Contrasting responses to aridity by different-sized decomposers cause similar decomposition rates across a precipitation gradient

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Authors' contributions

D.H., N.S. and V.T. conceived this study and designed the experiments. V.T, N.S. and D.H performed the field experiment. N.S. and V.T. performed lab analyses. J.A.D., Y.H. and E.G.R.

sorted and identified animal samples. N.S. analyzed the data. N.S., V.T and D.H wrote the manuscript, and all authors provided critical feedback and approved submission.

Data sharing plans

All data used in the manuscript has been deposited in an open repository and can be found on the following link https://figshare.com/s/96ff438c98ae4a6afbc4

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Abstract

Litter decomposition is expected to be positively associated with precipitation despite evidence that decomposers of varying sizes have different moisture dependencies. We hypothesized that higher tolerance of macro-decomposers to aridity may counterbalance the effect of smaller decomposers, leading to similar decomposition rates across climatic gradients. We tested this hypothesis by placing plant litter baskets of different mesh sizes in seven sites along a sharp precipitation gradient, and by characterizing the macro-decomposer assemblages using pitfall trapping. We found that decomposers responded differently to precipitation levels based on their size. Microbial decomposition increased with precipitation in the winter while macro-decomposition peaked in arid sites during the summer. This led to similar overall decomposition rates across the gradient except in hyper-arid sites. Macro-decomposer richness, abundance and biomass peaked in arid environments. Our findings highlight the importance of macro-decomposition in arid-lands, possibly resolving the dryland decomposition conundrum, and emphasizing the need to contemplate decomposer size when investigating zoogeochemical processes.

Keywords

litter decomposition, climate, detritivores, dryland, zoogeochemistry, dryland decomposition conundrum

Introduction

Litter decomposition is a key process determining elemental cycling in terrestrial ecosystems[1]. Decomposition is controlled by climate, litter quality and origin, and the identity and abundance of microbial and faunal decomposers[2–4]. Climate regulates decomposition rates directly, but also indirectly by influencing food-web structure and dynamics[5]. Thus, understanding how climate and decomposers interact is a key step in explaining variation in plant litter decomposition across ecosystems and seasons, and in forecasting the consequences of climate change and biodiversity loss on elemental cycling.

Theory suggests that decomposition is positively associated with moisture and temperature[4]. Cross-site studies, reviews, and meta-analyses verified this global pattern, showing that plant litter decomposition in microbial litter bags is indeed faster under warm and wet conditions than under cool and dry conditions[6–11]. This well accepted realization implicitly assumes that microorganisms dominate plant litter decomposition, largely ignoring the growing recognition that animals may play an important role in litter cycling. This role includes mineralizing and excreting assimilated plant nutrients, fragmenting and partly decomposing plant material, and transporting detritus to microbial havens[12–19].

Attempts to explore how climate affects faunal decomposition revealed a similar positive association with temperature and precipitation[20,21]. This global pattern, however, may be confounded by compiling the effect of all decomposer fauna together, ignoring the well-established understanding that soil animals of various size groups respond differently to climate[4,22]. Specifically, larger arthropods can survive and remain active during hot and dry periods when smaller organisms cannot[23]. Indeed, handful evidence shows that macro-

detritivorous arthropods dominate litter and wood decomposition in warm drylands, especially during warm and dry seasons[24–26]. This suggests that the conceptualization of how animals and climate interact to regulate decomposition rates requires considering the effects of meso-decomposers and those of macro-decomposers separately, particularly in warm drylands.

Detritivorous animals are expected to be exceptionally abundant in arid ecosystems where plant detritus is prevalent year around but green plant material is available predominantly in short pulses following precipitation events[27]. Macrofauna are physiologically and morphologically more adapted to aridity than mesofauna[23]. Moreover, their large size enables them to remain active during long dry periods by shuttling between existing and self-engineered climatic havens and the hostile foraging grounds on the surface[28]. Consequently, macro-decomposition should be especially important in hot moisture-deprived habitats and periods, whereas the activity of microbes and mesofauna is expected to be minimal.

The predicted negative association between moisture and macro-decomposition in drylands may be reversed in hyper-arid environments. In these environments, the extreme climatic conditions and scarce and unpredictable plant litter availability may limit macro-decomposer populations, diminishing macro-decomposition rates with increasing aridity. Consequently, and in sharp contrast to smaller organisms, macro-decomposition should follow a hump-shaped response to precipitation that peaks in arid ecosystems.

To test this novel hypothesis, we examined the climate dependency of plant litter decomposition by microorganisms, meso-decomposers and macro-decomposers along a sharp aridity gradient spanning from mean annual precipitation of only 22 mm to 526 mm. This gradient represents hyper-arid, arid, semiarid and dry sub-humid Mediterranean climates. We repeated the experiment during hot summer with no precipitation and again during cooler and

wetter winter. We hypothesized that both microbial and mesofaunal decomposition should increase with increasing precipitation during the winter, but during the dry summer contribute only minimally to plant litter decomposition across the aridity gradient. In the dry summer, macrofaunal decomposition should follow a hump-shaped response to precipitation, increasing from hyper-arid to arid sites and decreasing gradually in more mesic semi-arid and Mediterranean sites. We also predicted that the opposing climatic dependencies of macrofauna and microorganisms and mesofauna should lead to similar overall decomposition rates across the precipitation gradient except in the hyper-arid sites in which decomposers activity is predicted to be minimal regardless of organism size (**Fig. 1**). To reveal the mechanism, we sampled macro-decomposers across the aridity gradient and the two seasons, using pitfall traps. We predicted hump-shaped relationships between precipitation and the abundance, richness, and biomass of macro-decomposers that peak in arid ecosystems.

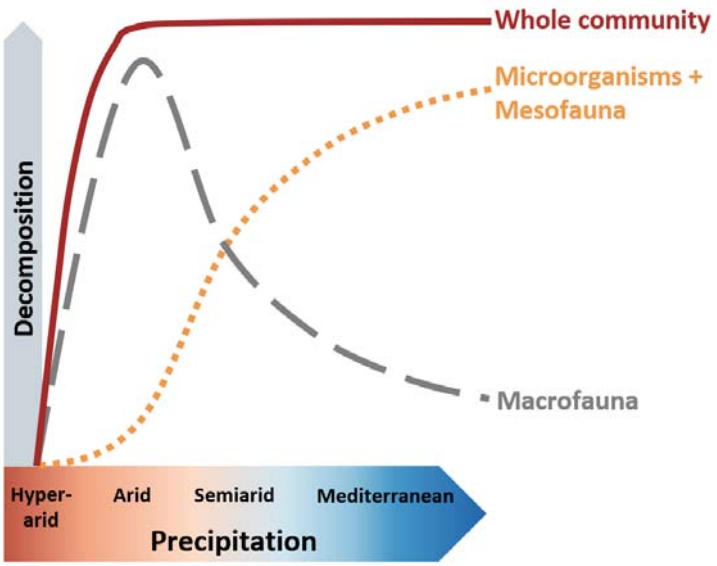

Figure 1 - Hypothetical climate dependence of litter decomposition by microorganisms and mesofauna (dotted orange curve), by macrofauna (grey – dash), and by the whole decomposer community (maroon - solid).

Methods

We performed a manipulative litter mass loss experiment across seven sites representing a sharp mean annual precipitation (MAP) gradient ranging from hyper-arid desert to Mediterranean maquis (Fig. 2A, Table 1). All sites were chosen to be on calcareous soils formed upon sedimentary limestone rock in natural habitats. The mean annual temperature varies only slightly across sites from 18.7ºC to 22.3 ºC. The exact study sites were determined to ensure minimal human disturbance during the year-long experiment. In each of the seven sites we installed litter baskets of three different mesh sizes that control organismal access to litter: Micro-baskets allowing entry of only microorganisms (<200 μm), meso-baskets allowing entry of microorganisms and mesofauna (<2 mm), and macro-baskets that were identical to the meso-baskets but with side openings that allow entry of macrofauna (<2 cm). Litter baskets were filled with leaf litter belonging to the annual grass *Stipa capensis* Thunb. that is native to all seven study sites. This approach allowed us to compare decomposition rates across sites without using exogenous litter that may decompose in a very different rate than local litter[3]. Twenty-five blocks, each including the three basket types (Fig. 2B), were installed in each site for two consecutive experimental periods - a wet cool winter and a dry hot summer (2 periods x 7 sites x 3 treatments x 25 blocks = 1050 baskets in total). We also characterized the macro-decomposer assemblage in each site during the two seasons using pitfall trapping.

Table 1 - Properties of the seven experimental sites

Site	Abb.	Coordinates	MAT* [□]	MAP* [mm]	AI_U* (MAP/PET)	Climate	Winter experiment	Summer experiment
Ramat Hanadiv	RH	32°33’22.4”N 34°56’26.6”E	20.2	526	0.518	Dry subhumid Mediterranean	3.12.2020 – 27.6.2021	27.6 – 27.10.2021
Bet Guvrin	BG	31°35’54.7”N 34°54’14.2”E	20.9	403	0.370	Semiarid	2.12.2020 – 13.6.2021	13.6 – 21.10.2021
Havat Shikmim	HS	31°30'49.7”N 34°41'18.8”E	19.8	367	0.364	Semiarid	2.12.2020 – 13.6.2021	13.6 – 21.10.2021
Sayeret Shaked	SS	31°16’05.7”N 34°39’12.9”E	20.0	148	0.145	Arid	26.11.2020 – 23.5.2021	23.5 – 21.10.2021
Avdat	AV	30°47’02.3”N 34°46’13.3”E	18.7	84	0.089	Arid	26.11.2020 – 23.5.2021	23.5 – 21.10.2021
Meishar	MS	30°27’04.2”N 34°56’03.0”E	20.8	33	0.029	Hyperarid	10.12.2020 – 12.7.2021	12.7 – 8.11.2021
Nahal Shita	NS	30°08'29.4"N 35°07'36.6"E	22.3	22	0.017	Hyperarid	10.12.2020 – 12.7.2021	12.7 – 8.11.2021

* Climatic data extracted from http://www.meteo-tech.co.il/hanadiv_new/hanadiv_en.asp (RH), courtesy of Shaily Dor-Haim (SS), and extracted from https://ims.gov.il/en (all other sites).

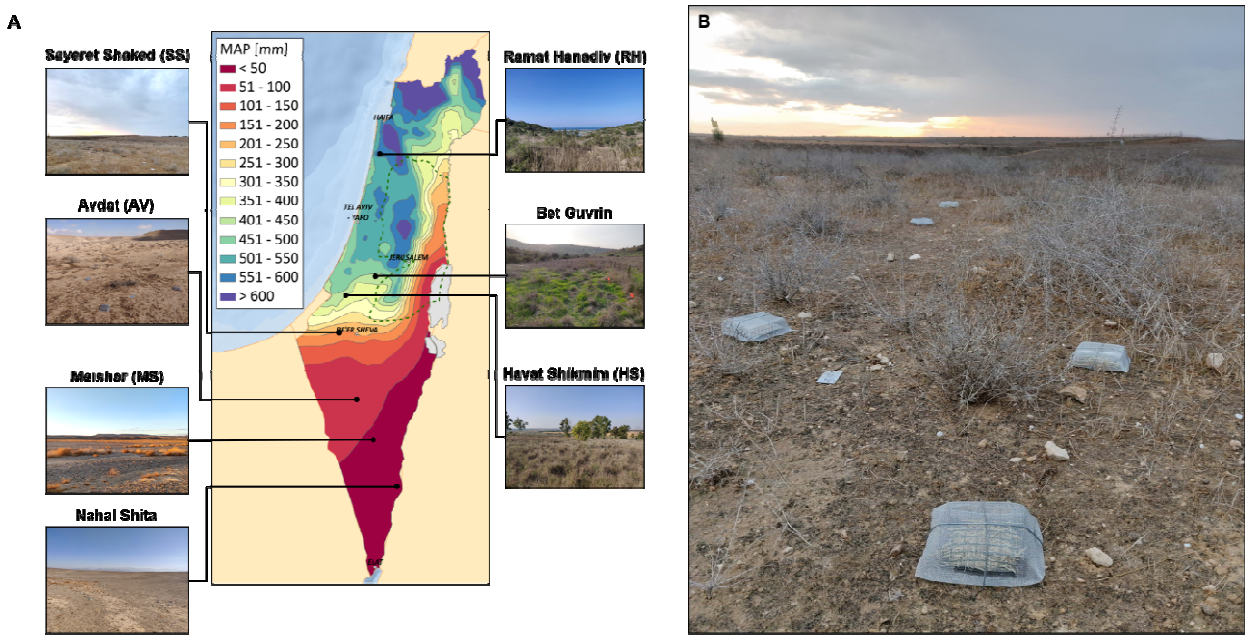

Figure 2 - (A) Locations and landscapes of the seven experimental sites across a precipitation gradient from 22 to 526 mm mean annual precipitation (MAP). (B) A block of three litter baskets in the Sayeret Shaked site. Macro-basket in front, meso-basket on the right and micro-basket on the left. The precipitation map courtesy of the Hebrew University GIS center.

Litter basket experiment

We collected *S. capensis* litter from the Avdat site in the summer of 2020 and air dried it. We sorted the litter to remove litter belonging to any other species and assigned 3 ± 0.0001 g (Mettler Toledo MS105DU) to each litter basket. Thirty additional litter samples were oven dried at 60 ºC for 48 hours and weighed again for determination of initial moisture content. The 14 x 13 x 3.6 cm litter baskets were prepared of a 12 mm mesh galvanized welded metal, lined at the bottom with a 1.5 mm fiberglass mesh to prevent litter loss, and covered from all sides (including top and bottom) with a 2 mm metal mesh to exclude termites. In the macro-baskets, three 2 x 2 cm windows were cut at each of the four sides. The windows were cut approximately 1 cm above ground level to allow macrofaunal access but prevent accidental litter spill. This may slightly reduce macrofaunal access, making our estimations of the macrofaunal effect conservative. In the micro-baskets, we placed the litter within a polyethylene 200 μm mesh bag. In the macro- and meso-baskets, we laid a 2 cm heavy metal mesh over the litter to minimize litter loss due to wind.

We installed the first batch of 525 litter baskets in the field in November-December 2020. All blocks were placed around similarly sized bushes of locally distributed species and tethered to the ground using metal stakes. We collected the baskets in May-July 2021 and replaced them with a new similar batch that was later collected in October-November 2021. At the end of each season, the collected baskets were transported to the laboratory in sealed Ziplock bags. Any litter spilled during transportation was weighed and the weight loss was incorporated in the calculations. Leaf litter in each basket was first screened for adulteration from leaf litter of other species, following which the *S. capensis* litter was oven dried at 60 ºC for 48 hours and weighed. To account for dust accumulation on the litter we applied an ash correction procedure[29]. We burned and weighed five sub-samples from each site-season-treatment combination (550 ºC for 5

hours) and calculated the combination-specific mean ash content. The final litter mass was corrected for ash content based on these calculations. We burned and weighed 15 additional samples of *S. capensis* litter that were not placed in the field and calculated the mean ash content of the initial litter. The initial litter mass was corrected accordingly. The rate of litter removal from each basket was calculated as the difference between the ash corrected final dry litter mass and the ash and moisture corrected initial litter mass, divided by the number of days the litter spent in the field.

Pitfall trapping

We characterized the macro-decomposer assemblages by setting up 20 pitfall traps for 5-7 days at each site during each experimental period. Wet season traps were opened in February 2021, whereas the dry season traps were opened between late August and early October. We installed traps by placing two 10 cm diameter X 7.5 cm deep plastic containers one inside another such that the opening was flushed with the ground. We added to each trap 150 ml of preservative, which comprised of 40% absolute ethanol, 40% distilled water and 20% Propylene glycol. Traps were covered with steel mesh of large mesh size to prevent small mammals and reptiles from falling inside. At the end of the 5-7 days, samples were collected and transferred to 70% ethanol. Samples were sorted and identified to morphospecies level in the lab. Only animals larger than 2 mm were included in the analysis. Sub-samples were freeze-dried and weighed (Mettler Toledo MS105DU) for biomass estimation of each morphospecies.

Analytical procedures

We first fitted a linear mixed model (LMM) to the litter removal rate data, including experimental site, experimental season, mesh size and all interaction terms as fixed effects. The random effect of the experimental spatial blocks was found insignificant using a simulation test

with 9999 simulations (RLRT=2.1, P-value=0.07). Therefore, we assessed the effects of the site, season and mesh size on the litter removal rate using a full factorial analysis of variance, followed by Tukey HSD pairwise comparisons. We calculated the contribution of each size group to litter mass loss by block. Microbial contribution was defined as the mass loss from micro-baskets; mesofaunal contribution was calculated as the difference between mass loss from meso- and micro-baskets; macrofaunal contribution was calculated as the difference between mass loss from macro- and meso-baskets; whole-community decomposition was defined as the mass loss from macro-baskets. We modeled the relationship between MAP and each of these contributions using Locally Estimated Scatterplot Smoothing (LOESS). We used the same method to model the relationship between MAP and the macro-decomposer abundance, biomass and morphospecies richness in each season. We assessed differences in the macro-decomposer assemblage among experimental sites and seasons using a principal coordinates analysis (PCoA) with individual traps as the sampling units and Bray-Curtis index (BC) as the dissimilarity metric. We tested for differences across sites and seasons in macro-decomposer assemblage using a permutational multivariate analysis of variance (PERMANOVA), followed by pairwise comparisons between sites using the Benjamini-Hochberg P-value adjustment. BC indices between site-season combinations were calculated as well, based on the summed abundances across traps. To explore which macro-decomposer groups dominate the different sites and seasons, we classified the identified morphospecies to ten macro-decomposer taxa: Archaeognatha (bristletails), Coleoptera (beetles), Diplopoda (millipedes), Formicidae (ants), Gastropoda (snails and slugs), Grylloidea (crickets), Isoptera (termites), Lumbricina (earthworms), Oniscidea (woodlice) and Zygentoma. Then we summed the abundance, richness and biomass from each group in each trap. We used the abundance data to fit the group scores

onto the PCoA ordination. Litter removal data was analyzed using the 'stats', 'lme4'[30] and 'RLRsim'[31] packages from R software (version 4.3.0)[32], whereas assemblage data was analyzed using the 'vegan' package[33].

Results

Litter removal rate differed across seasons, sites and mesh sizes, and all interactions between these factors were found significant as well (**Table 2**). On average, the litter removal rate was 2.6-fold higher in winter than in summer, 1.6-fold higher in meso- than in micro-baskets and 1.3-fold higher in macro- than in meso-baskets. Litter removal was negligible in the hyperarid sites during both seasons, while it was highest in the arid sites during summer and in the more mesic sites during winter (**Fig. 3**). Within site and season comparisons between mesh sizes yielded significant differences only in Avdat, Sayeret Shaked and Havat Shikmim, indicating that faunal effects on decomposition were found only under arid to dry-semiarid conditions (**Fig. 3**). Both macro- and mesofaunal effects were detected in the arid sites (Avdat, Sayeret Shaked), whereas the semiarid Havat Shikmim site exhibited only a mesofaunal effect during both seasons (**Fig. 3**). The macrofaunal, mesofaunal and microorganismal contributions to litter mass loss peaked under arid, semiarid and Mediterranean climate conditions, respectively (**Fig. 4**). Whole-community litter removal rates were dictated by microorganisms in winter and by macrofauna in summer, resulting in comparable rates across the aridity gradient from Mediterranean to arid climate at the annual scale (**Fig. 4**). In total, the whole-community litter removal rate peaked in Sayeret Shaked (MAP=148 mm) and significantly decreased under drier and wetter conditions (**Fig. 4**).

Macro-decomposer abundance, biomass and morphospecies richness peaked in the arid sites during both seasons (**Fig. 5**). The macro-decomposer assemblage differed significantly

across sites ($F_{6,229}$=10.6, P-value<0.001) and across seasons ($F_{1,229}$=13.1, P-value<0.001), where woodlice, millipedes and snails were substituted by ants and termites with increasing aridity (**Fig. 6A, B**). Assemblage was significantly affected by the interaction between site and season too ($F_{6,229}$=5.4, P-value<0.001). The experimental site explained much of the assemblage variability across traps (R^2=0.18), whereas experimental season accounted for a smaller fraction (R^2=0.04), and site-season interaction played an intermediate role (R^2=0.10). All pairwise comparisons across sites yielded significant differences in assemblage (**Table S1**). In general, ants were the most abundant group, whereas beetles accounted for most of the biomass. However, under mesic conditions, woodlice (Ramat Hanadiv site), millipedes (Ramat Hanadiv and Bet Guvrin) and snails (Havat Shikmim) were dominant (**Fig. 6C**). The Ramat Hanadiv assemblage was distinctively different from all other sites (**Fig. 6A**), as demonstrated by very high Bray-Curtis dissimilarity indices compared to the other sites, regardless of the season (**Table S2**). There were parallels between the spatial and temporal axes of aridity, as winter communities in the most arid sites (Nahal Shita, Meishar and Avdat) were relatively similar to the summer communities of the more mesic sites (Sayeret Shaked, Havat Shikmim and Bet Guvrin) (**Fig. 6A,B**; **Table S2**). The arid sites, where macro-decomposer assemblages flourished and were responsible for the highest litter mass loss, showed interesting seasonal dynamics. Bray-Curtis dissimilarity across seasons was higher in Sayeret Shaked than in Avdat (BC=0.79 and 0.72, respectively). Cross-site dissimilarity between Sayeret Shaked and Avdat was higher in winter than in summer (BC=0.85 and 0.72, respectively).

Table 2 - Results of a full-factorial analysis of variance in litter removal rate across mesh sizes, experimental sites and seasons.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	6	0.002092	0.000349	171.946	<0.001
Season	1	0.000679	0.000679	334.94	<0.001
Mesh size	2	0.000267	0.000133	65.77	<0.001
Site : Season	6	0.00112	0.000187	92.044	<0.001
Site : Mesh size	12	0.000392	3.27E-05	16.11	<0.001
Season : Mesh size	2	1.77E-05	8.9E-06	4.368	0.0129
Site : Season : Mesh size	12	0.000129	1.08E-05	5.306	<0.001
Residuals	1008	0.002044	0.000002		

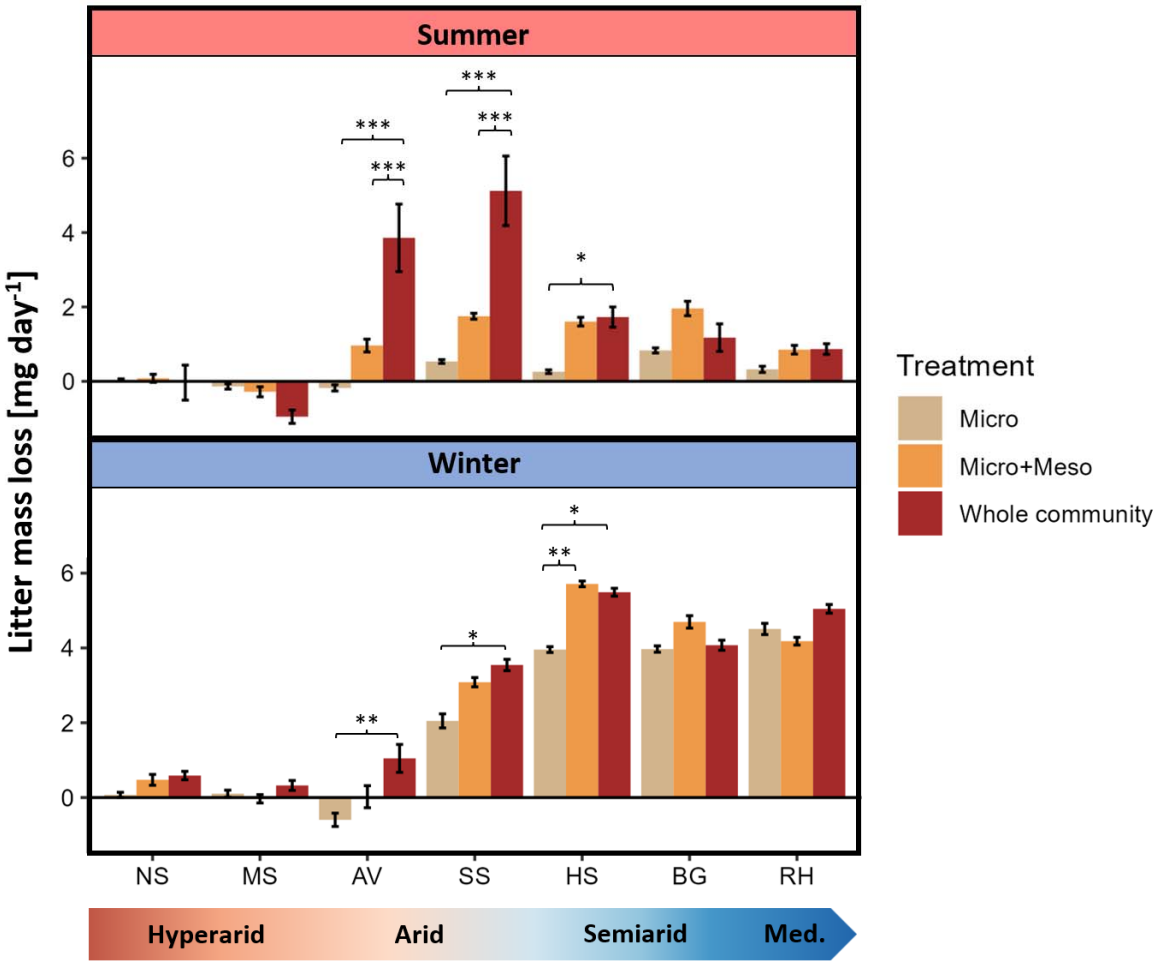

Figure 3 - Litter removal rate (mean ± se) from baskets with different mesh sizes across sites and seasons. Asterisks represent significant differences between mesh sizes within site and season: * P-value<0.05, **P-value<0.01, ***P-value<0.001. NS – Nahal Shita; MS – Meishar; AV – Avdat; SS – Sayeret Shaked; HS – Havat Shikmim; BG – Bet Guvrin; RH – Ramat Hanadiv. Negative values may represent cases in which physical cleaning and ash correction failed to correct for all dust accumulation on the litter or cases in which exogenous litter may have penetrated the baskets. Our findings were not sensitive to these negative values.

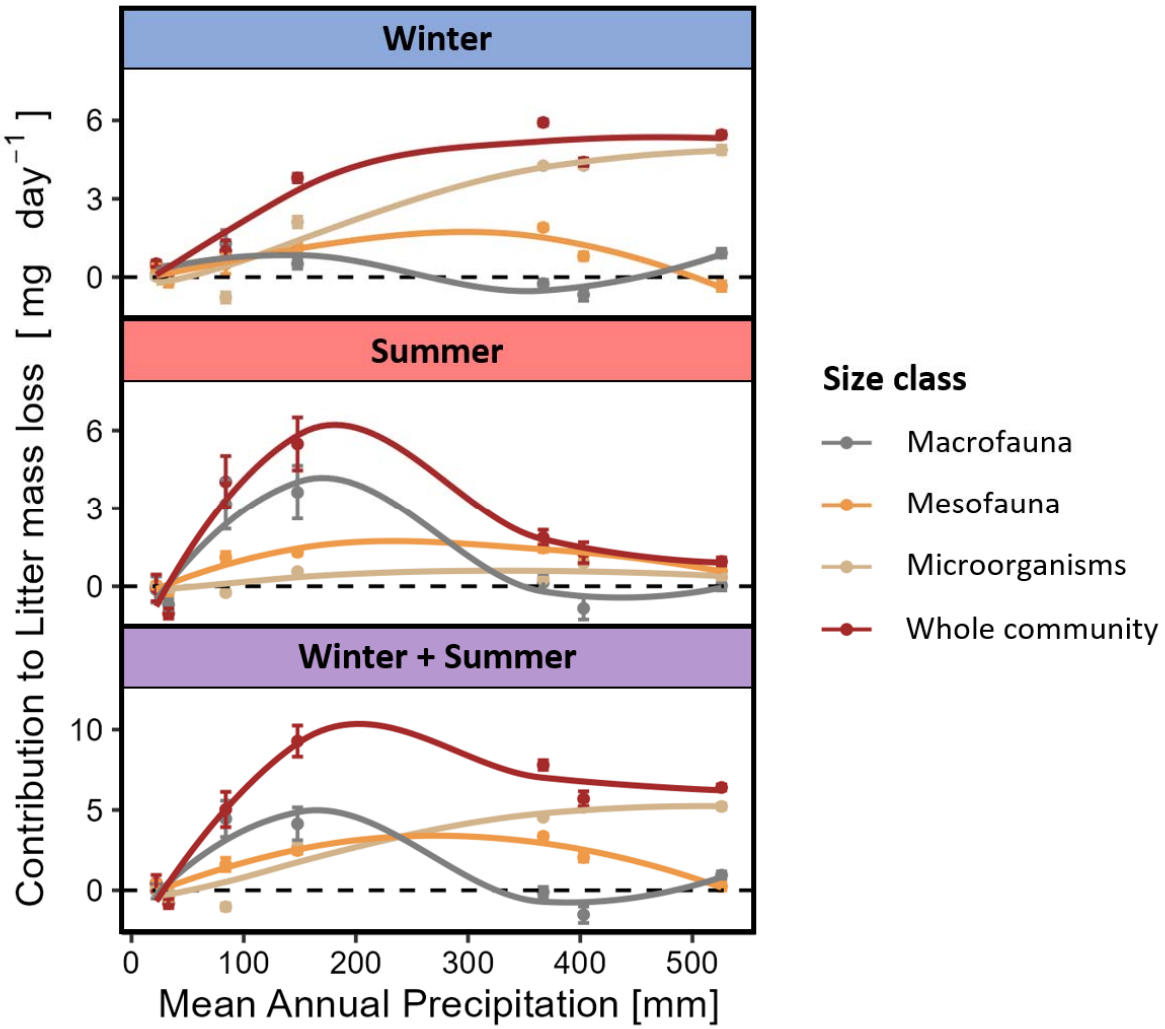

Figure 4 - Contribution of different organism size classes to litter removal (mean ± se) across the precipitation gradient during summer, winter and both seasons combined. Macrofaunal contribution was calculated as the within-block difference between macro- and meso-baskets; mesofaunal contribution as the difference between meso- and micro-baskets; microbial and whole community contributions represent litter removal rates in the micro- and macro-baskets, respectively. Curves were fitted to data using local estimation scatterplot smoothing (LOESS). Negative values may represent cases in which physical cleaning and ash correction failed to correct for all dust accumulation on the litter or cases in which exogenous litter may have penetrated the baskets. Our findings were not sensitive to these negative values.

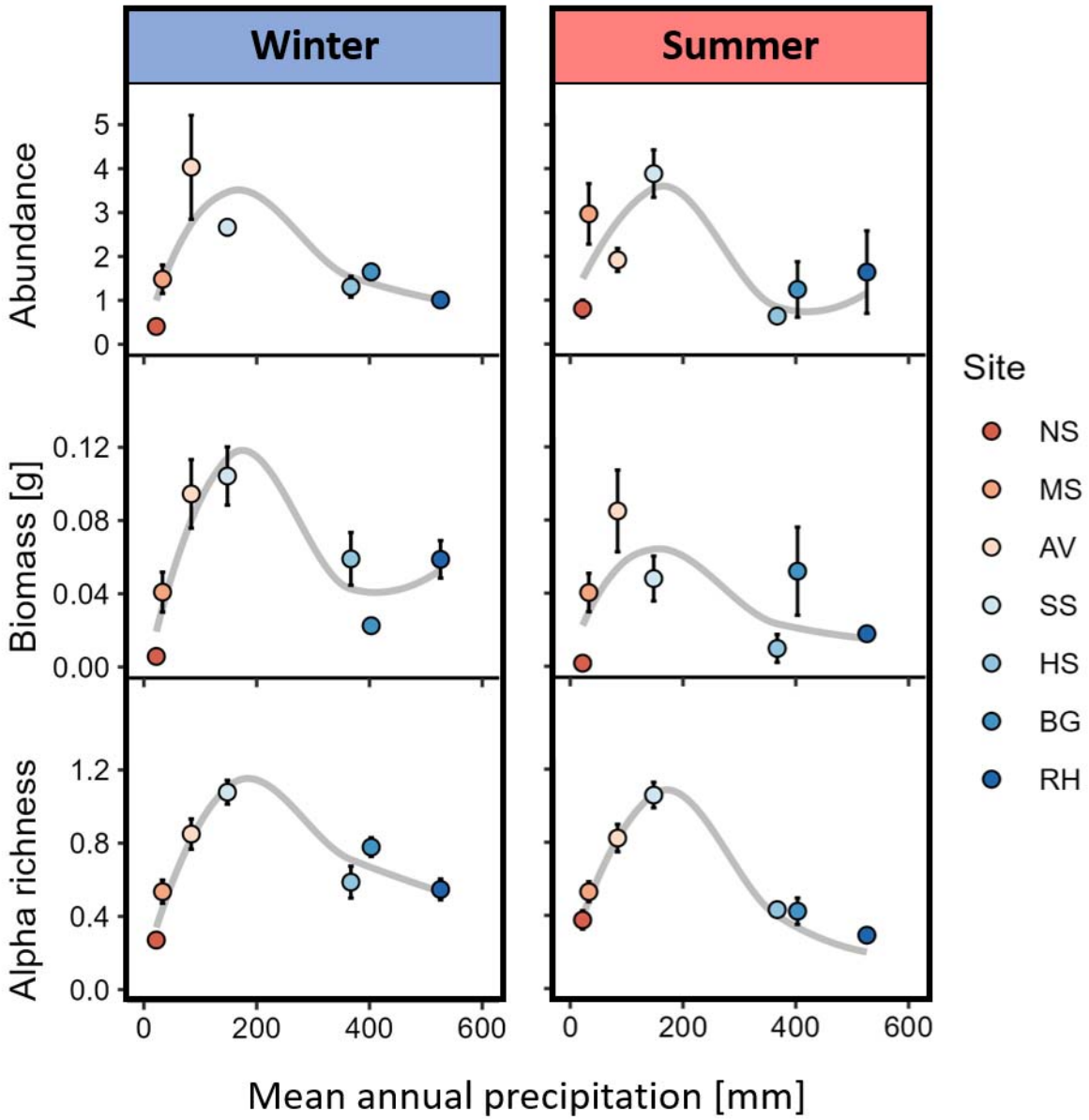

Figure 5 - Macro-decomposer abundance, biomass and alpha morphospecies richness across the precipitation gradient in the two experimental seasons (mean ± se). Values are averaged across traps and divided by the number of trapping days. NS – Nahal Shita; MS – Meishar; AV – Avdat; SS – Sayeret Shaked; HS – Havat Shikmim; BG – Bet Guvrin; RH – Ramat Hanadiv.

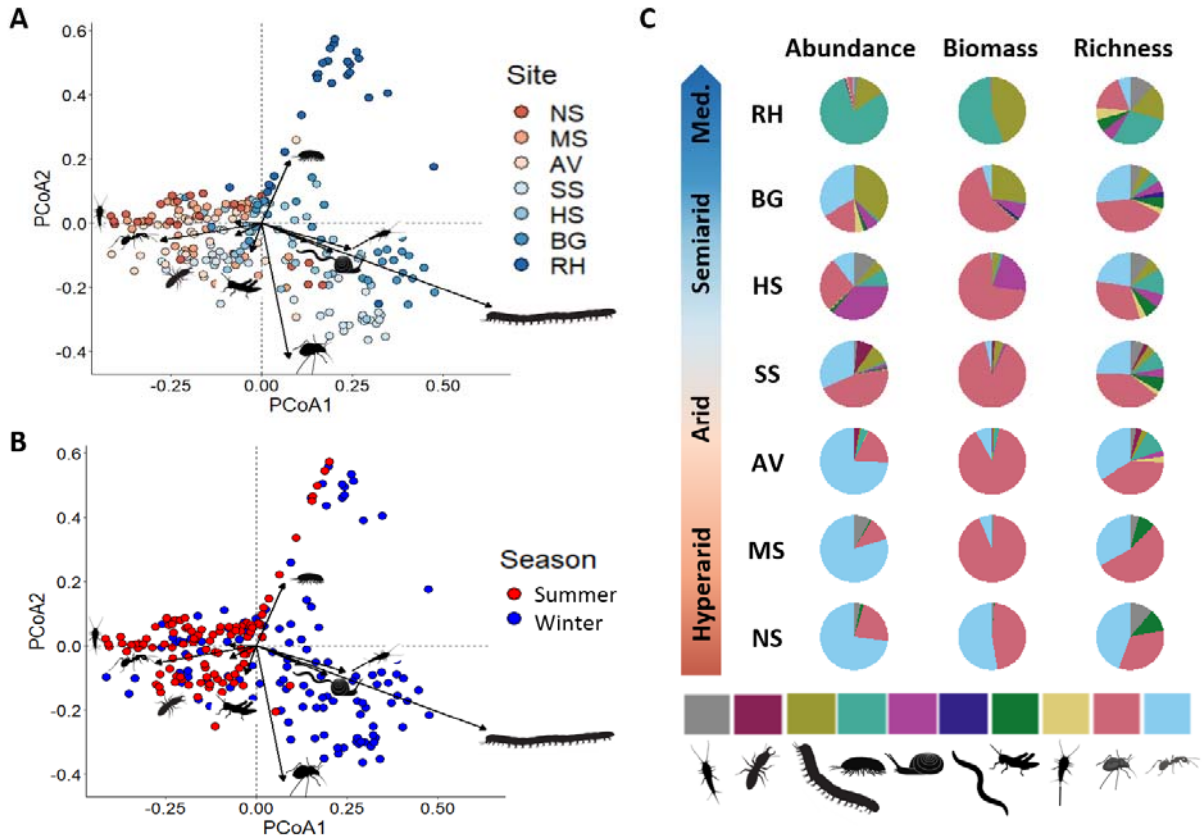

Figure 6 - (A) and (B) Graphical representation of the first two axes of a principal coordinate analysis on the macro-decomposer assemblage data. Colors represent experimental sites in A and seasons in B. Arrows represent taxonomic group scores fitted onto the PCoA ordination. (C) Distribution of abundance, biomass and morphospecies richness among macro-decomposer taxonomic groups in each site across the aridity gradient. NS – Nahal Shita; MS – Meishar; AV – Avdat; SS – Sayeret Shaked; HS – Havat Shikmim; BG – Bet Guvrin; RH – Ramat Hanadiv. Color codes (left to right in panel C): grey – Zygentoma, burgundy – termites, olive green – millipedes, turquoise – woodlice, pink – snails and slugs, purple – earthworms, dark green – crickets, pale yellow – bristletails, red – beetles, pale blue – ants.

Discussion

Our goal was to investigate how climate interacts with soil biota of different size categories to influence litter decomposition. We used litter baskets of different mesh sizes that were placed along a sharp precipitation gradient during hot-dry summer and again during colder-wetter winter. Our results suggest that decomposers respond differently to precipitation levels based on their size, leading to similar overall decomposition rates across the gradient, except in hyper-arid sites. We found that microbial decomposition was minimal during the summer. In the winter, microbial decomposition was positively associated with precipitation, governing the whole-community decomposition. In both seasons, mesofaunal decomposition was moderate and followed a hump-shaped response to precipitation, peaking in semiarid sites. Macro-decomposition contributed minimally to whole-community decomposition during the winter, but during the summer dominated decomposition in the two arid sites. Using pitfall trapping, we found that macro-decomposer richness, abundance and biomass followed a hump-shaped response to precipitation, peaking in arid environments.

The puzzle of why plant litter decomposition in arid-lands is decoupled from annual precipitation and is faster than expected based on microbial decomposition models has bothered scientists for half a century[7,34,35], and was later termed the desert decomposition conundrum[36]. Attempts to resolve this conundrum have focused predominantly on abiotic weathering agents, such as photodegradation[37,38] and thermal degradation[39], alternative sources of moisture such as fog, dew and atmospheric water vapor[40] and soil–litter mixing[36,41]. We, in turn, hypothesized that the opposing climatic dependencies of macrofauna and that of microorganisms and mesofauna should lead to similar overall decomposition rates across precipitation gradients, except in hyperarid environments in which decomposers activity is predicted to be minimal regardless of

organism size. Our results largely agree with this hypothesis. Whole-community decomposition was minimal in hyper-arid sites in both summer and winter. In the winter, microbial decomposition dominated the whole-community decomposition, demonstrating a positive response to precipitation that reached a maximum in the most mesic Mediterranean site. In contrast, macro-decomposition has contributed only little to the whole-community decomposition during the winter, but dominated the arid sites' decomposition in the summer. These findings supported the long-suggested but largely overlooked hypothesis that macro-decomposition governs plant litter decomposition in deserts[7,34,35]. The opposing climatic dependencies of micro- and macro-decomposers have led to similar or even higher annual decomposition rates in arid sites compared to those measured in more mesic sites. Consequently, we highlighted that differential climatic dependencies of different-sized decomposers rather than abiotic factors explain the discrepancy between classic decomposition models and the observed decomposition rates in drylands. This realization provided a plausible resolution to the longstanding desert decomposition conundrum, and exposed a hidden mechanism that may account for unexplained variation in plant litter decomposition across biomes.

Canonically, faunal decomposition is expected to be positively associated with temperature and moisture[20]. We, however, hypothesized that climate dependencies of mesofauna and macrofauna should differ due to the lower sensitivity of macrofauna to high temperature and low moisture, and the ability of macro-decomposers to shuttle between the hostile environment aboveground and the climatic havens belowground[28]. We also hypothesized that low and unpredictable resource availability in hyper-arid environments should limit macro-decomposer populations. Consequently, we predicted that macro-decomposers should be more prevalent in arid environments in comparison to hyper-arid or more mesic environments. Furthermore, ample

resource availability may increase niche space[42], resulting in higher macro-decomposer diversity, which in turn can facilitate decomposition through synergistic effects of functionally complementary species[43–46]. Thus, we predicted that macro-decomposition should reflect the variation in the abundance, richness and biomass of macro-decomposers across the precipitation gradient. Our findings supported these predictions. The richness, abundance and biomass of macro-decomposers followed a hump-shaped relationship with precipitation, peaking in arid environments and diminishing toward hyper-arid or semiarid and Mediterranean sites. Macro-decomposer assemblages were dominated by ants and beetles across the aridity gradient except in the Mediterranean site that was dominated by isopods and millipedes. During the summer, the observed hump-shaped relationship between macro-decomposition and precipitation tightly echoed the variation in richness, abundance, and biomass of macro-decomposers, revealing the mechanistic foundation for the cross-system variation in macro-decomposition.

In winter, macro-decomposer abundance, richness, and biomass were similar to or even higher than those measured during the summer across all sites. Despite this resemblance, macro-decomposition did not reflect the observed variation in macro-decomposer assemblages. This discrepancy could be explained by between-seasons differences in the structure of the macro-decomposer assemblages (**Fig. 6B**). The macro-decomposer summer assemblage in Sayeret Shaked was more similar to the Avdat summer assemblage than to the Sayeret Shaked winter assemblage. The Avdat assemblages were more similar to each other across seasons than the Sayeret Shaked assemblages. This may explain why macro-decomposition in winter was higher in Avdat than in Sayeret Shaked. Termites (*Hodotermitidae* sp.), that play an important role in decomposition, were more abundant in summer compared to the winter in Sayeret Shaked but not in Avdat. Moreover, our data revealed that several beetle taxa (*Adelostoma* sp., *Akis reflexa*

(Fabricius, 1775), *Dailognatha crenata* (Reiche & Saulcy, 1857), *Tentyrina* sp., *Zophosis* sp.) were prevalent in both arid sites during the summer but were absent or very scarce in the winter. Phenological differences in the behavior of dominant macro-decomposers may also contribute to the seasonal differences[47]. For instance, *Hemilepistus reaumuri* (Milne Edwards, 1840), an abundant isopod species in Avdat, and *Anacanthotermes ubachi* (Navás, 1911), a common termite species in Sayeret Shaked, consume detritus predominantly during the summer and autumn and disperse and reproduce during the winter[48,49]. Future studies should explicitly test these explanations. Regardless, the whole-year association between macro-decomposition and the abundance, richness, and biomass of macro-decomposers strongly support our hypothesis.

Theory suggests that plant litter decomposition by meso-decomposers should increase with moisture. This pattern was supported by a cross-biome experiment[50]. Thus, we hypothesized that both meso-decomposition and microbial decomposition should increase with precipitation and be more prominent in the winter than in the summer. Our results did not coincide with these hypotheses. Litter decomposition by mesofauna followed a unimodal pattern across the precipitation gradient, peaking under semiarid conditions in both seasons (**Fig. 4**). Meso-decomposition and macro-decomposition were similar in the hyper-arid and Mediterranean sites. However, meso-decomposition was higher than macro-decomposition in the semiarid sites and much lower than macro-decomposition in the arid sites. These results suggest that meso-decomposers, like macro-decomposers, have adaptations that allow them to strive in moisture-deprived environments. Yet, meso-decomposition peaked in more mesic conditions than macro-decomposition, implying higher moisture dependency. Our findings highlight the need to explore the moisture dependency of mesofauna in greater details, and to generate

different predictions for how mesofauna and microorganisms may affect plant litter decomposition.

Faunal decomposition in our study peaked in arid environments, contrasting the positive association between faunal decomposition and precipitation that was found in recent global meta-analyses[20,21]. This discrepancy may reflect underestimation of faunal decomposition rates in drylands, possibly because these studies either deliberately grouped cold and dry environments together[20,50], or focused solely on precipitation without accounting for differences in temperature[21]. In cold water-deprived environments and seasons, low temperatures may limit the populations and activity of ectotherm animals[4,22]. Therefore, ignoring the effect of temperature may lead to falsely smaller faunal effects on decomposition in drylands. This bias may contribute to the positive association between precipitation and faunal decomposition. To reveal the realistic relationships, future studies on faunal decomposition should explore the effects of temperature, precipitation and the interaction between them. It is important noting that temperature could affect decomposition both directly by determining the activity of ectotherms and indirectly by regulating moisture availability. Thus, using aridity indices that aim to correct for moisture availability cannot resolve the need to account also for temperature *per se*.

We used litter of one plant species that is common to all seven experimental sites. In this way, we were able to compare decomposition rates across sites without using litter that is exogenous to one or more sites. Decomposer communities are assumed to perceive litter quality based on the chemical composition of the focal litter, and that of past resource inputs that these communities have experienced[51]. Plant communities differ substantially between our sites, suggesting that each decomposer community has experienced very different resource inputs, and may have access to alternative litter of various qualities. Thus, it is likely that the perceived

quality of *S. capensis* litter differs between sites, possibly confounding our results. Moreover, our sites were distributed along a single precipitation gradient. Thus, our results may be confounded by other environmental factors that were not accounted for. To determine how general our findings are, future research should repeat our experimental approach using different litter sources, and across multiple climatic gradients.

In conclusion, our work revealed that decomposers of varying size categories have different moisture dependencies. This suggests that microorganisms, meso-decomposers and macro-decomposers should be considered separately in decomposition models, and emphasizes the need to contemplate animals' physiology and behavior when investigating zoogeochemical processes. Warm drylands cover 19% of the land surface worldwide and expand rapidly due to unsustainable land-use and climate change[52]. We highlight the importance of macro-decomposition in arid-lands that compensates for the minimal microbial decomposition, providing a plausible resolution to the long-debated dryland decomposition conundrum. Understanding the mechanisms that regulate decomposition in drylands is key for conserving and restoring fundamental ecosystem processes in these ever-growing areas, and in improving our understanding of global processes like C cycling. To date, the general conceptualization of decomposition is largely based on ample research from temperate ecosystems. Thus, prevailing theory centers on focal processes that dominate decomposition in these systems. Our work highlights that in other less studied ecosystems additional processes like the role of animal decomposers may be dominant, opening the door for new exciting research that may shake our conceptualization of decomposition processes.

References

1. Schlesinger, W. H. & Bernhardt, E. Biogeochemistry: An Analysis of Global Change. (Academic Press, 2020) doi:10.1016/B978-0-12-814608-8.09991-6.
2. Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R. & Wood, S. A. Understanding the dominant controls on litter decomposition. *J. Ecol.* **104**, 229–238 (2016).
3. Joly, F. X., Scherer-Lorenzen, M. & Hättenschwiler, S. Resolving the intricate role of climate in litter decomposition. *Nat. Ecol. Evol.* **7**, 214–223 (2023).
4. Swift, M. J., Heal, O. W. & Anderson, J. M. *Decomposition in Terrestrial Ecosystems*. (University of California Press, 1979).
5. Wu, X., Niklas, K. J. & Sun, S. Climate change affects detritus decomposition rates by modifying arthropod performance and species interactions. *Curr. Opin. Insect Sci.* **47**, 62–66 (2021).
6. Berg, B. *et al.* Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry* **20**, 127–159 (1993).
7. Meentemeyer, V. Macroclimate and lignin controls of litter decomposition rates. *Ecology* **59**, 465–472 (1978).
8. Bradford, M. A. *et al.* A test of the hierarchical model of litter decomposition. *Nat. Ecol. Evol.* **1**, 1836–1845 (2017).
9. Parton, W. *et al.* Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**, 361–364 (2007).
10. Aerts, R. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos* **79**, 439 (1997).
11. Zhang, D., Hui, D., Luo, Y. & Zhou, G. Rates of litter decomposition in terrestrial ecosystems: Global patterns and controlling factors. *J. Plant Ecol.* **1**, 85–93 (2008).
12. David, J. F. The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views. *Soil Biol. Biochem.* **76**, 109–118 (2014).
13. Frouz, J. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma* **332**, 161–172 (2018).
14. Griffiths, H. M., Ashton, L. A., Parr, C. L. & Eggleton, P. The impact of invertebrate decomposers on plants and soil. *New Phytol.* **231**, 2142–2149 (2021).
15. Auclerc, A. *et al.* Fostering the use of soil invertebrate traits to restore ecosystem functioning. *Geoderma* **424**, 116019 (2022).
16. Sagi, N., Zaguri, M. & Hawlena, D. Macro-detritivores assist resolving the Dryland Decomposition Conundrum by engineering an underworld heaven for decomposers. *Ecosystems* **24**, 56–67 (2021).
17. Coulis, M., Hättenschwiler, S., Coq, S. & David, J. F. Leaf litter consumption by macroarthropods and burial of their faeces enhance decomposition in a Mediterranean ecosystem. *Ecosystems* **19**, 1104–1115 (2016).

18. Joly, F. X., Coq, S., Coulis, M., Nahmani, J. & Hättenschwiler, S. Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition. *Funct. Ecol.* **32**, 2605–2614 (2018).
19. Joly, F. X. *et al.* Detritivore conversion of litter into faeces accelerates organic matter turnover. *Commun. Biol.* **3**, 660 (2020).
20. García-Palacios, P., Maestre, F. T., Kattge, J. & Wall, D. H. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecol. Lett.* **16**, 1045–1053 (2013).
21. Xu, X. *et al.* Cellulose dominantly affects soil fauna in the decomposition of forest litter: A meta-analysis. *Geoderma* **378**, 114620 (2020).
22. Johnston, A. S. A. & Sibly, R. M. Multiple environmental controls explain global patterns in soil animal communities. *Oecologia* **192**, 1047–1056 (2020).
23. Cloudsley-Thompson, J. L. Adaptations of arthropoda to arid environments. *Annu. Rev. Entomol.* **20**, 261–283 (1975).
24. Veldhuis, M. P., Laso, F. J., Olff, H. & Berg, M. P. Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology* **98**, 467-477 (2017)
25. Sagi, N., Grünzweig, J. M. & Hawlena, D. Burrowing detritivores regulate nutrient cycling in a desert ecosystem. *Proc. R. Soc. B Biol. Sci.* **286**, 20191647 (2019).
26. Zanne, A. E. *et al.* Termite sensitivity to temperature affects global wood decay rates. *Science* **377**, 1440–1444 (2022).
27. Ayal, Y., Polis, G. A., Lubin, Y. & Goldberg, D. How can high animal diversity be supported in low-productivity deserts? The role of macrodetritivory and habitat physiognomy. in *Biodiversity in drylands: towards a unified framework* (eds. Shachack, M., Gosz, J. R., Perevolotsky, A. & Pickett, S. T. A.) 34–45 (Oxford University Press, 2005).
28. Sagi, N. & Hawlena, D. Arthropods as the engine of nutrient cycling in arid ecosystems. *Insects* **12**, 726 (2021).
29. Barney, J. N. *et al.* Global Invader Impact Network (GIIN): toward standardized evaluation of the ecological impacts of invasive plants. *Ecol. Evol.* **5**, 2878–2889 (2015).
30. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48 (2015).
31. Scheipl, F., Greven, S. & Kuechenhoff, H., Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Comput. Stat. Data Anal.* **52**, 3283-3299 (2008).
32. R Core Team. R: A language and environment for statistical computing. (2022).
33. Oksanen, J. *et al.* vegan: Community Ecology Package. (2022).
34. Noy-Meir, I. Desert ecosystems□: Higher trophic levels. *Annu. Rev. Ecol. Syst.* **5**, 195–214 (1974).
35. Whitford, W. G. Exceptions to the AET model: Deserts and clear-cut forest. *Ecology* **62**, 275–277 (1981).
36. Throop, H. L. & Archer, S. R. Resolving the Dryland Decomposition Conundrum: Some new perspectives on potential drivers. in *Progress in Botany* (eds. Lüttge, U., Beyschlag, W., Büdel, B. & Francis, D.) **70**,

171–194 (Springer-Verlag Berlin Heidelberg, 2009).

37. Austin, A. T. & Vivanco, L. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442**, 555–558 (2006).

38. Austin, A. T. Has water limited our imagination for aridland biogeochemistry. *Trends Ecol. Evol.* **26**, 229–235 (2011).

39. Day, T. A., Bliss, M. S., Placek, S. K., Tomes, A. R. & Guénon, R. Thermal abiotic emission of CO_2 and CH_4 from leaf litter and its significance in a photodegradation assessment. *Ecosphere* **10**, (2019).

40. Evans, S., Todd-Brown, K. E. O., Jacobson, K. & Jacobson, P. Non-rainfall moisture: A key driver of microbial respiration from standing litter in arid, semiarid, and mesic grasslands. *Ecosystems* **23**, 1154–1169 (2020).

41. Throop, H. L. & Belnap, J. Connectivity dynamics in dryland litter cycles: Moving decomposition beyond spatial stasis. *Bioscience* **69**, 602–614 (2019).

42. Macarthur, R. H. Patterns of species diversity. *Biol. Rev.* **40**, 510–533 (1965).

43. Heemsbergen, D. A. *et al.* Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* **306**, 1019–1020 (2004).

44. Gessner, M. O. *et al.* Diversity meets decomposition. *Trends Ecol. Evol.* **25**, 372–380 (2010).

45. Boyero, L. *et al.* Impacts of detritivore diversity loss on instream decomposition are greatest in the tropics. *Nat. Commun.* **12**, 1–11 (2021).

46. Zeng, X. *et al.* Soil invertebrates are the key drivers of litter decomposition in tropical forests. *Authorea Prepr.* (2023) doi:10.22541/AU.167776750.08748069/V1.

47. Bonato Asato, A. E., Wirth, C., Eisenhauer, N. & Hines, J. On the phenology of soil organisms: Current knowledge and future steps. *Ecol. Evol.* **13**, e10022 (2023).

48. Zaady, E., Groffman, P. M., Shachak, M. & Wilby, A. Consumption and release of nitrogen by the harvester termite *Anacanthotermes ubachi navas* in the northern Negev desert, Israel. *Soil Biol. Biochem.* **35**, 1299–1303 (2003).

49. Shachak, M., Chapman, E. A. & Steinberger, Y. Feeding, energy flow and soil turnover in the desert isopod, Hemilepistus reaumuri. *Oecologia* **24**, 57–69 (1976).

50. Wall, D. H. *et al.* Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob. Chang. Biol.* **14**, 2661–2677 (2008).

51. Strickland, M. S., Osburn, E., Lauber, C., Fierer, N. & Bradford, M. A. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Func. Ecol.* **23**, 627-636 (2009).

52. Cartereau, M. *et al.* Global bioregionalization of warm drylands based on tree assemblages mined from occurrence big data. *Front. Biogeogr.* **14**, e56435 (2022).

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Competing interests

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