These conditions accelerate the same or at least similar chemical processes typical of natural ageing during long-term storage (Delouche & Baskin, 2021). Although this method may not perfectly replicate natural ageing, the longevity of seeds in artificial ageing correlates with the longevity of seeds stored in seed banks both across and within species (Ninoles et al., 2022; Probert et al., 2009). Nevertheless, artificial ageing is the best method we currently have to compare seed longevity among accessions.

Seed survival in artificial ageing differs between species, and to some degree also between higher taxa like plant families, although large plant families harbour substantial variation in seed longevity (Probert et al., 2009; Walters et al., 2005a). Studies aiming to detect general patterns in seed longevity beyond evolutionary history yielded mixed results. Endospermic seeds survive shorter in storage than non-endospermic ones (Probert et al., 2009). The influence of seed weight is less clear; some studies suggest that seeds of small-seeded species survive longer (Satyanti et al., 2018), while others report no effect of seed weight (Davies et al., 2020; Merritt et al., 2014; Probert et al., 2009). Seed longevity is also affected by climatic conditions at seed collection sites: Seeds from hot or dry environments generally survive longer than those from cooler or wetter conditions (Merritt et al., 2014; Probert et al., 2009; Zani & Müller, 2017). Furthermore, seed longevity should hypothetically depend on the seed's chemical composition because high oil content should reduce seed longevity due to ongoing lipid peroxidation in storage (Narayana Murthy & Sun, 2000; Pritchard & Dickie, 2003), yet the results of empirical studies are inconsistent (Nagel et al., 2015; Probert et al., 2009; Walters et al., 2005a).

In contrast to between-species comparison, there is less comprehensive information on within-species variability on seed longevity in storage. Most data come from cultivated crops or model species (e.g. Bizouerne et al., 2023; Franks et al., 2018; Guzzon et al., 2021; Lee et al., 2019), with only a few studies addressing natural populations of wild species (Genna et al., 2020; Kochanek et al., 2009; Mondoni et al., 2011; White et al., 2023). These indicate that the variation in seed longevity within a species can be as substantial as the variation between species from the same ecosystem (Kochanek et al., 2009; Mondoni et al., 2011). The predictors of seed longevity on the level of populations, genotypes, or varieties appear to be similar to

103 those driving between-species differences: In general, lighter seeds of the same
104 species typically survive longer than heavier seeds (Franks et al., 2019; Guzzon et
105 al., 2018; Lee et al., 2019, but see Mira et al., (2019)). Consequently, seeds of
106 genotypes or varieties with lighter seeds tend to survive longer in storage than
107 accessions with heavier seeds, although this effect is inconsistent across studies
108 (Guzzon et al., 2021; Schutte et al., 2008). The climate at the seeds' origin seems to
109 be also a critical factor, with populations from warmer and dryer environments
110 producing longer-lived seeds than populations from colder and more humid
111 environments (Mondoni et al., 2011, 2014, but see Kochanek et al. (2009)). The
112 differentiation in seed longevity among populations of the same species can be
113 driven by two, mutually not exclusive mechanisms: genetic differentiation (Mondoni et
114 al., 2014) or phenotypic plasticity, where parental growing conditions influence seed
115 longevity (Kochanek et al., 2010; Mondoni et al., 2014; Sinniah et al., 1998). While
116 the studies above provide valuable insights, we are still missing a comprehensive
117 assessment of intraspecific variability in seed longevity across wild species, its
118 magnitudes and predictors.

119 To fill this gap, we focused on more than 40 common grassland species represented
120 by up to 11 accessions from across Europe. We exposed the seeds to artificial
121 ageing, estimated their longevity, and analysed the data on two levels: Comparison
122 across accessions within the species and comparison across species.

123 We expect that (1) seed longevity under artificial ageing conditions differs between
124 species and accessions within species. The variation among species will be larger
125 than the variation within species. (2) Within species, longevity will increase with mean
126 annual temperature and annual precipitation at the seed origin and decrease with
127 seed mass. (3) Across species, longevity will decrease with seed weight and be
128 influenced by seed chemical composition, particularly oil content, and the plant
129 family.

MATERIALS AND METHODS

Study species and seed material

We focused on 41 species common in European grasslands, belonging to 11 families distributed across the phylogenetic tree of angiosperms (Table 1). They represent a wide variety of traits, some potentially associated with seed longevity, specifically seed weight, seed oil and protein content (Probert et al., 2009). All species have orthodox seeds, i.e. they survive desiccation and freezing during storage.

To test for within-species variability, most species were represented by multiple origins, further called accessions. The number of accessions per species was driven by seed availability and varied strongly between species. More than half of the species were represented by at least four origins, while for six species we managed to obtain only one accession (Table 1). In total, the experiment included 188 accessions.

The experiment required large amounts of seeds. Seeds of 14 accessions were obtained by direct collection in nature or by collecting at least 50 young plants in the wild and growing them in a cold greenhouse to produce seeds. However, most seeds come from on-farm propagation for restoration purposes. We are aware that on-farm propagation may cause unintended selection, which could alter seed traits (Conrady et al., 2023; Ensslin et al., 2018). In the seeds we used, this effect will be rather minor because most producers are relatively new in this business and the propagation did not take place for many generations (*personal communication*). Using farm-propagated seeds further has the advantage that the maternal plants grew under optimal conditions and the seeds were harvested when fully ripe. This reduces the variability in seed quality, a characteristic that has a massive effect on storage behaviour (Rahman & Ellis, 2019; Sano et al., 2016; Sinniah et al., 1998).

Artificial ageing

To artificially age the seeds, we exposed them to 45° C and 60% relative humidity in a climate-controlled cabinet (Rumed ®, Rubarth Apparate GmbH, Laatzen, Germany). These conditions enhance similar chemical processes that are typical of

natural ageing during long-term storage and accelerate seed deterioration (Merritt et al., 2014; Probert et al., 2009).

We exposed the seeds to artificial ageing conditions for 0 (control group, fresh seeds), 1, 5, 9, 15, 20, 30, 40, 57 and 72 days (adjusted after Probert et al. (2009)). We put 3 replicates of 30 seeds of every accession and ageing duration into open 1.5 mL tubes in the ageing condition. The position of each accession in the ageing condition was randomised within the ageing duration. Before the ageing treatment, we manually scarified Fabaceae seeds with sandpaper to allow for moisture to be imbibed (Baskin, 2003). In total, our experiment contained 188 accessions, each with 10 ageing treatments and 3 replicates, that is 5,640 replicates containing 30 seeds each, that is 169,200 seeds.

Germination test

For germination tests, we used 6-well plates with a well-diameter of 39 mm (VWR International GmbH, Darmstadt, Germany, catalogue number: 734-2323), because they use space in the climate cabinet more efficiently than single petri dishes. For species with large seeds (*Bupleurum rotundifolium*, *Centaurea cyanus*, *Bromus hordeaceus*, *Arrhenatherum elatius*, *Lathyrus nissolia*, *Hordeum murinum*, *Hypochaeris radicata*, *Agrostemma githago*, *Poa annua*) we used petri dishes of 6 cm diameter to avoid overcrowding. We wrapped Petri dishes with seeds of *Bromus hordeaceus* in aluminium foil since light slightly inhibits germination (Andersson et al., 2002). After the intended ageing duration, we removed the seeds from the ageing conditions and transferred each replicate into one well or a petri dish laid out with two filter papers in a fully randomised design. We watered the seeds with a 0.025% Gibberellic acid solution to break dormancy and closed the plates with transparent Parafilm® to avoid evaporation. Germination took place in a climate-controlled cabinet (Rumed®, Rubarth Apparate GmbH, Laatzen, Germany) with a 14 h daily photoperiod at 20° C and 10 h darkness at 10° C.

We checked for germination every seven days and added distilled water if necessary. When a radicle was longer than 2 mm, we considered a seed viable and removed it from the dish. For each replicate with viable seeds, we finished the trial when no

more seeds germinated for at least four weeks. If in a replicate no seeds germinated at all for ten weeks, we considered the seeds not viable. If samples were affected by mould, we added 1 ml of a 0.0835% Difenoconazol solution.

Seed traits and climatic data

For each accession, we determined seed weight by weighing 2 replicates of 50 seeds and calculated the weight of a thousand seeds (further called seed weight for simplicity). We also obtained the mean annual temperature and precipitation for each accession location from WorldClim2 using the R package *raster* (Fick & Hijmans, 2017). In wild-collected seeds, we used the exact location of the seed collection. For farm-propagated seeds, we used the location of the farm, as the initial seeds used to establish the seed orchard were typically collected in the same region where the seed producer is located (Bucharova et al., 2019, Figure 1). The oil and protein content of the seeds was obtained from the Seed Information Database on species level (Society for Ecological Restoration et al., 2023).

Statistical analyses

Before data analysis, we calculated the initial germination rate of each of the 188 seed accessions. In some species, initial germination rates were higher in short-duration ageing treatments (one or five days) than in fresh seeds. This was likely because short exposure to ageing treatment can break dormancy (Hay et al., 2021; Mira et al., 2019). We thus defined “initial germination” for each accession as the highest average germination rate of the 0, 1 or 5 days in the ageing treatment. We removed accessions with initial germination below 50% and those particularly affected by mould (n = 39).

To analyse seed survival, we used generalized linear models (GLMs) with a quasibinomial error distribution (to account for overdispersion) and a probit link function. The probit transformation converts percentage responses onto a linear scale with a normal error distribution. We modelled the proportion of germinated seeds per replicate as a function of the number of days in ageing (Wolkis et al., 2025). The slope of the probit function directly describes the rate of seed viability

222 loss, and back transformation of the slope (-1/slope) yields σ, the number of days
223 needed for viability to drop by one probit (Hay et al., 2022; Klepka et al., 2025). We
224 are aware that most comparative studies of seed longevity in storage measured seed
225 longevity as p_{50}, the number of days needed for viability to decrease to 50%, yet this
226 parameter is heavily dependent on the initial seed viability (see Klepka et al. (2025)
227 for details). While the initial viability can be affected by the environmental effects, e.g.
228 during seed storage before the experiment, σ is assumed to be a genetic trait that
229 describes a species, population or genotype, and is thus the actual trait of interest
230 (Hay et al., 2022). We thus decided to use σ as a measure of seed longevity,
231 because it is independent of the initial seed viability of given accessions and directly
232 describes the slope of seed viability loss (Hay et al., 2022; Klepka et al., 2025).

233

234 ***Within-species variability***. We obtained the seed longevity estimate (σ) for each
235 accession. To do this, we related seed germination in each replicate to the time in
236 ageing conditions in a separate probit model for each accession. If the model failed
237 to give significant estimates for the slope, or if σ was higher than the maximum
238 ageing duration in our experiment (72 days), we excluded the accession from further
239 analyses (n = 14), since we assumed that in these cases the data cover only a very
240 short portion of the survival curve and the estimated parameters are therefore
241 unprecise. These models yielded separate σ-values for each accession.

242 We then tested whether the seed longevity (σ) differs between accessions within
243 species. This was possible for 26 species for which we had multiple accessions that
244 passed the initial check (initial germination >50% and significant accession-specific
245 σ). For this, we related the seed germination in each replicate to the accession
246 identity, the ageing duration and their interaction as explanatory variables in a
247 separate probit model for each species. A significant interaction between accession
248 identity and ageing duration indicates significantly different slopes between
249 accessions within species and therefore different seed longevities (σ). We further
250 tested whether the probability of detecting significant differences in σ between
251 accessions within species depended on the number of accessions representing each
252 species in our data set. To do this, we related the presence of significant difference

253 between accessions in each species (binomial yes/no) to the number of accessions
254 per species in a generalised linear model with binomial error distribution.

255 To understand drivers of within-species variability in seed longevity in storage, we
256 related accession-specific longevity (σ) as the response variable to the accession-
257 specific seed weight, mean annual temperature and precipitation at the accession's
258 origin as explanatory variables in a multiple linear mixed model. We included the
259 species' identity as a random factor. For this analysis, we scaled the seed weight
260 within each species to standardise the variable across species, and included only
261 species that were represented by at least 2 accessions.

262 We quantified the proportion of within-species variance explained by the fixed effects
263 using marginal and conditional R^2 estimates from the MuMIn package. This allowed
264 us to calculate the contribution of the within-species predictors relative to the
265 variance remaining after accounting for species identity.

266 ***Between-species variability***. We obtained the seed longevity estimate (σ) for each
267 species, common across accessions, regardless whether we detected significant
268 differences among accessions in the previous step. For this, we related seed
269 germination in each replicate (and from all accession of given species) to time in
270 ageing in a probit model for each species. For species with more than one accession,
271 we added accession identity as an explanatory variable to allow for different
272 intercepts (initial viability) in individual accessions. These models yielded one σ for
273 each species. To understand drivers of between-species variability in seed longevity
274 in storage, we related the log-transformed species-specific σ as the response
275 variable to the species' mean seed weight and plant family as explanatory variables
276 in a multiple linear regression model. As protein and oil contents were only available
277 for 15 study species, we evaluated their effects in a separate multiple linear
278 regression model.

279 All data analyses were performed using R version 4.4.2 (2024-10-31 ucrt) (R
280 Development Core Team, 2024). We log-transformed σ as the response variable to
281 ensure that model assumptions were met. For all models, we verified that model
282 assumptions were met by graphically evaluating the residuals (Zuur et al., 2010).

283 **RESULTS**

284 The estimated seed longevity (σ) significantly varied among accessions within 58%
285 of the species for which we had multiple accessions, specifically in 15 out of 26
286 species (Table S1). The probability of detecting significant differences among
287 accessions within species increased with the number of included accessions
288 (R^2=0.20, p=0.016, Figure S1). Within-species variation was the highest in *Prunella*
289 *vulgaris*, where σ varied more than 4-fold (Figure 2), specifically between 12.66 and
290 53.14 days. This within-species variability was hard to predict, as accession-specific
291 predictors explained only 14.4% of the variability among accessions, after correcting
292 for species identity. Specifically, seed longevity decreased with seed weight and
293 increased with the mean annual temperature at the accession origin, but was
294 unrelated to the mean annual precipitation (Table 2, Figure 3).

295 The estimated seed longevity also varied among species (Figure 2), and species s
296 identity explained 66% of the total variability among accessions. The average seed
297 longevity was shortest for *Thlaspi arvense* (σ = 5.04 days) and longest for *Lotus*
298 *pedunculatus* (σ = 66.70 days). The species seed longevity was unrelated to the
299 species-specific seed weight (Table 3A, Figure 4A) or the seed oil and protein
300 content (Table 3B, Figure 4B, C), but we found significant differences between plant
301 families (Table 3A, Figure 4D).

DISCUSSION

Effective conservation of seeds in ex-situ seed banks requires an understanding of seed storage behaviour not only for individual species but also for accessions within the very same species. We found, for multiple species common in European grasslands, that accessions of the same species commonly differ in seed longevity in storage. This intraspecific variability was partially explained by seed weight and mean annual temperature at the accession origin, but the predictive power of these variables was rather low (2.1% explained variability across all species). On the other hand, species identity was a strong predictor of seed longevity, explaining 66% of the variability among accessions. Our results thus suggest that seed longevity can be reliably predicted at the species level, but predicting accession-specific seed longevity in storage remains challenging.

Intraspecific variability in seed longevity

Seed longevity in storage varied considerably within-species, with accession-specific seed longevity differing significantly in 15 out of 26 species with multiple accessions. The probability of detecting significant differences among accessions within a species increased with the number of accessions included in the study. This suggests that with more accessions available, significant differences would likely be detected in even more species. Consequently, within-species differences in seed longevity in storage are likely very common.

Within-species, seed longevity was partially explained by the mean annual temperature at the collection site, a pattern that was reported previously (Mondoni et al., 2011). Other studies attributed such a positive correlation between temperature and seed longevity mainly to the species identity because they had species represented by single accessions (Merritt et al., 2014; Probert et al., 2009). We did not find any effect of the annual precipitation on seed longevity, which contrasts with previous studies, both within and across species (Merritt et al., 2014; Probert et al., 2009; White et al., 2023). This is likely because the mean annual precipitation was correlated with mean annual temperature (r=0.34), and as we used multivariate models, we were not able to tease apart the effect of both climate variables.

333 We found a negative relationship between the accession-specific seed weight and
334 seed longevity, with lighter seeds surviving significantly longer. Previous studies
335 primarily tested the relationship between seed weight and longevity across species,
336 yielding mixed results (Davies et al., 2020; Merritt et al., 2014; Pritchard & Dickie,
337 2003; Probert et al., 2009; Satyanti et al., 2018). Similarly, research on variability
338 within individual species has also produced inconsistent findings (Franks et al., 2018;
339 Genna et al., 2020; Guzzon et al., 2018, 2021; Mira et al., 2019; Schutte et al., 2008).
340 These inconsistent study findings underscore that seed mass remains an unreliable
341 predictor and highlight the complexity of seed longevity and its drivers. Nevertheless,
342 our results provide new evidence suggesting that, for a variety of wild grassland
343 species, lighter seeds may have a slight but consistent advantage over heavier seeds
344 of the same species in long-term storage survival.

345 The intraspecific variability in seed longevity may be driven by two mutually non-
346 exclusive mechanisms – phenotypic plasticity or genetic differentiation. For example,
347 Mondoni et al. (2011) detected that seeds collected in populations in warmer
348 environments survived longer in artificial ageing than conspecific seeds collected in
349 cooler environments. A large proportion of this effect was caused by phenotypic
350 plasticity, but the pattern was still significant, although weaker, in the second
351 generation grown in a common environment, which indicates that the effect is
352 partially heritable and thus genetic (Mondoni et al., 2014). Indeed, genes associated
353 with seed longevity in storage were identified in some crops and model species
354 (Bizouerne et al., 2023; Nagel et al., 2015; Raquid et al., 2021; Renard et al., 2020).
355 Our study worked with seeds that were collected in natural sites or produced in the
356 region of origin; we thus cannot discriminate whether the observed effects are plastic
357 or genetic.

358 After accounting for species identity, within-species predictors explained 14.4% of the
359 remaining variability among accessions. Still, species identity was the strongest
360 predictor of seed longevity and explained 66.9%. Our findings align with those of
361 Kochanek et al. (2009). On a continental scale, they collected data on seed longevity
362 in seven species represented by 2-8 populations, with populations within species
363 largely aggregated in a specific biome. Here, the species identity explained 69.1%
364 (adjusted R^2) of the variability among accessions, leaving 30% to variation among

accessions within species (own analysis of the data presented in Kochanek et al. (2009)). In contrast, a study by Mondoni et al. found that the intraspecific variability in seed longevity was much larger than the interspecific one. On a regional scale, they examined the seed longevity of six ecologically similar species that were each represented by two populations in contrasting environments, specifically high and low altitudes. Here, species identity explained only 6% of variability, leaving an astonishing 94% variation within species (own analysis of the data presented in Mondoni et al. (2011)). In our study, we detected that species explained about two-thirds of the variability in seed longevity among accessions, yet this number might be underestimated because we excluded the species with the most long-lived seeds for methodical reasons (see methods).

The comparison of our results with the findings of previous studies is complicated by different measures of seed longevity. We used σ, the rate of seed viability loss, which is independent of the initial seed viability and thus suitable for comparative studies across accessions and species. The vast majority of previous studies used p_{50}, the time till the seed viability decreases to half (e.g. Mondoni et al., 2011; Probert et al., 2009; Satyanti et al., 2018), a measure that is partially determined by the rate of seed viability loss (σ), but is heavily dependent on initial seed viability at the start of the experiment (Klepka et al., 2025). For example, using seeds with an initial viability ranging from 85 to 99.9%, but with the same rate of seed viability loss (σ), results in a threefold variation in p_{50}. The p_{50} estimate thus does not appropriately represent inherent differences between genotypes or populations (Hay et al., 2019). Direct comparison between our study and many previous studies is thus complex, unless raw viability data are available to calculate σ.

Interspecific variability in seed longevity

Across species, the only variable that significantly affected seed longevity was the plant family, with the observed differences between families being roughly in line with previous studies (Merritt et al., 2014; Mondoni et al., 2011; Probert et al., 2009; Walters et al., 2005b): Fabaceae seeds were relatively long-lived, probably due to their physical dormancy (Merritt et al., 2014), there was a large variability within Asteraceae (Merritt et al., 2014; Walters et al., 2005a), and three of the six shortest-

397 lived species in our study belonged to the Brassicaceae family (*Thlaspi arvense*,
398 *Cardamine hirsuta*, *Barbarea vulgaris*).

399 Neither seed weight nor chemical composition influenced seed longevity in our
400 artificial ageing experiment. In general, species-specific seed weight seems to be an
401 unreliable predictor of seed longevity in storage, as the effects reported in previous
402 literature strongly vary from negative, over no effect to, rarely, positive (Davies et al.,
403 2020; Merritt et al., 2014; Pritchard & Dickie, 2003; Probert et al., 2009; Satyanti et
404 al., 2018). Similarly, the chemical composition of the seeds did not predict seed
405 longevity, which corresponds to previous empirical studies of wild species (Kochanek
406 et al., 2009; Walters et al., 2005b). The expected effect of the chemical composition
407 on seed longevity in storage, especially oil content, is based on theoretical
408 expectations and comparisons among oil crops, cereals, and legumes (Narayana
409 Murthy & Sun, 2000; Pritchard & Dickie, 2003 Nagel et al., 2015), but the empirical
410 evidence provided by others and us shows that it is likely not true for wild species.

411

412 **CONCLUSIONS**

413 Our study demonstrates that in the majority of species, there is substantial within-
414 species variation in the rate of seed viability loss in storage. Conservation seed
415 banks sometimes design viability monitoring of individual accessions based on
416 species identity and initial seed viability only, assuming that accessions of the same
417 species lose viability at the same rate when stored under the same conditions (Hay &
418 Whitehouse, 2017). Our data show that this assumption is not valid and support the
419 existing concerns that this method might be suboptimal.

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AUTHOR CONTRIBUTIONS

Lea Klepka: Investigation, Formal analysis, Data Curation, Writing – original Draft, Visualization, Funding Acquisition. Sacha Liepelt: Investigation, Writing – Review&Editing, Anna Bucharova: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are not publicly available at the time of submission but will be deposited in an appropriate public repository upon acceptance of the manuscript. Data will be made available to editors and reviewers upon reasonable request.

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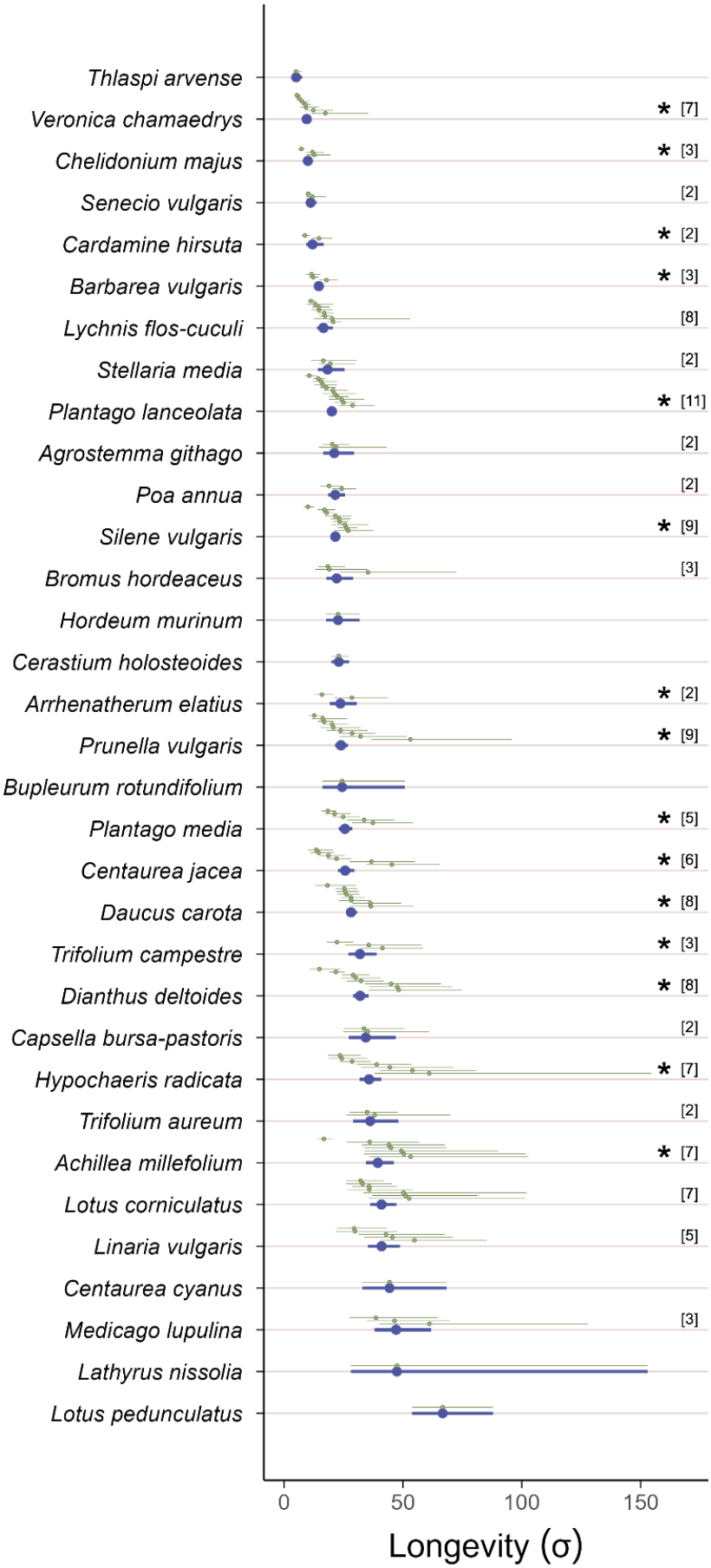
Figure 1: Origins of the 135 seed accessions used in the study and included in the analyses. Each point represents the location of a seed producer as a proxy for the origins of the individual seed accessions and thus, is the origin of multiple species. In three cases, the points represent the location of own seed collection.

Figure 2: Estimated seed longevity (σ) and 95% confidence intervals for 33 species and 135 accessions. Blue points and bars represent species-level estimates; green points and bars show accession-level estimates. Asterisks mark significant differences between accessions within species. Numbers in brackets indicate the number of accessions for species represented by multiple accessions.


Thlaspi arvense
Veronica chamaedrys
Chelidonium majus
Senecio vulgaris
Cardamine hirsuta
Barbarea vulgaris
Lychnis flos-cuculi
Stellaria media
Plantago lanceolata
Agrostemma githago
Poa annua
Silene vulgaris
Bromus hordeaceus
Hordeum murinum
Cerastium holosteoides
Arrhenatherum elatius
Prunella vulgaris
Bupleurum rotundifolium
Plantago media
Centaurea jacea
Daucus carota
Trifolium campestre
Dianthus deltoides
Capsella bursa-pastoris
Hypochaeris radicata
Trifolium aureum
Achillea millefolium
Lotus corniculatus
Linaria vulgaris
Centaurea cyanus
Medicago lupulina
Lathyrus nissolia
Lotus pedunculatus
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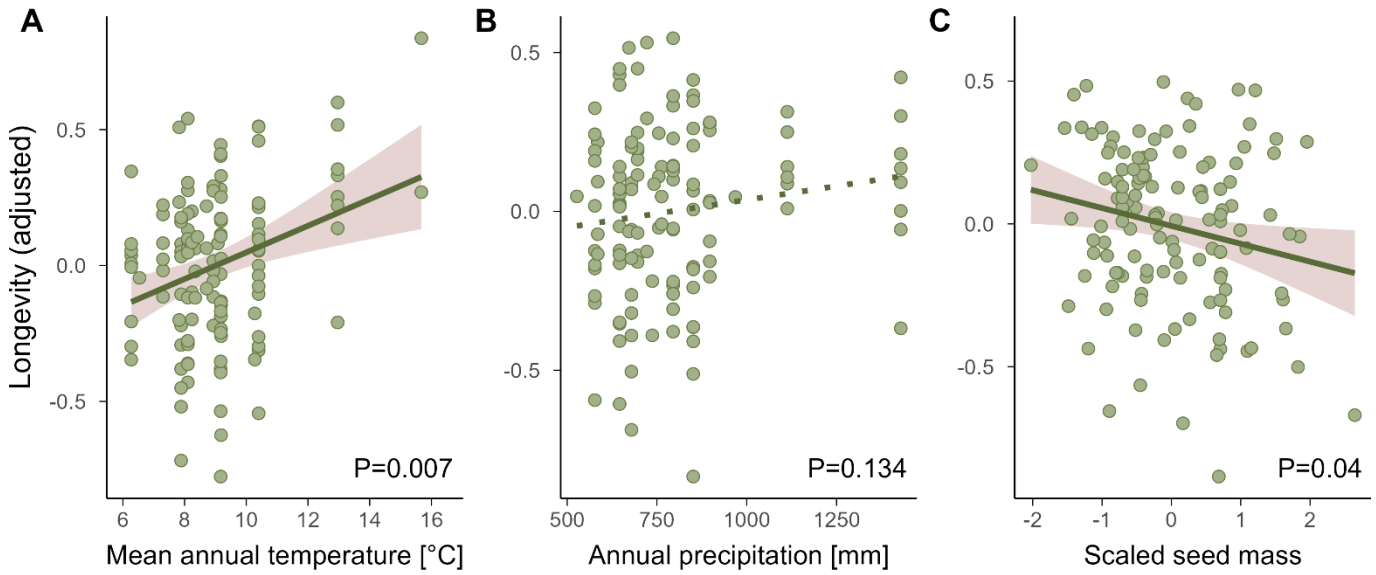
Longevity (σ)

650

651 Figure 3: Relationship between seed longevity (σ) of each accession, accession-
652 specific seed traits, and environmental variables. Each point represents a seed
653 accession. Seed longevity was adjusted for species identity. (A) Mean annual
654 temperature, (B) annual precipitation at the origins of the accessions, and (C)
655 accession-specific seed mass (scaled); For full model results, see Table 2.



656

Figure 4: Relationship between species seed longevity (σ) and species-specific seed traits. Each point represents one species. (A) Seed mass, average across accessions of the same species; species-specific (B) protein and (C) oil content in the seeds; and (D) plant families. The dashed lines indicate non-significant relationships. For full model results, see Table 3.

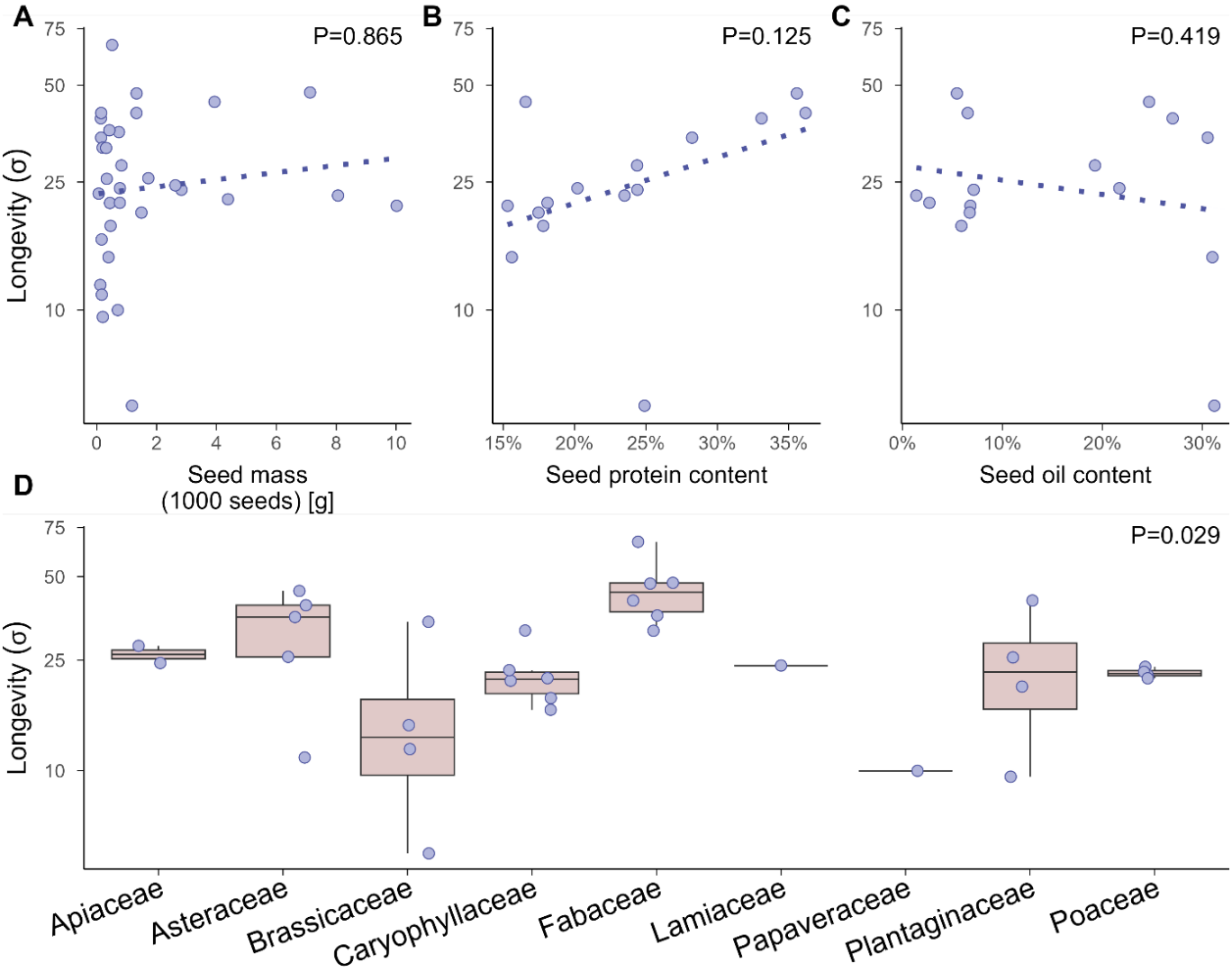


Table 1: Species included in the study. The number of accessions is the number of accessions used for the analyses, and in brackets is the initial number of accessions. Seed weight is the weight of 1000 seeds, averaged across all accessions of the same species. Oil and protein content are obtained from the Seed Information Database (Society for Ecological Restoration et al., 2023). Life cycle: A = annual, P = perennial, B = biennial. *: Information of conspecific

Species	**Number of accessions [initial number]**	**Seed weight [g]**	**Family**	**Life cycle**	**Oil content [%]**	**Protein content [%]**
Achillea millefolium	7 [10]	0.14	Asteraceae	P	27.03	33.1
Agrostemma githago	2 [2]	10.02	Caryophyllaceae	A	6.8	15.3
Ajuga reptans	0 [4]	1	Lamiaceae	P		
Anthemis arvensis	0 [1]	0.37	Asteraceae	A/B		
Arrhenatherum elatius	2 [5]	2.83	Poaceae	P	7.13	24.4
Barbarea vulgaris	3 [4]	0.39	Brassicaceae	A/B	31	15.6
Bromus hordeaceus	3 [3]	4.38	Poaceae	A		
Bupleurum rotundifolium	1 [1]	2.63	Apiaceae	A		
Capsella bursa-pastoris	2 [2]	0.15	Brassicaceae	A	30.53	28.23
Cardamine hirsuta	2 [2]	0.12	Brassicaceae	A		
Centaurea cyanus	1 [7]	3.94	Asteraceae	A	24.67	16.57
Centaurea jacea	6 [8]	1.72	Asteraceae	P		
Cerastium holosteoides	1 [1]	0.07	Caryophyllaceae	B/P		
Chelidonium majus	3 [5]	0.71	Papaveraceae	B		
Daucus carota	8 [9]	0.83	Apiaceae	A/B	19.26	24.38
Dianthus deltoides	8 [8]	0.2	Caryophyllaceae	P		
Galium wirtgenii	0 [1]	0.63	Rubiaceae	P		
Geranium pusillum	0 [1]	1	Geraniaceae	A		
Hordeum murinum	1 [1]	15.41	Poaceae	A	1.4	23.5
Hypochaeris radicata	7 [7]	0.74	Asteraceae	P		
Lamium album	0 [2]	1.57	Lamiaceae	P		
Lamium purpureum	0 [3]	0.69	Lamiaceae	A		
Lathyrus nissolia	1 [1]	7.13	Fabaceae	A		
Linaria vulgaris	5 [7]	0.15	Plantaceae	P		
Lotus corniculatus	7 [7]	1.33	Fabaceae	P	6.53	36.18
Lotus pedunculatus	1 [2]	0.52	Fabaceae	P		
Lychnis flos-cuculi	8 [8]	0.16	Caryophyllaceae	P		
Medicago lupulina	3 [6]	1.33	Fabaceae	A	5.45	35.57
Papaver rhoeas	0 [9]	0.1	Papaveraceae	A	43.47	24.53

Plantago lanceolata	11 [11]	1.49	Plantaginaceae	P	6.73	17.47
Plantago media	5 [6]	0.34	Plantaginaceae	P(/B/A)		
Poa annua	2 [2]	0.44	Poaceae	A/B		
Prunella vulgaris	9 [9]	0.77	Lamiaceae	P	21.7	20.2
Scandix pecten-veneris	0 [1]		Apiaceae	A		
Senecio vulgaris	2 [2]	0.17	Asteraceae	A		
Silene vulgaris	9 [9]	0.77	Caryophyllaceae	P	2.7	18.1
Stellaria media	2 [3]	0.46	Caryophyllaceae	A	5.9	17.8
Thlaspi arvense	1 [3]	1.18	Brassicaceae	A	31.2	24.9
Trifolium aureum	2 [2]	0.42	Fabaceae	A		
Trifolium campestre	3 [5]	0.31	Fabaceae	A/B		
Veronica chamaedrys	7 [8]	0.14	Plantaginaceae	P		

669

670 Table 2: **Intraspecific** variability in seed longevity in storage, results of the linear
671 mixed model testing the effect of accession-specific seed weight, mean annual
672 temperature, and annual precipitation on accession-specific seed longevity in storage
673 with species identity as random factor. Analysis of variance with error type III.
674 Significant effects (P < 0.05) are highlighted in bold.

	df	Chi Sq	p-value	$_{marg}R^2$	$_{cond}R^2$
				0.05	0.72
Accession-specific seed weight	1	4.23	**0.040**		
Mean annual temperature	1	7.30	**0.007**		
Annual precipitation	1	2.25	0.134		

675

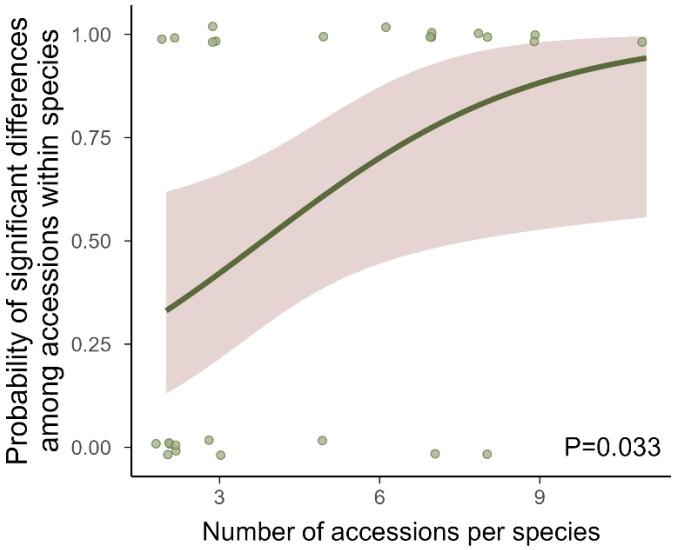
676 Table 3: **Interspecific** variability in seed longevity in storage, results of the linear
677 model testing the effect of (A) the family, the species-specific seed weight, and (B)
678 the protein and oil content on species-specific seed longevity. Analysis of variance
679 with error type III. Significant effects ($p < 0.05$) are highlighted in bold.

	df	Resid.df	*F*	*p*	R^2
A		23			0.49
Family	8		2.72	**0.029**	
Species-specific seed weight	1		0.03	0.865	
B		12			0.22
Protein content	1		0.77	0.125	
Oil content	1		0.70	0.419	

680

Figure S1:

Relationship between the number of accessions per species and the probability of detecting significant differences among accessions within species. The line shows a logistic regression with the 95% confidence interval.



686 Table S1: Species-specific seed survival models. Bold type indicates a significant
687 effect of the parameter. A significant interaction between the accession identity and
688 the ageing duration means significantly different seed longevities between
689 accessions within species.

Species	Number of Accessions	Ageing Duration			Accession Identity			Accession × Ageing		
		Df	F-value	p-value	Df	F-value	p-value	Df	F-value	p-value
Achillea millefolium	7	1	20.05	**<0.001**	6	1.24	0.290	6	5.96	**<0.001**
Agrostemma githago	2	1	37.33	**<0.001**	1	0.24	0.623	1	0.07	0.788
Arrhenatherum elatius	2	1	66.81	**<0.001**	1	1.10	0.298	1	6.41	**0.014**
Barbarea vulgaris	3	1	124.86	**<0.001**	2	56.90	**<0.001**	2	5.52	**0.006**
Bromus hordeaceus	3	1	16.95	**<0.001**	2	11.07	**<0.001**	2	2.49	0.089
Capsella bursa-pastoris	2	1	30.59	**<0.001**	1	1.98	0.165	1	0.03	0.871
Cardamine hirsuta	2	1	194.27	**<0.001**	1	4.24	**0.044**	1	8.65	**0.005**
Centaurea jacea	6	1	50.24	**<0.001**	5	7.59	**<0.001**	5	9.85	**<0.001**
Chelidonium majus	3	1	101.61	**<0.001**	2	19.83	**<0.001**	2	5.23	**0.007**
Daucus carota	8	1	84.95	**<0.001**	7	11.50	**<0.001**	7	2.50	**0.017**
Dianthus deltoides	8	1	99.55	**<0.001**	7	5.94	**<0.001**	7	8.28	**<0.001**
Hypochaeris radicata	7	1	80.70	**<0.001**	6	10.98	**<0.001**	6	5.19	**<0.001**
Linaria vulgaris	5	1	23.02	**<0.001**	4	11.62	**<0.001**	4	2.09	0.086
Lotus corniculatus	7	1	26.03	**<0.001**	6	4.06	**0.001**	6	1.58	0.155
Lychnis flos-cuculi	8	1	82.17	**<0.001**	7	18.94	**<0.001**	7	1.98	0.059
Medicago lupulina	3	1	23.12	**<0.001**	2	9.84	**<0.001**	2	1.21	0.305
Plantago lanceolata	11	1	123.03	**<0.001**	10	12.22	**<0.001**	10	5.14	**<0.001**
Plantago media	5	1	56.65	**<0.001**	4	22.08	**<0.001**	4	5.59	**<0.001**
Poa annua	2	1	94.97	**<0.001**	1	0.02	0.877	1	2.47	0.122
Prunella vulgaris	9	1	37.96	**<0.001**	8	4.85	**<0.001**	8	6.50	**<0.001**
Senecio vulgaris	2	1	149.25	**<0.001**	1	2.91	0.093	1	0.81	0.372
Silene vulgaris	9	1	139.81	**<0.001**	8	12.98	**<0.001**	8	7.27	**<0.001**
Stellaria media	2	1	46.77	**<0.001**	1	1.25	**0.268**	1	0.31	0.579
Trifolium aureum	2	1	29.80	**<0.001**	1	5.75	**0.020**	1	0.12	0.732
Trifolium campestre	3	1	87.20	**<0.001**	2	2.68	0.074	2	4.83	**0.010**
Veronica chamaedrys	7	1	128.71	**<0.001**	6	10.05	**<0.001**	6	5.46	**<0.001**

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