

Letter

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

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Data accessibility

All data will be available on FigShare

AUTHOR CONTRIBUTIONS

MS and JK conceived the research idea within the GLOWA Jordan River project and collected the data.

ND developed the seed bank and vegetation comparison, performed the statistical analysis, and wrote the first draft of the paper. All authors substantially contributed to the writing of the manuscript.

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ABSTRACT

Ecological theory predicts that the soil seed bank stabilizes the composition of plant communities in the face of environmental variability. Using one of the longest seed bank-vegetation databases, we tested whether the composition of the seed bank is more stable than the standing vegetation in annual communities across a rainfall gradient. The composition of the seed bank differed from the vegetation throughout the years with a higher abundance of small-seeded and persistent-seeded species. Year-to-year variability in composition increased with increasing aridity, but its magnitude was similar in the seed bank and the vegetation. Importantly, the rate of long-term compositional change was much slower in the seed bank. These results support the hypothesis that the seed bank can buffer against climatic shifts and increases the resistance of plant communities to directional trends. We conclude that the seed bank plays a crucial role in the stability of plant communities under global changes.

INTRODUCTION

Understanding the factors driving community stability is a key goal in ecology (Collins 2000; Cleland *et al.* 2013; de Mazancourt *et al.* 2013; Komatsu *et al.* 2019). 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 (Cohen 1966; Angert *et al.* 2009; Ooi 2012).

Seed banks are especially important for ecosystems with high rainfall variability, such as drylands (Kigel 1995; Huang *et al.* 2016). Currently, drylands cover 45% of the world's land surface (Prăvălie 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; Tielborger *et al.* 2014). These communities are frequently characterized by high temporal variability in species composition driven by asynchronized fluctuations among populations of coexisting species (Hobbs *et al.* 2007; Bar-Massada & Hadar 2017). 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 environmental variability can vary across ecosystems. Classical theory predicts that a higher dormancy fraction will be favored in systems with high rainfall uncertainty such as deserts, while lower dormancy will be favored in more predictable environments (Cohen 1966;

Venable & 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 (Thompson 1987; Kigel 1995).

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 (Osem *et al.* 2006; Bossuyt & Honnay 2008) 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 analyzed long-term seed bank dynamics, focusing on the ten most dominant species within a desert annual community (Venable & Kimball 2012). Here, we analyze one of the longest databases (nine-years) on soil seed bank and standing vegetation dynamics along a rainfall gradient 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), i.e. 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 (Tielborger *et al.* 2014; Sternberg *et al.* 2015), we predicted that the seed bank will experience weaker long-term compositional shifts than the vegetation.

We aimed to explain the differences in composition between the seed bank and the vegetation using a trait-based approach. We predicted that small-seeded species will have higher relative abundance in the seed bank because they often have higher fecundity (Jakobsson & Eriksson 2000), while large-seeded species will be more common in the standing vegetation because their seedlings have a higher survival probability (Ben-Hur *et al.* 2012). We also hypothesized that seed bank affinity will be affected by seed persistence, i.e., that species with higher seed persistence will be more common in the seed bank (and vice versa).

The composition of the seed bank was estimated by collecting soil cores every year and following seedling emergence in each core for three consecutive years. This unique approach enables the encapsulation of both the transient seed bank (i.e., seeds germinating during the first year) and the persistent seed bank (i.e., seeds germinating during the second and third years).

METHODS

Study sites

The study was conducted at three sites located along a steep rainfall gradient 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; Tielborger *et al.* 2014).

Briefly, the three sites represent three different ecosystem types: 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'). 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, personal observations). Each site included five plots of 250 m² (10 m × 25 m). The Mediterranean and semi-arid sites include additional plots with rainfall manipulations that were not considered in the current manuscript.

Vegetation and seed bank sampling

The annual sampling of the vegetation was conducted 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 x 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. Plant species were cut at the ground level, identified, and counted in the lab.

Soil seed bank samples were collected each year (2000–2009) in September before the onset of the rainy season in the same plots as the vegetation samples, aiming to relate the seed bank to the ensuing vegetation. As for the vegetation, ten random soil samples were taken from each plot. Soil cores were sampled over an area of 5×5 cm and a depth of 5 cm, including the surface litter. Each sample was brought to the lab. There it was thoroughly mixed, and stones and coarse roots were removed. The soil and plant litter containing seeds 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 (beginning early October) 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 (mid-March). The overall germinable seed bank in each soil sample was assessed by repeating the germination procedure for each tray during three consecutive growing seasons (winters). 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 soil 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).

Statistical Analyses

We aggregated all vegetation and seed bank samples for each year in each site, and the mean abundance of each species was calculated for each year. This aggregation aimed to minimize sampling error and variability in composition due to spatial heterogeneity. In the main analyses, seed bank composition was estimated by pooling all seedlings that germinated from each soil core during the three consecutive years of germination. We also performed additional, separate analyses for each year of germination to distinguish between the transient (first year) and the more persistent (second and third years) seed banks (see Appendix S1 for details).

All analyses were based on species' *relative abundance* to control for differences in density between the seed bank and the vegetation. In our analysis, we focused on the annual species that comprise most of the community in all sites in terms of biomass, abundance, and richness (Tielborger *et al.* 2014). Analyses of variability in composition were based on the Bray–Curtis index (Bray & Curtis 1957) among years. This commonly used index is a real distance metric (i.e., obeys the triangle inequality and equals half the Manhattan distance) when applied to relative abundance data. For each site, we used non-metric multidimensional scaling (NMDS), the most robust ordination method (Minchin 1987), for visualizing differences in composition between the seed bank and the vegetation. We tested whether the composition of the seed bank and the vegetation differ with PERMANOVA tests using the ‘vegan’ R package (Oksanen *et al.* 2019).

Temporal trends were investigated in both the vegetation and the seed bank using a time-lag analysis (Collins *et al.* 2000) i.e., regressing time-lag (the temporal distance between each pair of years [log transformed]) and compositional distance. 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. We also compared the compositional distance from the first year with time (second year

onward) as a complementary approach and found very similar patterns (Fig. S9). In all analyses of temporal trends in the vegetation and seedbank, the year 2005 (for which vegetation data was unavailable) was excluded to avoid any potential bias (e.g., if environmental conditions were very different during 2005).

We compared the mean compositional distance among consecutive years (in the seed bank and the vegetation, hereafter year-to-year variability) using a permutation t-test (Hothorn *et al.* 2019). Additionally, we compared the slopes of the time lag–compositional distance relationships in the vegetation and the seed bank using the method proposed by Nekola & White (Nekola & White 1999). This approach, which incorporates the dependence among replications of pairwise distance, was implemented using the ‘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 persistence, and functional group (grasses vs. forbs). These traits were chosen because of their importance for community assembly in the region (Harel *et al.* 2011; DeMalach *et al.* 2019). Seed mass data was 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 persistence index was calculated based on variability in the number of seedlings found in the soil cores during the three consecutive years: $\sqrt{\sum_{i=1}^3 \frac{(i-1) \cdot A_i}{2T}}$, 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 persistence index is bounded between zero (when all seeds germinated during the first year) and one (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 three years. The persistence index cannot capture persistence for more than three years but such long-term persistence was negligible under net-house conditions (see ‘Vegetation and seed bank sampling’ section above).

We related species traits and species composition using the affinity indices approach (DeMalach *et al.* 2019). First, *seed bank affinity* is species' relative abundance in the seed bank compared with that in the vegetation:

$$\text{seed bank affinity} = \frac{A_{\text{seedbank}}}{A_{\text{seedbank}} + A_{\text{vegetation}}}$$

Here, A_{seedbank} 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 zero (when a species appears only in the vegetation) to one (appears only in the seed bank). Similarly, the *succession affinity* index represents species' relative abundance in later years compared with the first year of the study: $\text{succession affinity} = \sum_{i=1}^9 \frac{(i-1) \cdot A_i}{8T}$. Here, i represents the year of sampling (the study lasted for nine years), A_i represents the relative abundance of the species in year i and T is the sum of species' relative abundances in all years. The eight in the numerator is a normalization factor constraining the values of the index between zero (when the species appears only in the first year) and one (when the species appears only in the last year).

We estimated the effect of the three major traits on affinity indices using linear regressions for the 40 most dominant species in each site (to avoid bias caused by rare species with more stochastic occurrences). The use of the affinity indices approach for testing trait-environmental relationships (DeMalach *et al.* 2019) reduces some of the problems associated with the classical community weighted mean approach (Peres-Neto *et al.* 2017; Miller *et al.* 2018).

In the regression, seed mass (mg) was \log_e transformed and the functional group was incorporated as a dummy variable (coded one for grasses and zero for forbs). 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 the wrong identification of some species (see Tables S1–S3 for sample size in the different analyses). 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.

RESULTS

The composition of the seed bank (all three germination years pooled) significantly differed from the composition of the vegetation in the Mediterranean ($P = 0.019$), semi-arid ($P < 0.001$) and arid ($P < 0.001$) sites (Fig. 1, Fig. S1–S3). As expected, the compositional distance from the vegetation was higher for the more persistent seed bank than for the transient seed bank (Fig. S4–S6).

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 persistence in all sites (Fig. 2, Fig. S7, Table S1) i.e., small-seeded species and species with higher seed persistence in the soil were more common in the seed bank than in the vegetation (but significance levels were marginal in the semi-arid site, Table S1). Additionally, we found no effects of plant functional group membership (grasses vs. forbs) on seed bank affinity (Fig. 2, Table S1), i.e., the effect of functional membership *per se* was not significant once the lower persistence and higher seed mass of the grasses (Fig. S8) were controlled for in the multiple regression (Table S1). Species' seed mass and their persistence index were not correlated in any of the sites (Fig. S8).

Directional trends in community composition exist in the Mediterranean and the semi-arid sites as indicated by the positive relationship between time-lag (temporal distance among years) and compositional distance (Fig. 3a–d, Fig. S9a–d). In contrast, there was no relationship between time-lag and compositional distance in the arid site indicating that there is no directional trend in composition in this ecosystem type (Fig. 3e–f, Fig. 9e–f).

The results did not support our hypothesis that the seed bank undergoes lower year-to-year variability than the vegetation (Fig. 3, blue triangles). Differences in year-to-year variability between the seed bank and the vegetation in the semi-arid and arid sites were not significant ($P = 0.493$, $P = 0.32$). In

the Mediterranean site, year-to-year variability was even slightly higher in the seed bank than in the vegetation ($P = 0.013$).

Compositional shifts in the vegetation of the Mediterranean and semi-arid sites and the seed bank of the Mediterranean site were related to an increase in the relative abundance of large-seeded species (Fig. S10, Tables S2, S3). Importantly, we found that the rates of these directional changes (the slopes in Fig. 3) were lower in the seed bank compared with the vegetation ($P = 0.012$ and $P < 0.001$ for the Mediterranean and semi-arid sites) thereby supporting the hypothesis that the seed bank is more resistant to directional changes than the vegetation (in the arid site there were no directional changes). The difference in the slopes was highest in the semi-arid site (about 3.5 times steeper) leading to divergence in composition between the seed bank and vegetation with time (Fig. S11).

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 persistent-seeded species are overly represented in the seed bank.

Differential composition in the seed bank and the vegetation

In this study, we focused on three traits: seed mass, seed persistence, and functional group membership. These traits partially explained variability in species' seed bank affinity ($R^2 = 0.33$, $R^2 = 0.17$, $R^2 = 0.54$, for the Mediterranean, semi-arid and arid sites, respectively) but additional traits could have increased the explanatory power.

As we hypothesized, species' seed persistence increased their seed bank affinity (Fig. 2) because in persistent-seeded species individuals spend most of their life as seeds and only one growing season as

plants. Our persistence index was based on persistence in net-house conditions with constant irrigation during the growing season which depleted the seed bank after three consecutive growing seasons (see Methods). In natural conditions, however, persistence 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. Therefore, we speculate that the real effect of seed persistence on seed bank affinity is even stronger than implied by our analyses.

The negative effect of seed mass on seed bank affinity (Fig. 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; Lebrija-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 reduces their abundance in the vegetation. Furthermore, seed size is frequently correlated with environmental factors controlling germination, particularly light conditions (Thompson 1987; Kigel 1995).

In our main analyses, we focused on the total seed bank which includes both the less dormant seed bank (transient seed bank germinating during the first year after collection) and the more persistent seed bank (seeds germinating during the second and third years). Comparison of the separate analyses of the transient and total seed banks (all years pooled, Fig. 1; see Appendix S1 for details) showed similar patterns of germination (Fig. S4) because the proportion of seeds germinating during the first year was much higher than in the following two years.

Overall, germination patterns in the total seed bank, the transient seed bank, and the persistent seed bank were qualitatively similar. In all cases, the composition of the seed bank was different than that of the standing vegetation (Fig. S4–S6). Moreover, our conclusion that the seed bank undergoes similar year-to-year variability as the vegetation but slower rates of long-term shifts is valid for the total seed bank, the transient seed bank, and the persistent seed bank (Fig. S12–S14).

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 (Fig. S15).

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 methods), 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 persistence 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 fluctuations in environmental conditions. 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).

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 (Fig. 3). Directional changes in composition in both sites (Fig. 1, 3) are probably related to removal

of livestock grazing during the establishment of the research sites (Osem *et al.* 2004; Golodets *et al.* 2010; 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. As expected by theory (Pianka 1970; DeMalach & Kadmon 2018) small-seeded species were replaced by large-seeded species when grazing was removed (Fig. S10).

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 sensitivity of Californian grasslands to prolonged drought was attributed to a depleted seed bank (Harrison *et al.* 2020). Conversely, the high stability of Middle-Eastern annual communities to grazing and rainfall changes was attributed to the high resistance of their seed bank (Sternberg *et al.* 2003; Tielborger *et al.* 2014). Our results provide empirical support for the above assertion. We have demonstrated that in these Middle-Eastern communities, the seed bank is more resistant than the vegetation to long-term changes. 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 many plant communities. The crucial stabilizing role of soil seed banks against climatic variability and increasing resistance should be further considered in climate change studies.

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454

455 **Competing interests**

456 We have no competing interests

457

FIGURE CAPTIONS

Figure 1: Community composition in the seed bank (red circles) and vegetation (green triangles) in the three sites represented using non-metric multidimensional scaling (NMDS) based on the Bray–Curtis index. Numbers represent years of sampling (1 – 2001, 2 – 2002, ..., 10 – 2010). The pink and cyan polygons represent the minimal compositional space occupied by the seed bank and the vegetation. The red and the green arrows represent the temporal trajectories of the community composition of the seed bank and the vegetation. (a) Mediterranean site, stress = 0.15. (b) Semi-arid site, stress = 0.08 (c) Arid site, stress = 0.13.

Figure 2. The effects of seed mass, seed persistence index, and functional group membership (coded zero for forbs and one for grasses) on species' seed bank affinity (relative abundance in the seed bank compared with that in the vegetation) in the three sites. Effect size (points) represents standardized regression coefficients (see Table S1 for a detailed summary). Error bars represent confidence intervals. The dashed line represents zero effect. $N_{\text{(Mediterranean)}} = 40$, $N_{\text{(Semi-arid)}} = 40$, $N_{\text{(Arid)}} = 14$.

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. (e, f) Arid site. The x-axis has a logarithmic scale.

478 **Fig. 1**

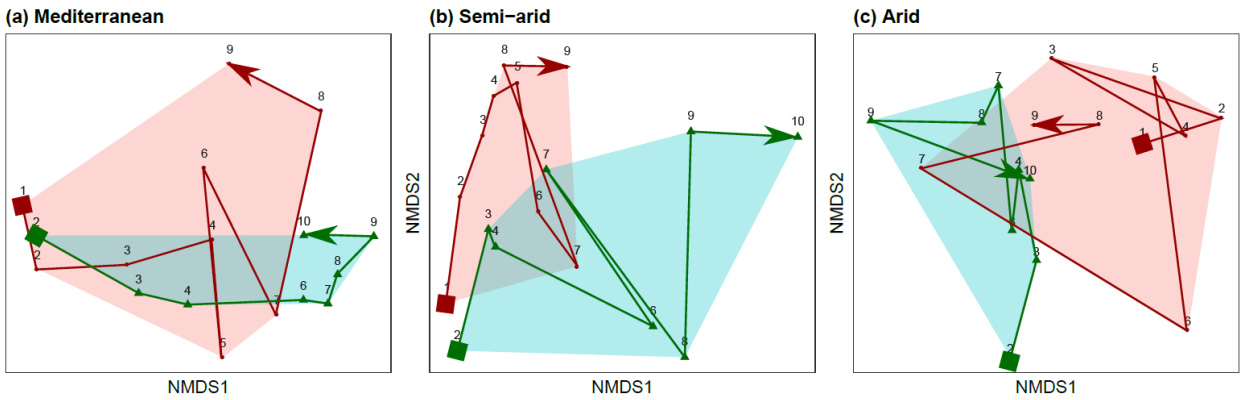


Fig. 2

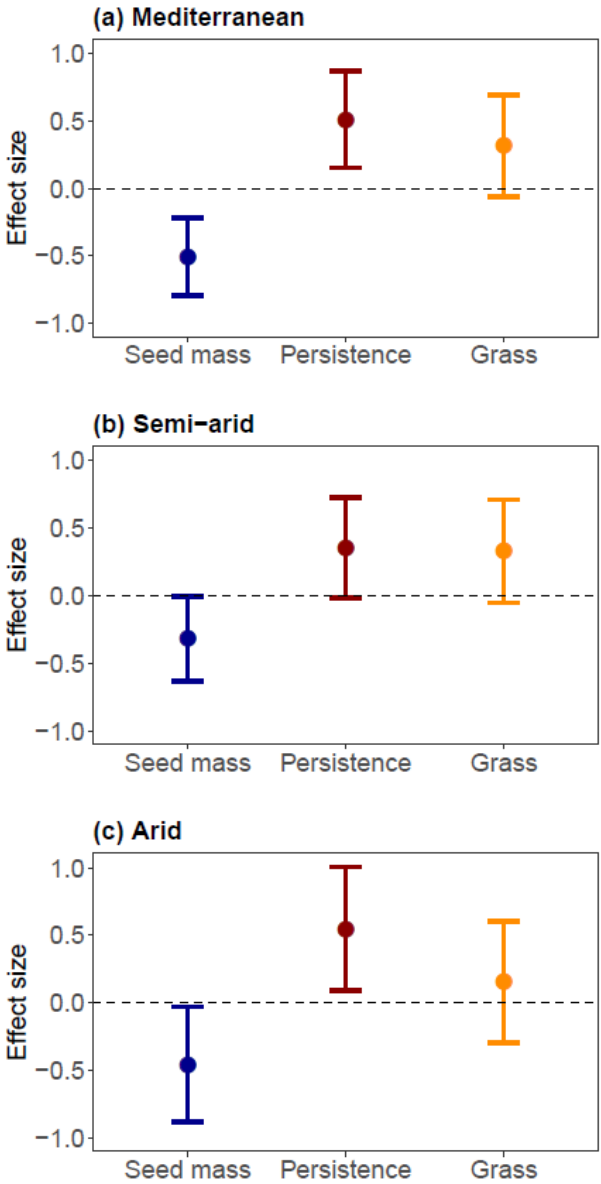
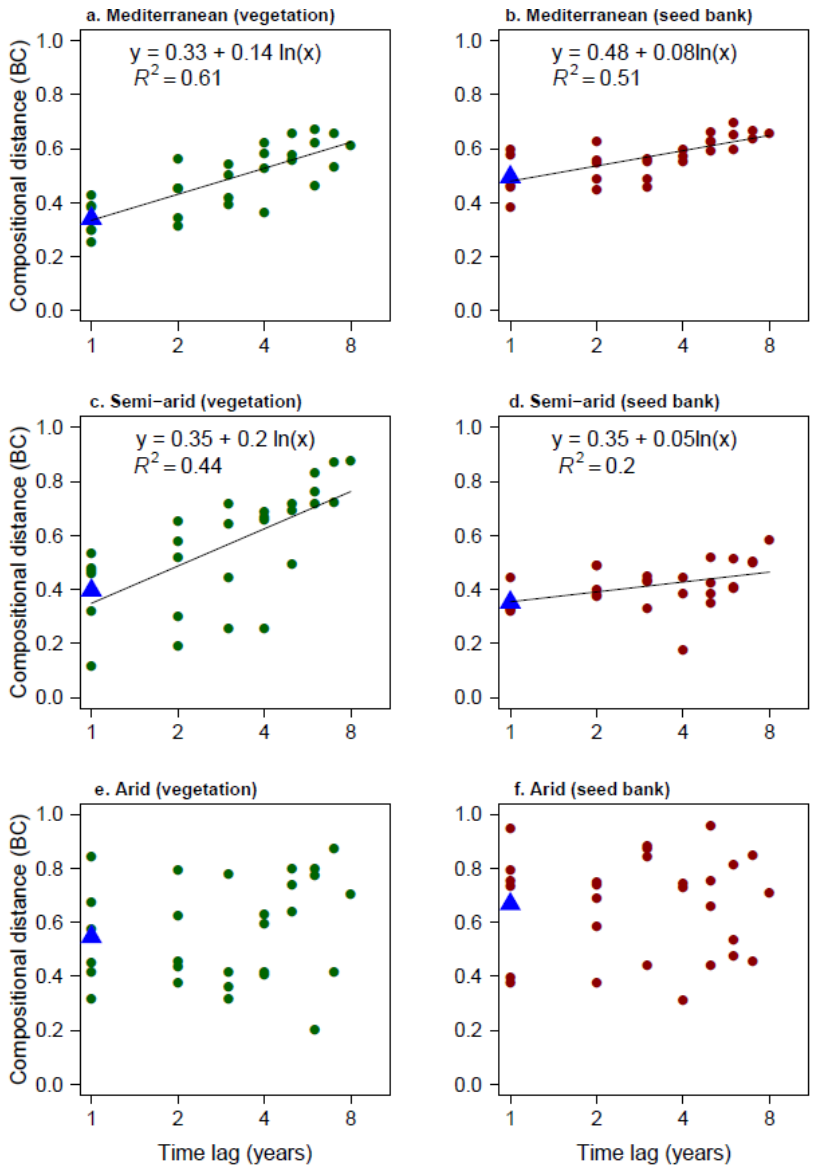


Fig. 3



SUPPORTING INFORMATION

Appendix S1

In the main analyses, seed bank was defined as the total number of seedlings emerging from soil cores, i.e., pooling together the three consecutive years of germination. Additionally, we applied a complementary approach where separate analyses were conducted for each of the three years of germination. Results from the first year largely represent the contribution of species with transient seed banks which germinated during the year of seed dispersal and soil sampling, while the second and third year represent species with more persistent seed banks.

In the arid site, the seed bank composition during the second and third year of germination included a single species – *Filago desertorum*, which emerged in the second germination year of 2001, 2002, 2004 and 2009 sampling years, and the third germination year of 2003 sampling. No seedlings emerged during the third germination year of 2004 and 2006 sampling years. We chose not to exclude years with a single species (these years have identical locations in an NMDS plot and zero distance in time-lag analysis), but years without emerged species were excluded (compositional distance could not be computed).

Overall, the results of these separate analyses were qualitatively similar to the main analysis (Fig S4–S6, S12–S14). Regardless of the type of seed bank analyzed, year-to-year variability of the vegetation was higher compared to the seed bank, and the slope of the time-lag analyses was steeper in the vegetation compared with the seed bank.

508 **Table S1: Results of linear models of species' seed bank affinity as a function of their seed mass**
509 **(log_n transformed [mg]), seed persistence index, and functional group membership (0 – forbs, 1 –**
510 **grasses).** Standardized estimates for the regression coefficients are calculated by standardizing both the
511 explanatory and the dependent variables to enable comparison among variables varying in units (see
512 methods)
513
514

	Mediterranean				Semi-arid				Arid			
	(raw)	Std.	Std.		(raw)	Std.	Std.		(raw)	Std.	Std.	
	estimate	estimate	error	p	estimate	estimate	error	p	estimate	estimate	error	p
(intercept)	0.16	0.00	0.13	0.212	0.15	0.00	0.20	0.463	0.20	0.00	0.14	0.184
Seed mass	-0.06	-0.51	0.02	0.001	-0.06	-0.32	0.03	0.053	-0.08	-0.45	0.04	0.063
Persistence	0.69	0.51	0.25	0.008	0.71	0.35	0.38	0.068	0.74	0.55	0.31	0.040
Grass	0.14	0.32	0.09	0.107	0.22	0.33	0.13	0.102	0.10	0.16	0.15	0.512
N	40				40				14			
R ²	0.33				0.17				0.54			

515

516 **Table S2: Results of linear models of species' succession affinity in the vegetation as a function of**
517 **their seed mass (ln transformed [mg]), seed persistence index, and functional group membership (0**
518 **– forbs, 1 – grasses).** Standardized estimates for the regression coefficients are calculated by
519 standardizing both the explanatory and the dependent variables to enable comparison among variables
520 varying in units (see methods)
521

	Mediterranean				Semi-arid				Arid			
	(raw)	Std.	Std.		(raw)	Std.	Std.		(raw)	Std.	Std.	
	estimate	estimate	error	p	estimate	estimate	error	p	estimate	estimate	error	p
(intercept)	0.30	0.00	0.07	<0.001	0.63	0.00	0.11	<0.001	0.55	0.00	0.15	0.002
Seed mass	0.04	0.47	0.01	0.002	0.04	0.35	0.02	0.033	0.01	0.07	0.04	0.789
Persistence	0.21	0.23	0.14	0.153	-0.03	-0.02	0.22	0.908	0.02	0.02	0.32	0.950
Grass	0.13	0.38	0.06	0.028	-0.07	-0.18	0.08	0.368	-0.01	-0.01	0.17	0.961
N	40				40				22			
R ²	0.45				0.13				0.00			

522

523

Table S3: Results of linear models of species' succession affinity in the seed bank as a function of their seed mass (\log_n transformed [mg]), seed persistence index, and functional group membership (0 – forbs, 1- grasses). Standardized estimates for the regression coefficients are calculated by standardizing both the explanatory and the dependent variables to enable comparison among variables varying in units (see methods)

	Mediterranean				Semi-arid				Arid			
	(raw)	Std.	Std.		(raw)	Std.	Std.		(raw)	Std.	Std.	
	estimate	estimate	error	p	estimate	estimate	error	p	estimate	estimate	error	p
(intercept)	0.25	0.00	0.12	0.034	0.50	0.00	0.15	0.002	0.53	0.00	0.10	<0.001
Seed mass	0.05	0.40	0.02	0.014	0.01	0.09	0.02	0.625	0.01	0.08	0.03	0.676
Persistence	0.42	0.32	0.23	0.068	0.01	0.01	0.29	0.96	-0.24	-0.20	0.21	0.277
Grass	0.11	0.26	0.08	0.164	-0.02	-0.04	0.11	0.859	0.10	0.14	0.13	0.459
N	40				40				33			
R ²	0.28				0.01				0.08			

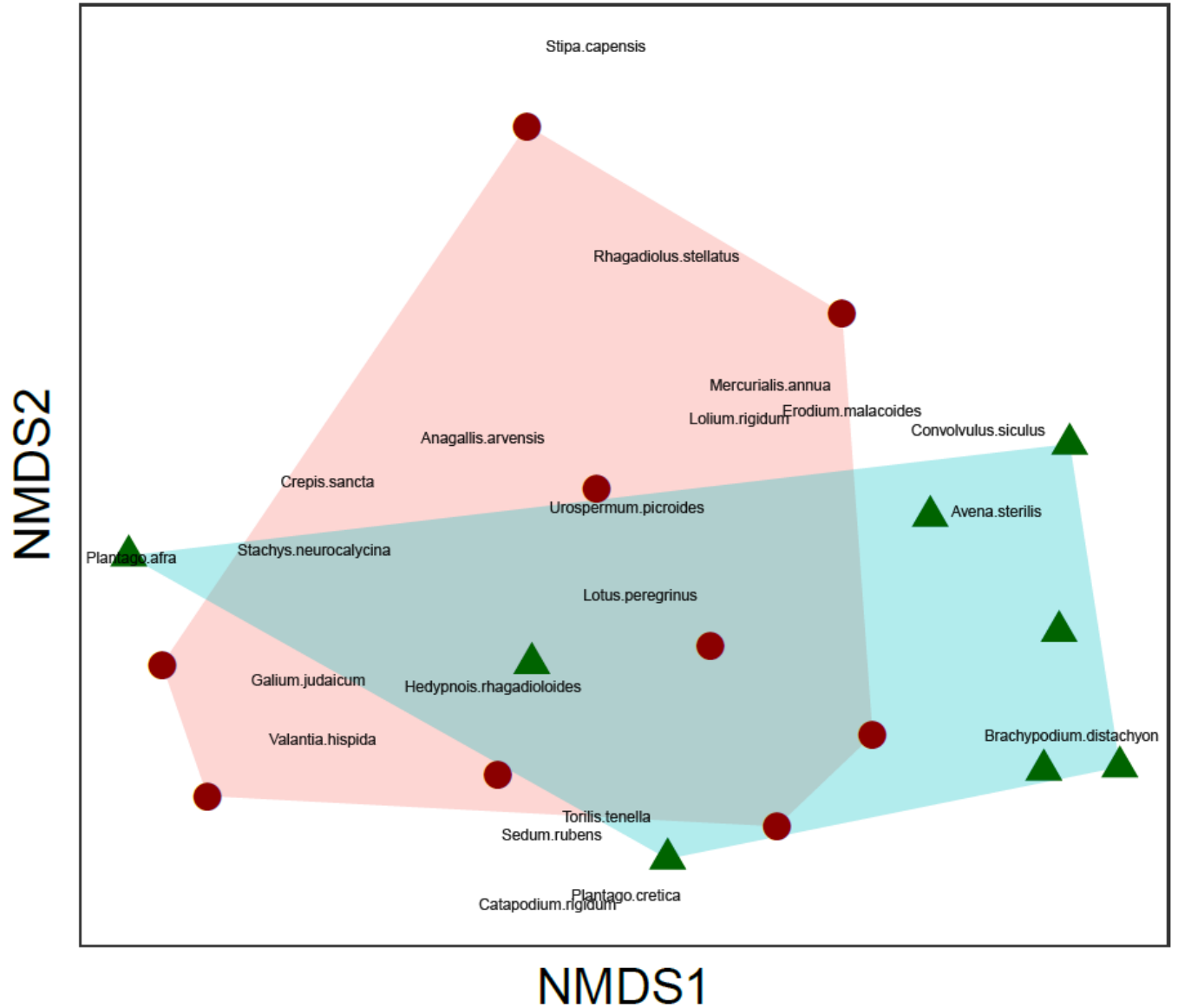


Fig. S1: Community composition in the seed bank (brown circles) and vegetation (green circles) in the Mediterranean site represented using non-metric multidimensional scaling (NMDS) of the 30 most dominant species (instead of all species as in the main text) based on Bray–Curtis dissimilarity. The pink and cyan polygons represent the minimal compositional space occupied by the seed bank and the vegetation. Stress = 0.11.

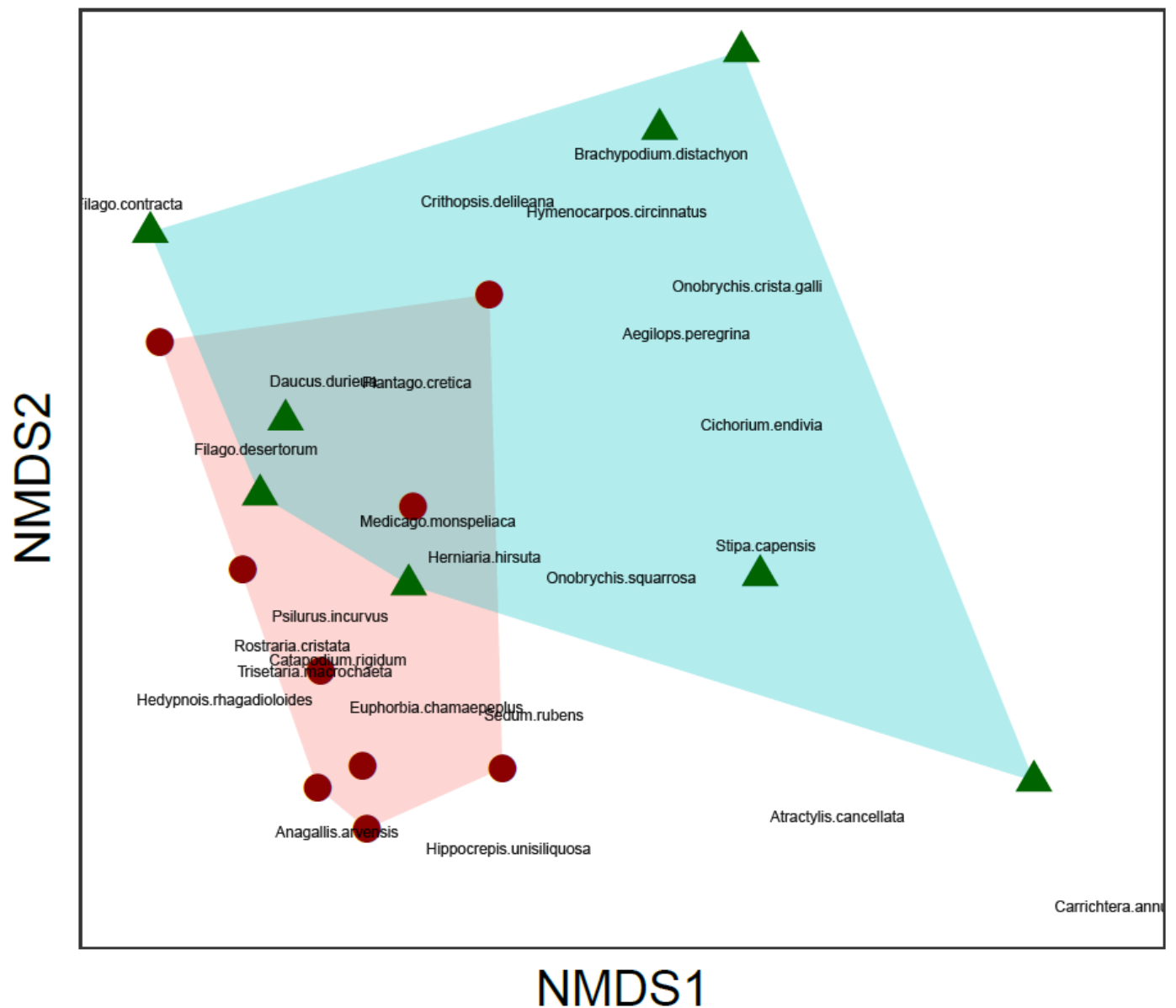


Fig. S2: Community composition in the seed bank (brown circles) and vegetation (green circles) in the Semi-arid site represented using non-metric multidimensional scaling (NMDS) of the 30 most dominant species (instead of all species as in the main text) based on Bray–Curtis dissimilarity. The pink and cyan polygons represent the minimal compositional space occupied by the seed bank and the vegetation. Stress = 0.06

(c) Arid

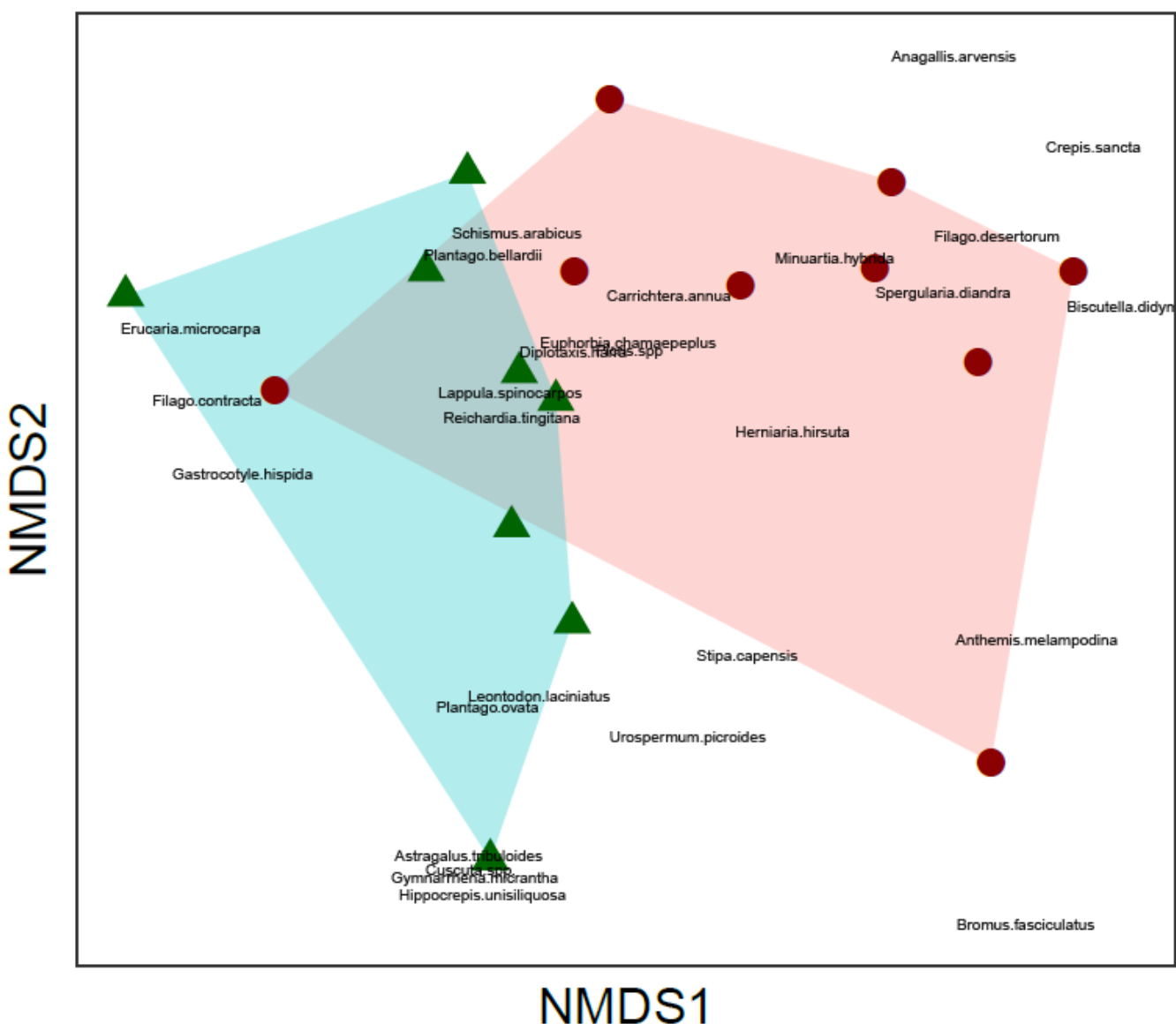


Fig. S3: Community composition in the seed bank (brown circles) and vegetation (green circles) in the Arid site represented using non-metric multidimensional scaling (NMDS) of the 30 most dominant species (instead of all species as in the main text) based on Bray–Curtis dissimilarity. Names of all species used in the analysis are shown. The pink and cyan polygons represent the minimal compositional space occupied by the seed bank and the vegetation. Stress = 0.13

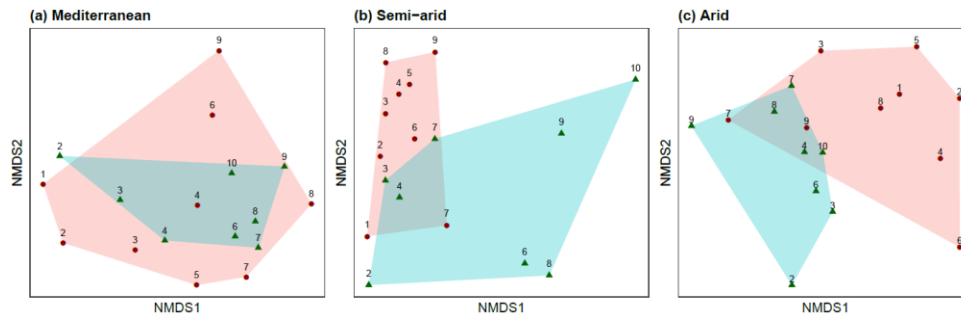


Fig. S4: Community composition in the seed bank from *the first germination season* (brown circles) and vegetation (green circles) in the three sites represented using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity. (a) Mediterranean site, stress=0.15, $P(\text{PERMANOVA}) = 0.006$. (b) Semi-arid site, stress=0.09, $P(\text{PERMANOVA}) < 0.001$ (c) Arid site, stress=0.12, $P(\text{PERMANOVA}) < 0.01$

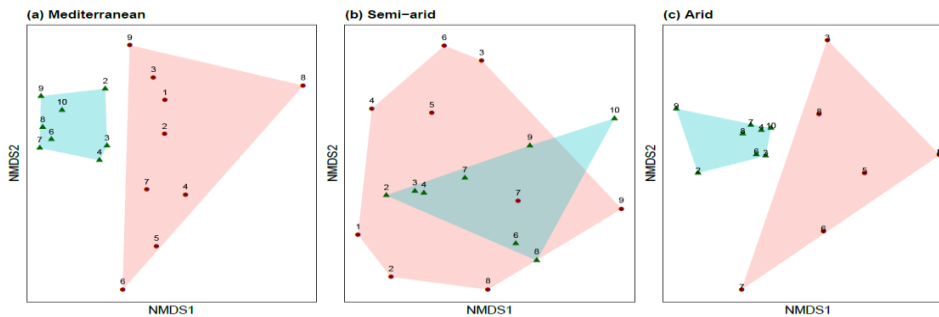


Fig. S5: Community composition in the seed bank from *the second germination season* (brown circles) and vegetation (green circles) in the three sites represented using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity. (a) Mediterranean site, stress=0.14, $P(\text{PERMANOVA}) = 0.01$. (b) Semi-arid site, stress=0.15, $P(\text{PERMANOVA}) < 0.001$ (c) Arid site, stress=0.09, $P(\text{PERMANOVA}) < 0.001$

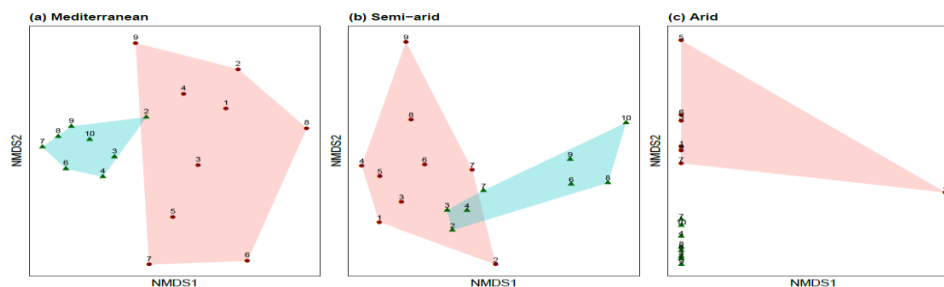


Fig. S6: Community composition in the seed bank from *the third germination season* (brown circles) and vegetation (green circles) in the three sites represented using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity. (a) Mediterranean site, stress=0.15, $P(\text{PERMANOVA}) = 0.001$. (b) Semi-arid site, stress=0.13, $P(\text{PERMANOVA}) < 0.001$ (c) Arid site, stress= 10^{-5} (stress close to zero implies unreliable estimation probably because there was almost no overlap between the seed bank and the vegetation), $P(\text{PERMANOVA}) < 0.001$

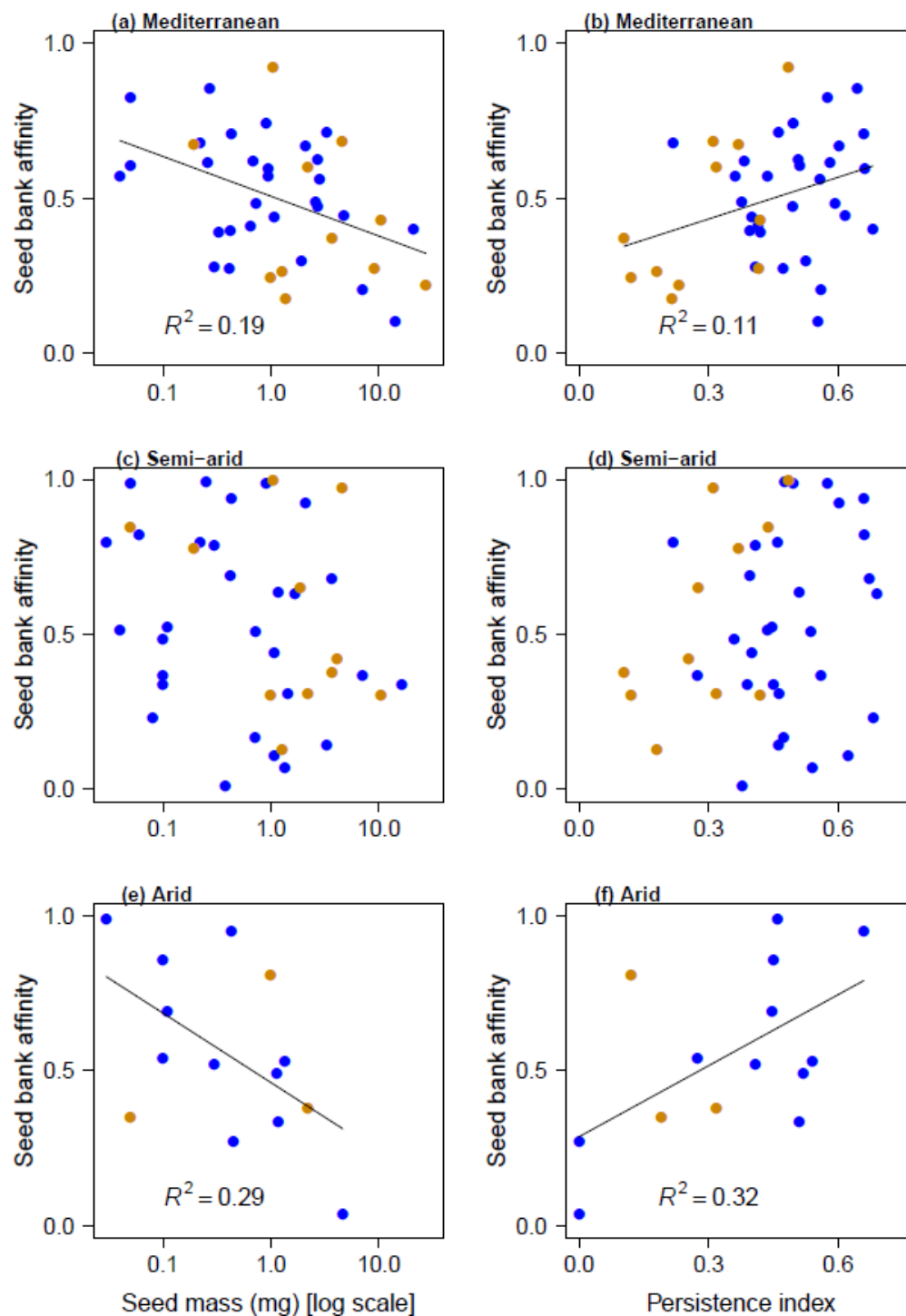


Fig. S7. Relationships between seed mass (left panels), seed persistence (right panels), and seed bank affinity. Orange points represent grass species while blue circles represent forb species. (a,b) Mediterranean site (c,d) Semi-arid site (e,f) Arid site. A trend line appears is shown when there is a statistically significant trend ($P < 0.05$). Only species that appear in both seed bank and the vegetation are shown. The x-axes in the left panels are in logarithmic scale.

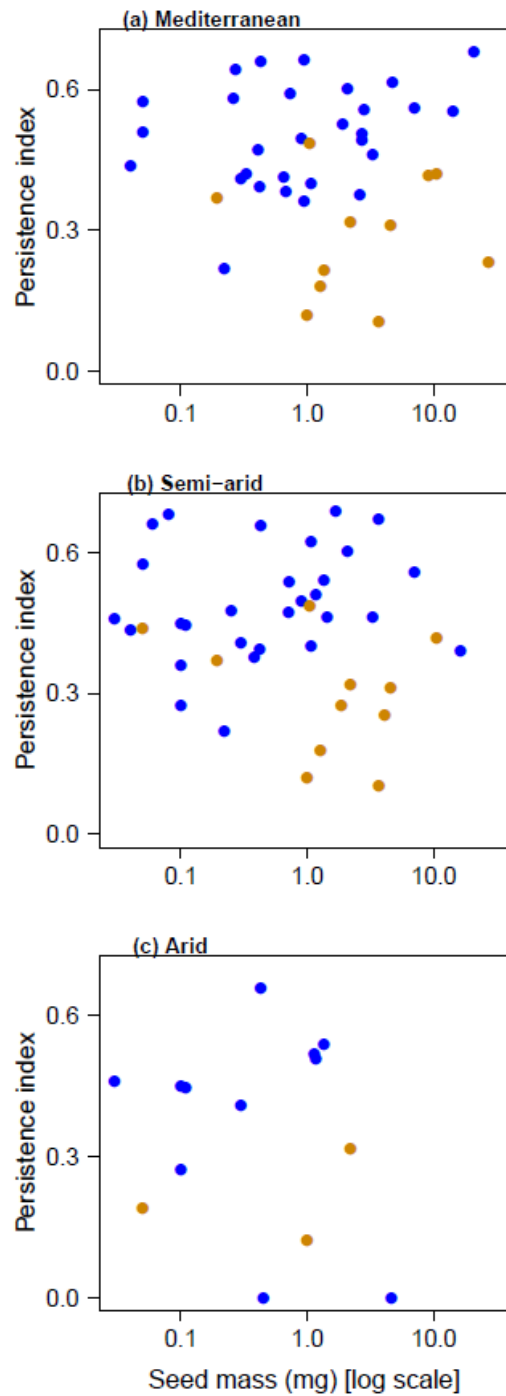


Fig. S8. Relationships between seed mass (left panels) and seed persistence (right panels). Orange points represent grass species while blue circles represent forb species. (a) Mediterranean site (b) Semi-arid site (c) Arid site. The relationships were not significant for any of the sites. The x-axes in the left panels are in logarithmic scale.

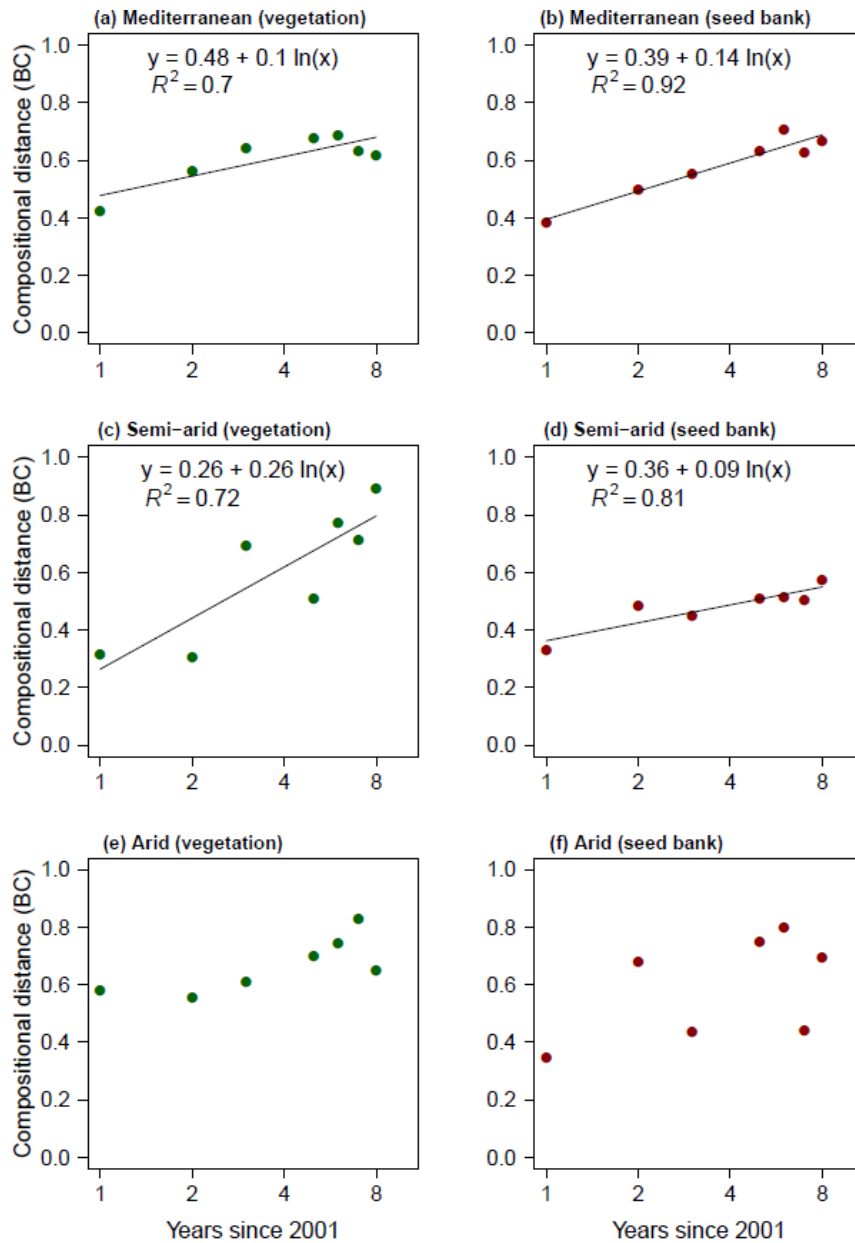
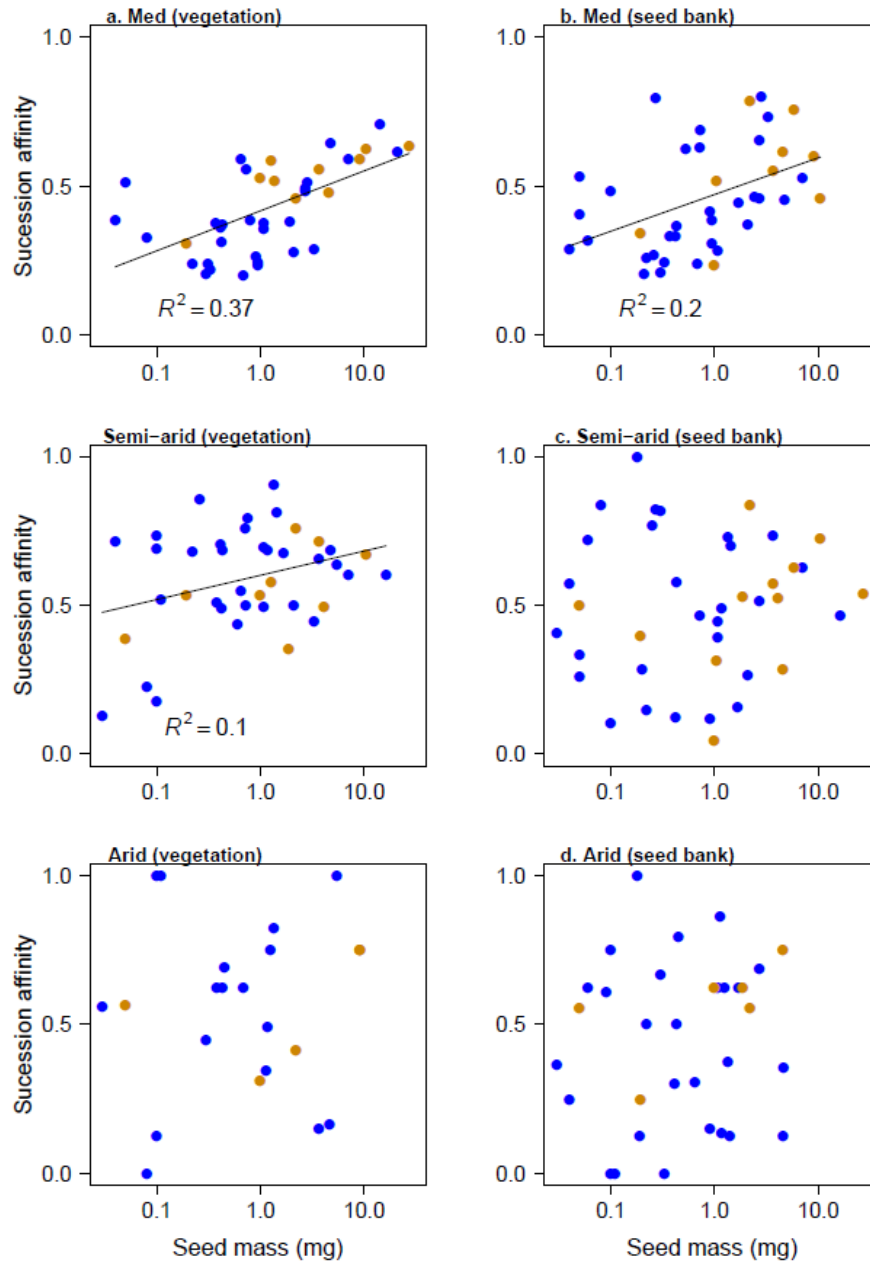


Fig S9: The relationship between the temporal distance from the first growing season (2001/2002) and the compositional distance (Bray–Curtis index) for the years 2002/2003–2009/2010. Note the log scale of the x-axis. A trend line appears when there is a significant linear trend ($P < 0.05$).



594

595 **Fig. S10.** Relationship between seed mass and succession affinity (species' tendency to occur during the
 596 later years of the study) in the vegetation and the seed bank. Orange points represent grass species while
 597 blue circles represent forb species. (a,b) Mediterranean site (b,c) Semi-arid site (e,f) Arid site. A trend line
 598 appears when there is a significant linear trend ($P < 0.05$). The x-axis is in logarithmic scale. $N_{\text{(Mediterranean vegetation)}} = 40$, $N_{\text{(Mediterranean seed bank)}} = 40$, $N_{\text{(Semi-arid vegetation)}} = 40$, $N_{\text{(Semi-arid seed bank)}} = 40$, $N_{\text{(arid vegetation)}} = 22$, $N_{\text{(arid seed bank)}} = 33$.
 600

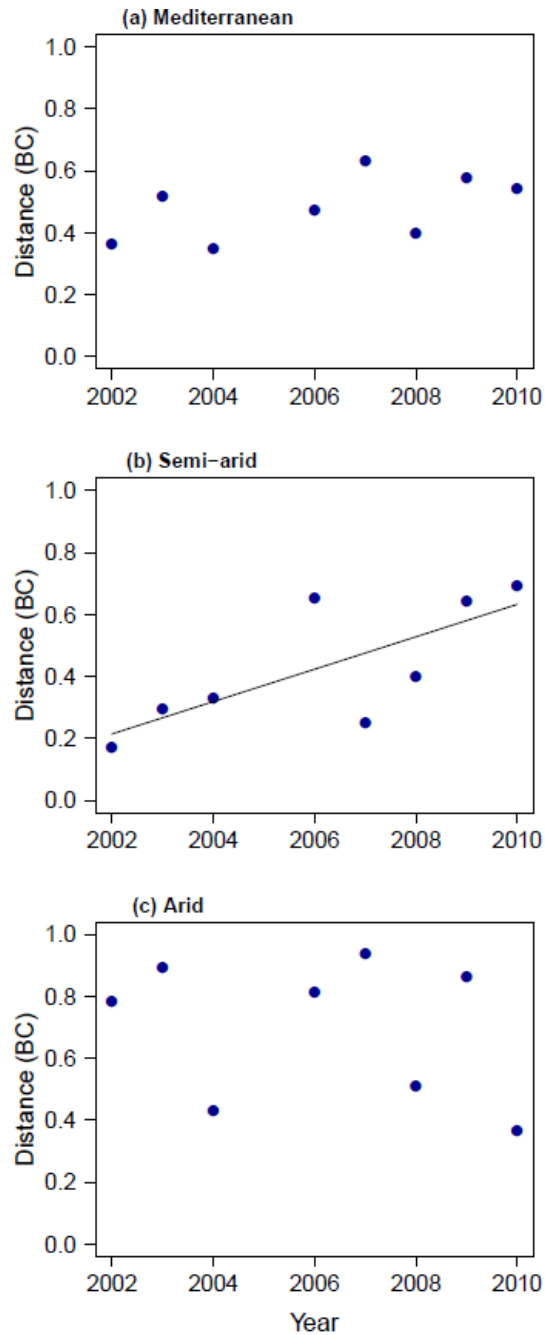


Fig. S11. Temporal dynamics of Bray–Curtis distance between the seed bank and the vegetation in the three sites. Each point represents the distance between the vegetation collected during March\April and the seed bank that was collected before the vegetation during September of the previous calendar year. A trend line appears when there is a significant linear trend ($P < 0.05$).

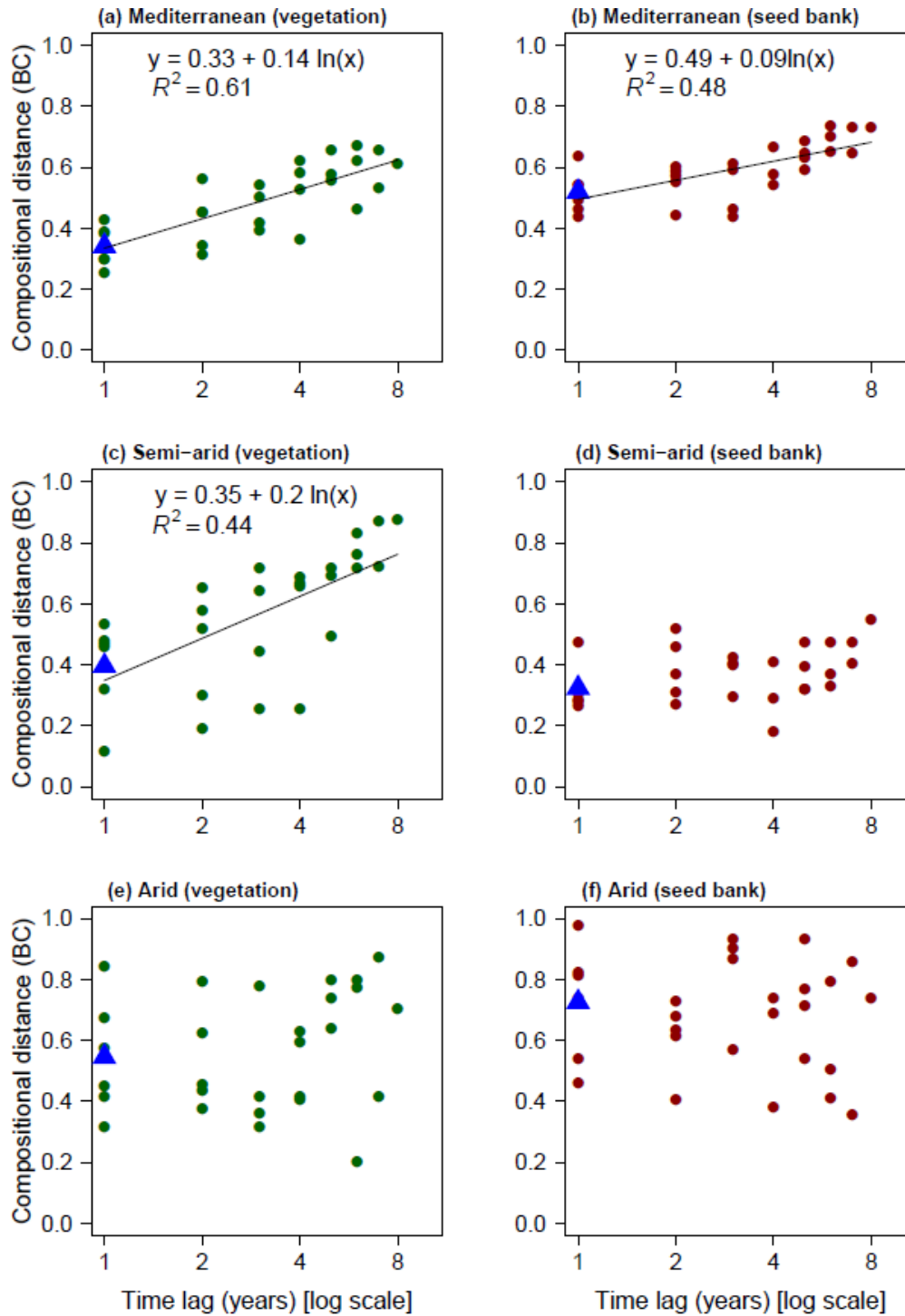


Fig. S12: Compositional distance (Bray–Curtis index) in the vegetation (left panels) and seed bank from *the first germination season* (right panels) as a function of time lag (temporal distance between years of sampling including all possible pairs). The blue triangle represents the mean compositional 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, $P(\text{year-to-year variability}) < 0.001$, $P(\text{slope}) < 0.05$. (c,d) Semi-arid site, $P(\text{year-to-year variability}) > 0.05$, $P(\text{slope}) < 0.001$. (e,f) Arid site, $P(\text{year-to-year variability}) > 0.05$, $P(\text{slope}) > 0.05$. The x-axis is in logarithmic scale.

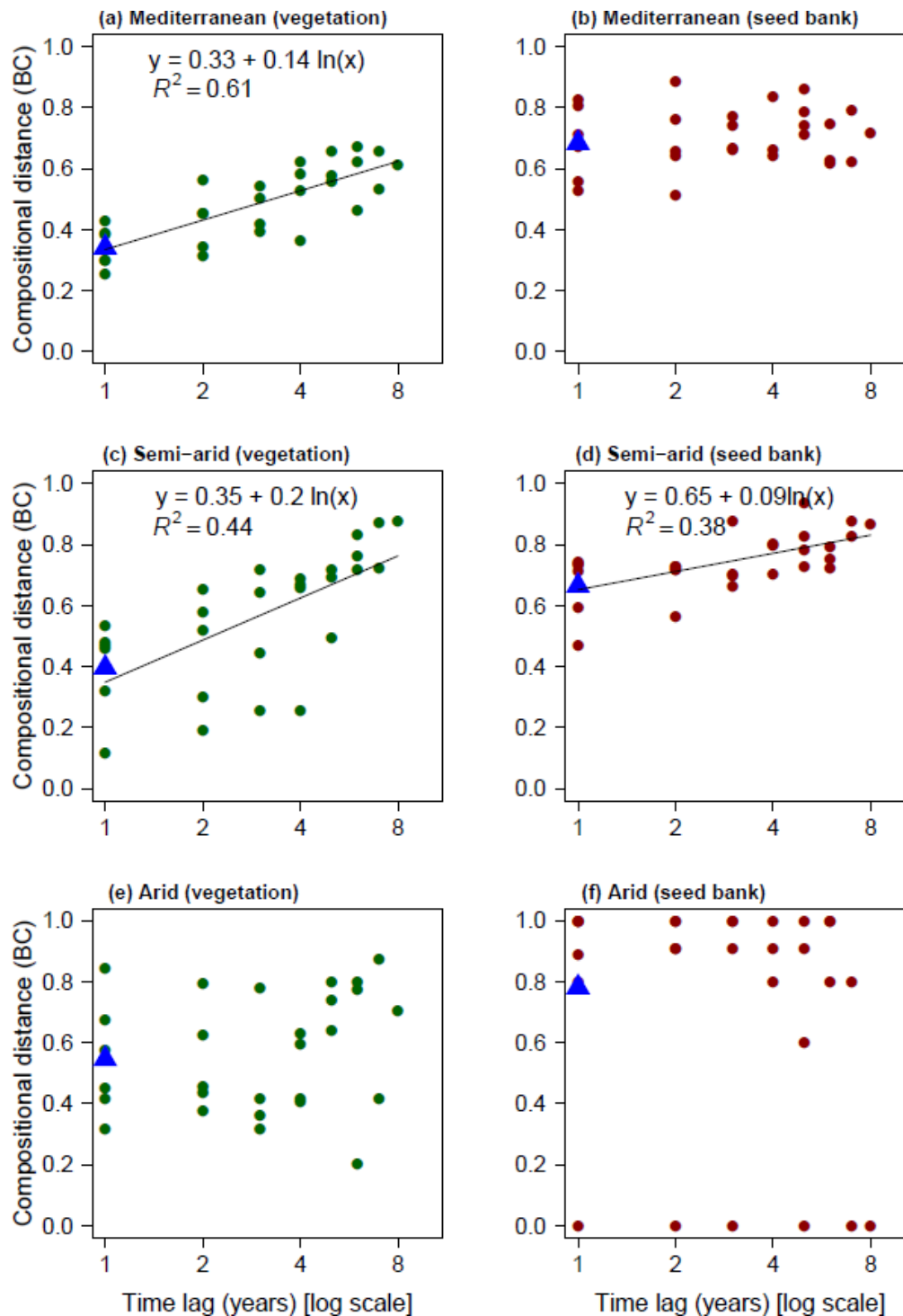


Fig. S13: Compositional distance (Bray–Curtis index) in the vegetation (left panels) and seed bank from *the second germination season* (right panels) as a function of time lag (temporal distance between years of sampling including all possible pairs). The blue triangle represents the mean compositional 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, $P(\text{year-to-year variability}) < 0.05$, $P(\text{slope}) = 0.01$. (c,d) Semi-arid site, $P(\text{year-to-year variability}) > 0.05$, $P(\text{slope}) < 0.001$. (e,f) Arid site, $P(\text{year-to-year variability}) > 0.05$, $P(\text{slope}) > 0.05$. The x-axis is in logarithmic scale.

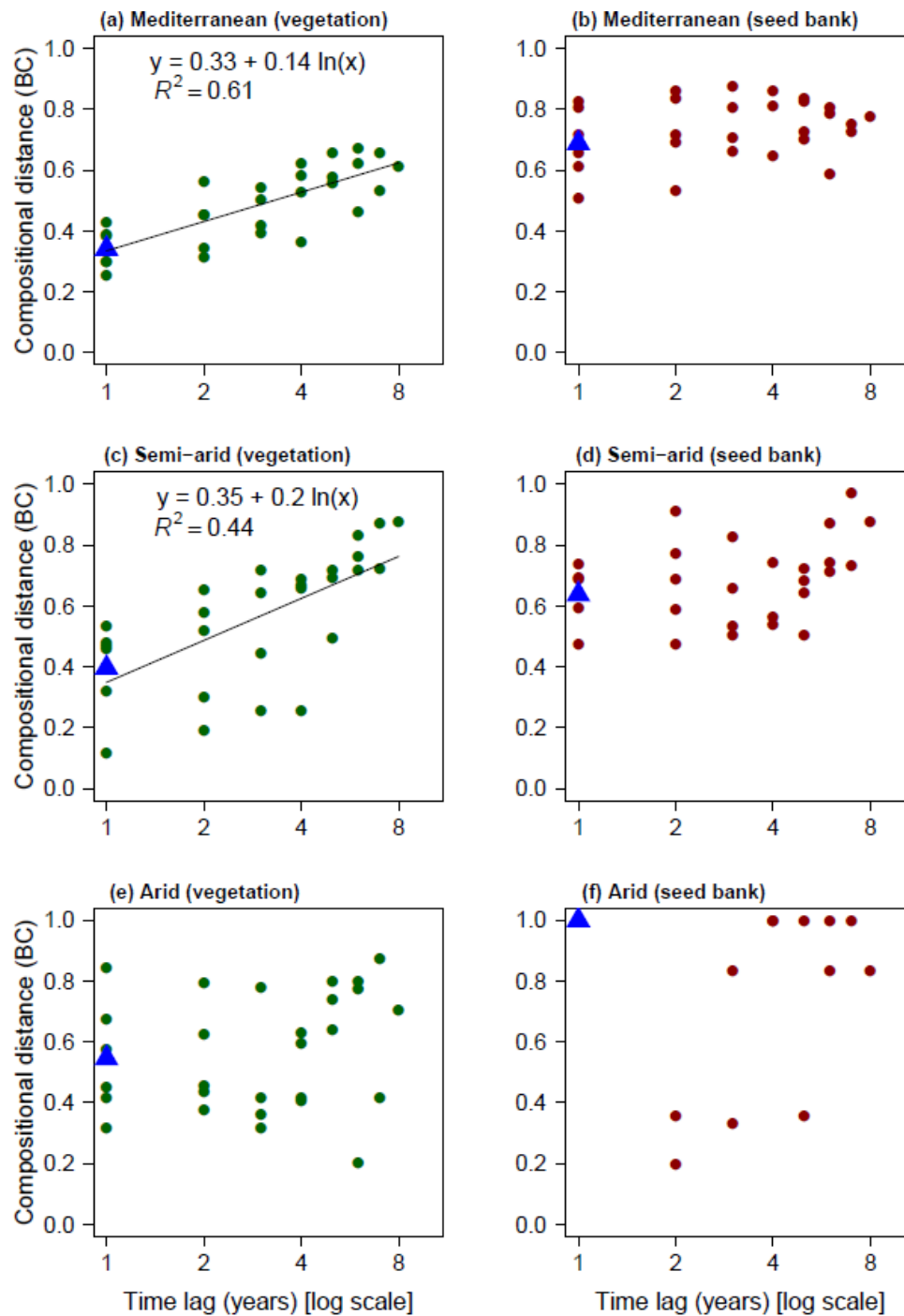


Fig. S14: Compositional distance (Bray–Curtis index) in the vegetation (left panels) and seed bank from the third germination season (right panels) as a function of time lag (temporal distance between years of sampling including all possible pairs). The blue triangle represents the mean compositional 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, $P(\text{year-to-year variability}) < 0.005$, $P(\text{slope}) < 0.001$. (c,d) Semi-arid site, $P(\text{year-to-year variability}) < 0.05$, $P(\text{slope}) < 0.005$. (e,f) Arid site, $P(\text{year-to-year variability}) < 0.05$, $P(\text{slope}) > 0.05$. The x-axis is in logarithmic scale.

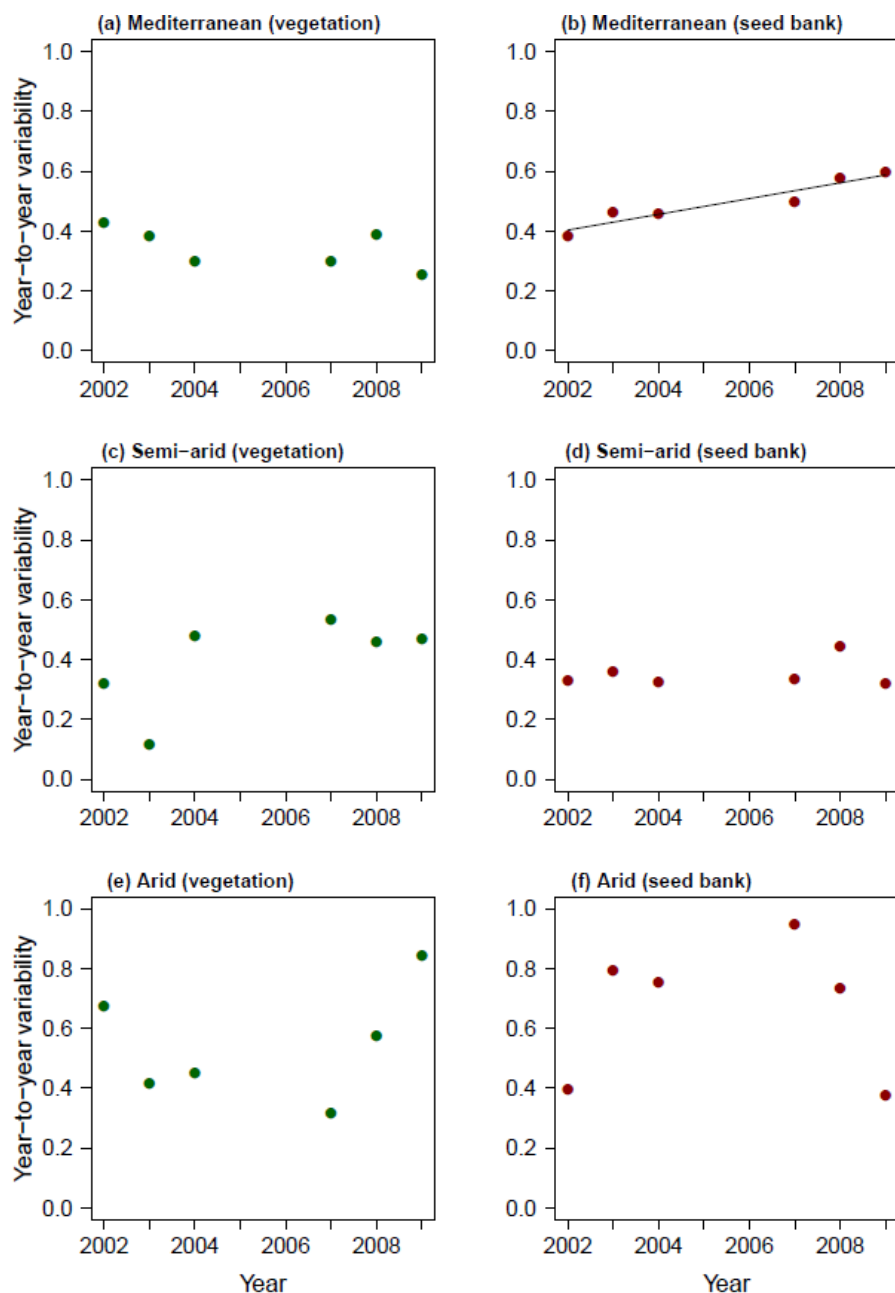


Fig. S15. Relationships between the year of sampling and year-to-year variability. Year-to year variability is the Bray–Curtis distance between each year compared with the previous year (e.g. ‘2002’ represents the distance between 2002\2003 and 2001\2002 growing seasons). A trend line appears when there is a significant linear trend ($P < 0.05$).