The soil seed bank can buffer long-term compositional changes in annual plant communities

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Abstract

1. Ecological theory predicts that the soil seed bank stabilizes the composition of annual plant communities in the face of environmental variability. However, long-term data on the community dynamics in the seed bank and the standing vegetation are needed to test this prediction.

2. We tested the hypothesis that the composition of the seed bank undergoes lower temporal variability than the standing vegetation in a 9-year study in Mediterranean, semi-arid and arid ecosystems. The composition of the seed bank was estimated by collecting soil cores from the studied sites on an annual basis. Seedling emergence under optimal watering conditions was measured in each soil core for three consecutive years, to account for seed dormancy.

3. In all sites, the composition of the seed bank differed from the vegetation throughout the years. Small-seeded and dormant-seeded species had a higher frequency in the seed bank than in the standing vegetation. In contrast, functional group membership (grasses vs. forbs) did not explain differences in species frequency between the seed bank and the vegetation after controlling for differences between grasses and forbs in seed mass and seed dormancy.

4. Contrary to predictions, the magnitude of year-to-year variability (the mean compositional dissimilarity between consecutive years) was not lower in the seed bank than in the vegetation in all sites. However, long-term compositional trends in the seed bank were weaker than in the vegetation in the Mediterranean and semi-arid sites. In the arid site where year-to-year variability was highest, no long-term trends were observed.

5. Synthesis. The effect of the seed bank on the temporal variability of the vegetation in annual communities depends on site conditions and time-scale. While the year-to-year variability of the seed bank is similar to the vegetation, the soil seed bank can buffer long-term trends.

Keywords
community composition, dormancy, drylands, rainfall gradient, resilience, seed size, temporal stability, temporal variability
1 | INTRODUCTION

Understanding the factors driving community stability is a key goal in ecology (Cleland et al., 2013; Collins, 2000; Komatsu et al., 2019; de Mazancourt et al., 2013). This goal is increasingly important in times of abrupt shifts in species composition driven by climate and land-use changes (Harrison et al., 2015; Liu et al., 2018; Song et al., 2018; Swenson et al., 2020). For plant communities, the natural storage of seeds in the soil (hereafter seed bank) is considered essential for compositional stability because seeds are highly resistant to environmental hazards (Angert et al., 2009; Cohen, 1966; Ooi, 2012).

Soil seed banks are especially important in ecosystems with high rainfall variability, such as drylands (Huang et al., 2016; Kigel, 1995). Currently, drylands cover 45% of the world's land surface (Praväll, 2016) and their cover is predicted to increase to 56% by the end of this century (Huang et al., 2016). Many drylands are dominated by annual plants that germinate each year from the seed bank (Angert et al., 2009; Tiellborger et al., 2014). These communities are frequently characterized by high temporal variability in species composition driven by asynchronized fluctuations among populations of coexisting species (Bar-Massada & Hadar, 2017; Hobbs et al., 2007). Theoretically, the seed bank can buffer two types of compositional changes, namely year-to-year variability (Cohen, 1966) and long-term community changes (Koopmann et al., 2017). Year-to-year variability may result from unpredictable differences among years in environmental conditions (e.g. precipitation, temperature). Long-term community changes are often caused by a trended variation in environmental conditions or management practices. Climate change models predict changes in both the mean and the variance of climatic conditions which will probably affect both year-to-year variability and long-term trends (Donat et al., 2016; Huang et al., 2016). Similarly, global land-use changes lead to directional changes in community composition (e.g. succession) but also affect year-to-year variability (Allan et al., 2014).

The role of the soil seed bank in buffering year-to-year environmental variability can vary across ecosystems. Classical theory predicts that a higher dormancy fraction will be favoured in systems with high rainfall uncertainty such as deserts, while lower dormancy will be favoured in more predictable environments (Cohen, 1966; Venable and Brown, 1988). However, the persistence of seeds in the soil is affected not only by dormancy but also by other factors such as seed predation, pathogen attack and mechanical decay (Kigel, 1995; Thompson, 1987).

While ecological theory highlights the role of the seed bank in stabilizing plant communities (Cohen, 1966; Venable & Brown, 1988), long-term monitoring of seed bank dynamics are scarce. Most empirical studies have focused on the short-term dynamics (<3 years) of seed banks (Bossuyt & Honnay, 2008; Osem et al., 2006) while several studies have used chronosequences as a substitute for the lack of long-term data from the same location (Dalling & Denslow, 1998; Török et al., 2018). We know of only one study that analysed long-term seed bank dynamics, focusing on the 10 most abundant species within a desert annual community (Venable & Kimball, 2012). Here, we compared temporal compositional trends in the seed bank and ensuing standing vegetation in annual plant communities spanning Mediterranean, semi-arid and arid ecosystems.

We hypothesized that year-to-year variability in the composition of the vegetation will increase with increasing aridity (because rainfall variability increases with aridity) while the seed bank will be more stable (Cohen, 1966; Venable & Brown, 1988), that is, the role of the seed bank in buffering year-to-year variability will increase with aridity. Additionally, assuming that the seed bank is a major driver of the high stability of Middle-Eastern communities (Sternberg et al., 2015; Tiellborger et al., 2014), we predicted that the seed bank will experience weaker long-term compositional trends than the vegetation.

A further aim of the study was to explain the differences in composition between the seed bank and the vegetation using a trait-based approach. Small-seeded species typically have higher fecundity (‘the size-number trade-off’, Jakobsson & Eriksson, 2000) and higher persistence in the soil (Funes et al., 1999; Thompson et al., 1993, 1998). However, small-seeded species often have lower survival at the seedling stage (Ben-Hur et al., 2012; Metz et al., 2010). Therefore, we predicted that small-seeded species will be relatively more common in the seed bank than in the vegetation. We also hypothesized that species with higher seed dormancy will be more common in the seed bank (Thompson, 1987).

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted at three sites located along a rainfall gradient (c. 100 km distance) in Israel. All sites were located over the same calcareous bedrock on south-facing slopes at similar altitudes and experienced similar mean annual temperatures that range from 17.7 to 19.1°C. The length of the growing season is determined by the rainfall, usually commencing in October–November and ending in April–May, with shorter seasons in drier sites. A detailed description of the sites appears in previous publications (Harel et al., 2011; Tiellborger et al., 2014).

Briefly, the three sites represent three different climatic regions: Mediterranean (Matta LTER; N 31°42′; E 35°03′), semi-arid (N 31°23′; E 34°54′) and arid (N 30°52′, E 34°46′). Thus, the sites have relatively low species overlap in terms of Jaccard’s similarity (Mediterranean–semi-arid: 0.64, Mediterranean–arid: 0.18 and semi-arid–arid: 0.22, see Tables S1–S3 for full species lists). The long-term mean annual rainfall in these three sites is 540, 300 and 90 mm with a coefficient of variation (CV) of 30%, 37% and 51% respectively (Tielborger et al., 2014). The mean annual rainfall during the years of the study (2000/2001–2009/2010) was 502, 245 and 79 mm with a CV of 24%, 32% and 48% respectively. All sites were fenced against grazing (by sheep and goats) in 2001. Before the establishment of the experimental plots, grazing intensity was high in the semi-arid site, intermediate in the Mediterranean site and negligible in the arid site (M. Sternberg, pers. obs.). Each site included
five plots of 250 m$^{-2}$ (10 × 25 m) with a minimum distance of 10 m between plots. The Mediterranean and semi-arid sites included additional plots with rainfall manipulations that were not considered in the current manuscript.

### 2.2 | Vegetation and seed bank sampling

The sampling of the vegetation was conducted annually at peak biomass—late March in the arid and semi-arid sites, and mid-April in the Mediterranean site, between the growing seasons of 2000/2001 and 2009/2010 (except in 2004/2005). Ten random samples (20 × 20 cm quadrats) of the herbaceous vegetation were taken in the open patches (i.e. patches without shrub cover) in each of the five plots (with a minimum distance of 1 m from the plot’s edges). Each sample was collected by cutting the vegetation at the ground level and brought to the laboratory. There, plants were sorted by species, and individuals of each species were counted.

The composition of the seed bank (including both transient and persistent fractions) was estimated by collecting soil cores on an annual basis (2000–2009) in September before the onset of the rainy season. Ten random soil samples were taken from each plot independently of the vegetation samples because the collection of the soil samples is likely to affect the vegetation in that particular sampling area (and vice versa). Soil cores were sampled over an area of 5 × 5 cm with a soil depth of 5 cm and included surface standing plant litter (c. 1–2 cm). Each sample was brought to the laboratory, thoroughly mixed, and stones and coarse roots were removed. The soil and plant litter was spread in drained plastic trays (12 × 14 cm, 6.5 cm depth) on a gauze sheet placed on top of a 3-cm-thick layer of perlite. The thickness of the soil layer varied between 0.75 and 1 cm. The trays were irrigated during winter (October–March) in a net-house at the Botanical Garden of Tel Aviv University. Emerging seedlings were identified, counted and continuously removed until no further emergence was observed a few weeks after the end of the growing season; Harel et al., 2011. This approach enables a better estimate of the abundance of species with high dormancy fraction. During summer, seed bank trays were naturally dried in the net-house to mimic typical hot, dry field conditions. At the end of the third season, each sample was passed through 5- and 0.30-mm sieves, to retrieve non-germinated seeds that were counted under a microscope (80× magnification). Since the number of retrieved non-germinated seeds was very low (<1% of the total number of emerged seedlings) and the procedure very time-consuming, this fraction of the seed bank was not considered in further analyses (see Harel et al., 2011).

The species lists for the three sites are found in the supporting information (Tables S1–S3).

### 2.3 | Statistical analyses

Our analysis focuses on the annual species that comprise most of the community in all sites in terms of biomass, abundance and richness (Tielborger et al., 2014). The seed bank composition was estimated by pooling all seedlings that germinated from each soil core during the 3 consecutive years of germination. We also performed additional, separate analyses for each year of germination (see Appendix S1 for details). All analyses were based on the Bray–Curtis index (Bray & Curtis, 1957) as a measure of dissimilarity among years and/or between the vegetation and the seed bank. We chose this index which is based on relative abundance data because presence–absence indices are sensitive to variability in the total density (no. of individuals per area) and the spatial scale of the sampling unit (Chase & Knight, 2013). Both the sampling-unit area and total density differed between the seed bank and the vegetation.

One major challenge in temporal analyses is that the dissimilarity in species composition across years can result from sampling errors instead of real temporal variability, especially in heterogeneous landscapes (Kaluzhny et al., 2014). We aimed to minimize the effects of sampling errors among replicates (due to spatial heterogeneity) by aggregating all vegetation and seed bank samples from each year in each site and taking the mean abundance of each species.

To visualize the temporal trends in species composition, we used non-metric multidimensional scaling (NMDS), the most robust ordination method (Minchin, 1987). We used PERMANOVA tests (‘adonis’ function of the \textit{vegan R} package, Oksanen et al., 2019) to test whether the community composition varies among years and between the seed bank and the vegetation. Additionally, we tested for homogeneity of dispersion (‘betadisp’ function of the \textit{vegan R} package), one of the assumptions of PERMANOVA tests (Alekseyenko, 2016).

The year-to-year variability was estimated based on the mean distance among all possible pairs of consecutive sampling years. The differences between year-to-year variability in the seed bank and vegetation were compared with a permutation t test using the \textit{coin R} package (Hothorn et al., 2019).

To investigate long-term compositional variability, we applied a time-lag analysis (Collins et al., 2000), that is, regressing time-lag [the temporal distance between each pair of years (log transformed)] and compositional dissimilarity (Bray-Curtis). The time-lag analysis is the temporal analog of the commonly used distance-decay approach for spatial analysis of compositional similarity (Nekola & White, 1999). The advantage of the time-lag approach is that it does not require using the first year as a reference point for all other years and allows more accurate estimation because of several replications for each distance class. In this analysis, the slope of the time-lag compositional distance relationship indicates the rate of long-term directional change in composition. We compared the slopes in the vegetation and the seed bank using the method proposed by Nekola and White (1999). This approach, which incorporates the dependence among replications of pairwise distance, was implemented using the \textit{Simba R} package (Jurasinski & Retzer, 2012).
We investigated whether species’ traits can explain differences in composition between the seed bank and the vegetation, as well as differences in temporal trajectories, focusing on seed mass, seed dormancy and functional group (grasses vs. forbs). These traits were chosen because of their importance for community assembly in the region (DeMalach et al., 2019; Harel et al., 2011). Seed mass data were taken from a previous study in the same sites (Harel et al., 2011) and were available for more than 90% of the individuals sampled. Additionally, a seed dormancy index was calculated for each species based on variability in the number of seedlings found in the soil cores during the three consecutive germination years: \( \sqrt{\sum_{i=1}^{3} \frac{100}{12T_i} - A_i} \), where \( i \) is the year of germination (not the year of sampling), \( A_i \) is the abundance of the species in year \( i \) (all soil samples combined) and \( T \) is the total abundance of the species (summed over all years). The dormancy index is bounded between 0 (when all seeds germinated during the first year) and 1 (when all seeds germinated during the third year). The square root reduces the skewness of the index resulting from the steep decrease in the number of germinating seeds over the 3 years. The dormancy index cannot capture dormancy for more than 3 years, but such long-term dormancy was negligible under net-house conditions (see ‘Vegetation and seed bank sampling’ section above).

We related species traits and species composition using affinity indices (DeMalach et al., 2019) as a solution for the problem of inflated type I error of the community-weighted mean approach (Miller et al., 2018; Peres-Neto et al., 2017). We defined seed bank affinity as species’ relative abundance in the seed bank compared with the sum of relative abundances in the vegetation and seed bank:

\[
\text{seed bank affinity} = \frac{A_{\text{seed bank}}}{A_{\text{seed bank}} + A_{\text{vegetation}}}.
\]

Here, \( A_{\text{seed bank}} \) and \( A_{\text{vegetation}} \) represent the relative abundance of the species in the seed bank and the vegetation respectively (all years pooled together). The seed bank affinity ranges from 0 (when a species appears only in the vegetation) to 1 (appears only in the seed bank). The very rare species that appeared only in the seed bank or in the vegetation were not included in the analyses of seed bank affinity to eliminate the possibility that differences result from low detection rate (see Tables S4–S6 for sample size in the different analyses).

We estimated the effect of the three major traits on seed bank affinity using linear models for species with relative abundance higher than 0.5% to avoid bias caused by rare species with more stochastic occurrences. In the regression, seed mass (mg) was \( \log_{10} \)-transformed and the functional group was incorporated as a dummy variable coded 1 for grasses and 0 for forbs. For each regression, we report both the coefficients without transformation (raw estimates) and standardized estimates (when both the explanatory variables and the dependent variable are standardized by subtracting their mean from each observation and then dividing by the standard deviation). Standardized coefficients enable comparison among variables with different units.

### 3 | RESULTS

The composition of the seed bank (all three germination years pooled) significantly differed from the composition of the vegetation in the Mediterranean (pseudo-\( F_{1,15} = 2.6, p = 0.016 \)), semi-arid (pseudo-\( F_{1,15} = 3.9, p = 0.003 \)) and arid (pseudo-\( F_{1,15} = 4.3, p < 0.001 \)) sites (Figure 1; Figures S1–S3). Heterogeneity of dispersion between the seed bank and the vegetation was found to be significant in the semi-arid community (pseudo-\( F_{1,15} = 5.1, p = 0.04 \)) and insignificant in the Mediterranean (pseudo-\( F_{1,15} = 2.08, p = 0.17 \)) and the arid (pseudo-\( F_{1,15} = 0.5, p = 0.48 \)) communities.

Species’ seed bank affinity (relative abundance in the seed bank compared with the vegetation) was negatively affected by seed mass and positively affected by seed dormancy in the semi-arid and arid...
sites (Figure 2; Table S4), that is, small-seeded species and species with higher seed dormancy were more common in the soil seed bank than in the vegetation (but significance levels were marginal in the arid site, Table S4). In the Mediterranean site, seed bank affinity was negatively affected by seed mass and unaffected by dormancy. Plant functional group membership (grasses vs. forbs) did not affect seed bank affinity in any of the sites (Figure 2; Table S4). Species’ seed mass and their dormancy index were not correlated in any of the sites (Figure S7).

The results did not support our hypothesis that the seed bank undergoes lower year-to-year variability than the vegetation (Figure 3, blue triangles). Differences in year-to-year variability (dissimilarity between pairs of consecutive years) between the seed bank and the vegetation were not significant in both the semi-arid ($Z_{1,10} = 0.69, p = 0.49$) and arid ($Z_{1,10} = -0.99, p = 0.32$) sites. In the Mediterranean site, year-to-year variability was even slightly higher in the seed bank than in the vegetation ($Z_{1,10} = -2.49, p = 0.013$).

Long-term directional trends in community composition occurred in the Mediterranean and the semi-arid sites as indicated by the positive relationship between time-lag (temporal distance among years) and compositional distance (Figure 3a–d; Figure S8a–d). In contrast, there were no significant relationships between time-lag and compositional distance in the arid site (Figure 3e–f; Figure S8e–f).

The rates of long-term changes in the Mediterranean and semi-arid sites (the slopes in Figure 3) were lower in the seed bank compared with the vegetation ($p = 0.013$ and $<0.001$ respectively) thereby supporting the hypothesis that the seed bank is more resistant to directional changes than the vegetation. The difference in

**FIGURE 2** The effects of seed mass, seed dormancy index and functional group membership (coded 0 for forbs and 1 for grasses) on species’ seed bank affinity. Effect size (points) represents standardized regression coefficients (see Table S4 for a detailed summary). Species’ seed bank affinity (relative abundance in the seed bank compared with that in the vegetation) is negatively affected by seed mass and positively affected by seed dormancy. Error bars represent confidence intervals. The dashed line represents zero effect. $N_{	ext{Mediterranean}} = 80$, $N_{	ext{Semi-arid}} = 43$ and $N_{	ext{Arid}} = 14$

**FIGURE 3** Compositional distance (Bray–Curtis index) in the vegetation (left panels) and seed bank (right panels) as a function of time-lag (temporal distance between years of sampling including all possible pairs). The blue triangle represents the mean compositional distance between two consecutive years (year-to-year variability). The slope of the relationship indicates the rate of long-term trends. (a, b) Mediterranean site, (c, d) Semi-arid site and (e, f) Arid site. The $x$-axis has a logarithmic scale. Trendlines were added when the relationship between time-lag and compositional distance was statistically significant ($p < 0.05$)
the slopes was highest in the semi-arid site (about 3.5 times steeper) leading to a larger divergence in composition between the seed bank and vegetation with time (Figure S9).

4 | DISCUSSION

Our findings support the hypothesis that the seed bank is more resistant than the vegetation to long-term compositional shifts in both the Mediterranean and the semi-arid sites. However, the hypothesis of lower year-to-year variability in the seed bank was not supported in any of the sites. Additionally, we demonstrated that the composition of the seed bank differs from the standing vegetation because small-seeded and species with high dormancy fraction are overly represented in the seed bank.

4.1 | Differential composition in the seed bank and the vegetation

The PERMANOVA demonstrates major differences in composition between the vegetation and the seed bank in all sites. In the case of the semi-arid site, the results should be treated with caution because the assumption of homogeneous dispersion has been violated. Nonetheless, such violation is unlikely to inflate type I error in our study because we had a balanced sample size in the seed bank and the vegetation (see details in Alekseyenko, 2016).

We aimed to explain differences in composition using three major traits: seed mass, seed dormancy and functional group membership. Seed bank affinity was partially explained by these traits ($R^2 = 0.07$, $R^2 = 0.18$, $R^2 = 0.54$, for the Mediterranean, semi-arid and arid sites respectively), but additional traits could have increased the explanatory power.

Dormant-seeded species were more common in the seed bank than in the vegetation (Figure 2), as expected for organisms that spend most of their life as seeds and only one growing season as developed plants. Our dormancy index was based on dormancy in net-house conditions with constant irrigation during the growing season which depleted the seed bank after three consecutive growing seasons (see Section 2). In natural conditions, however, dormancy could be much longer because of spatial heterogeneity in soil conditions, greater year-to-year variation in rainfall conditions and other differences between natural and experimental conditions (Kigel, 1995; Thompson, 1987). Therefore, we believe that the association between dormancy and seed bank affinity is even stronger than implied by our analyses.

The finding that small-seeded species were relatively more common in the seed bank (Figure 2) could be related to several factors. First, small-seeded species often have higher fecundity and are less sensitive to seed predation (Jakobsson & Eriksson, 2000; Lebría-Trejos et al., 2011; Petry et al., 2018) resulting in higher abundance in the seed bank. At the same time, small-seeded seedlings are more sensitive to abiotic stress (Moles & Westoby, 2004; Muller-Landau, 2010) and size-asymmetric competition (DeMalach et al., 2019) which may reduce their abundance in the vegetation compared with the seed bank. Furthermore, seed size is often correlated with persistence in the soil (Funes et al., 1999; Thompson et al., 1993, 1998) and with environmental factors controlling germination, particularly light conditions (Kigel, 1995; Thompson, 1987).

In our main analyses, we focused on the total seed bank which included all seeds that germinated during three consecutive watering years after the collection. Comparison of the separate analyses of seeds germinating in the first year only and total seed banks (all years pooled, Figure 1; see Appendix S1 for details) showed similar patterns of germination (Figure S4) because the proportion of seeds germinating during the first year was much higher than that in the following 2 years. Moreover, differences between the seed bank and the vegetation were found also when we compared the vegetation to the second and the third years of germination (Figures S5–S6). In sum, our conclusion that the seed bank undergoes similar year-to-year variability in composition as the vegetation but slower rates of long-term shifts is valid for the total seed bank, as well as the seed bank estimated for each germination year separately (Figures S10–S12).

All our analyses were based on the Bray–Curtis dissimilarity index which is mostly affected by changes in the relative abundance of common species. The common species in the three sites were found in both the seed bank and the vegetation (Tables S1–S3). However, in each site, some rare species were exclusively found in either the seed bank or the vegetation. Such patterns could be related to the four times larger area of the vegetation samples or the higher density of the seed bank.

4.2 | The role of the seed bank in buffering year-to-year variability

We used the mean compositional distance among each pair of consecutive years as an indicator of year-to-year variability. This type of short-term variability is often caused by stochastic differences among years in climatic conditions but can also be affected by directional trends (e.g. succession). In our case, we believe that year-to-year variability is mostly related to stochastic variability among years since in the overwhelming majority of cases we did not find a significant overall temporal trend in year-to-year variability (Figure S13).

Year-to-year variability in the composition of both the seed bank and the vegetation was highest in the arid site which is probably related to the high rainfall variability in this site. However, we caution that despite our aim to minimize alternative sources of variability among sites (see Section 2), it is difficult to reach generalizations based on three ecosystems.

In contrast with our prediction, year-to-year variability in the seed bank was not lower than in the vegetation. We attribute this finding to species-specific variability in fecundity among years (Venable, 2007) which may lead to high compositional variability in the seed bank.
Furthermore, seed bank composition could be affected by variability in dormancy among years due to fluctuations in temperature, soil moisture, granivores and pathogens (Venable, 2007). Nonetheless, our findings do not imply that the seed bank does not play a role in buffering temporal fluctuations in the vegetation. Even though the relationships between seed bank and vegetation dynamics are highly complex, seed banks can still serve as ‘insurance’ against population extinctions even when species abundance varies among years (Fischer & Stocklin, 1997).

4.3 | The role of the seed bank in buffering long-term shifts

We supported the hypothesis that seed bank composition is more resistant to long-term changes than the vegetation by showing lower rates of directional changes in both the Mediterranean and the semi-arid sites (Figure 3). Directional changes in composition in both sites (Figures 1 and 3) are probably related to the removal of livestock grazing during the establishment of the research sites (Golodets et al., 2010; Osem et al., 2004; Tielborger et al., 2014). The trend was stronger in the semi-arid site than in the Mediterranean site where past grazing was more intense, while grazing intensity was negligible in the arid site.

5 | CONCLUSIONS

Investigating the drivers of compositional stability is of major importance in times of major climate and land-use changes (Damschen et al., 2010; Duprè et al., 2010; Harrison et al., 2015; Komatsu et al., 2019). Several studies have speculated that patterns of vegetation stability are related to seed bank stability. For example, the high drought sensitivity of the vegetation in Californian grasslands was attributed to a depleted seed bank (Harrison et al., 2018). Furthermore, it has been shown that drought and nitrogen deposition deplete seed banks in several grasslands (Basto et al., 2015, 2018). Conversely, the high stability of Middle-Eastern annual communities to grazing and rainfall changes was attributed to the high resilience of their seed bank to these environmental factors (Sternberg et al., 2003; Sternberg et al., 2017; Tielborger et al., 2014). Our results provide empirical support for the above assertion. We have demonstrated that in the Mediterranean and the semi-arid communities, the seed bank undergoes weaker long-term shifts. Therefore, we argue that a better understanding of the buffering role of soil seed banks under climate change will significantly improve our predictions for the future distribution and persistence of annual plant communities.

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AUTHORS’ CONTRIBUTIONS

M.S. and J.K. conceived the research idea within the GLOWA Jordan River project and collected the data; N.D. developed the seed bank and vegetation comparison, performed the statistical analysis and wrote the first draft of the paper. All the authors substantially contributed to the writing of the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13555.

DATA AVAILABILITY STATEMENT

All data are available on FigShare https://figshare.com/articles/dataset/The_soil_seed_bank_can_buffer_long-term_compositional_changes_in_annual_plant_communities/13175987 (DeMalach, Sternberg, & Kigel, 2020).

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**SUPPORTING INFORMATION**

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

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