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Small spaces have large impacts: Microsites determine plant litter decomposition rates in drylands

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Our understanding of carbon and nutrient dynamics in globally vast and socioeconomically critical dryland ecosystems lags behind mesic systems. Litter decomposition models consistently underestimate measured decomposition in these regions. Both models and measurements largely represent spatially dominant intercanopy areas; however, little litter resides in these interspaces as transport vectors move litter to other microsites such as beneath plant canopies and buried in soil. Abiotic and biotic conditions differ among microsites, but few studies have characterized microsite impacts on decomposition. We collated data on microsites where litter accumulates. In microsites with sufficient available data, we used meta-analysis to test hypotheses on decomposition relative to litter in intercanopy spaces. Decomposition was lower under woody plant canopies than in intercanopy spaces. Buried litter decomposed faster than surface litter. There was no difference in decomposition between surface litter and litter suspended aboveground to simulate standing dead. All microsite contrasts had exceptions, suggesting that site-specific characteristics influence microclimate and subsequent decomposition. Extrapolation of decomposition rates to the landscape-level (using estimates of microsite-specific decomposition rates multiplied by litter pools), suggests that decomposition estimates based on intercanopy data alone underrepresent landscape-level decomposition. Thus, despite advances in the understanding of mechanistic decomposition drivers in drylands advancing, most studies are spatially unrepresentative analyses in intercanopy areas and this will underestimate decomposition at the landscape level. Expanding the ecological relevance of decomposition processes to be useful for predicting larger-scale carbon and nutrient dynamics requires improved characterization of dryland litter distribution, coupled with a mechanistic understanding of decomposition in microsites where litter accumulates.

arid and semiarid | decomposition | microhabitat | carbon cycle | UV photodegradation

Significance

Predicting rates by which dead plant material breaks down is essential for global carbon models. Dryland ecosystems are critical to the global carbon cycle, as they cover >40% of the terrestrial area, but modeled predictions of dryland litter decomposition frequently do not match measurements. We suggest that extreme spatial heterogeneity in drylands has been insufficiently addressed in models and measurements. Spatial heterogeneity in microsites, largely the result of patchy vegetation, causes high variability in microclimate and uneven distribution of litter pools. We synthesize existing data on decomposition rates among microsites and illustrate how failure to consider microsite heterogeneity can affect landscape-level decomposition estimates. Inclusion of data from a diverse range of microsites should greatly improve representation of dryland decomposition models.

Nearly half of the world's terrestrial surface is covered by dryland ecosystems, where annual potential evapotranspiration far exceeds precipitation (dryland mean annual precipitation to potential evapotranspiration ratio < 0.65; 1). Understanding dryland biogeochemical processes is critical: globally, drylands account for a third of soil carbon (C) and net primary production (2, 3) and are a major contributor to interannual variability in the atmospheric C pool (4). Chronic water limitation shapes many ecological processes in these systems. However, mechanistic understanding of biogeochemical processes in drylands lags behind that of mesic systems (5), in part due to controlling mechanisms in drylands that differ from those of more frequently studied wetter systems (6). These "dryland mechanisms" are magnified by extreme spatial and temporal heterogeneity in abiotic and biotic conditions in drylands (6). Filling gaps in our understanding of dryland biogeochemical processes requires integrating mechanistic knowledge of process controls with an understanding of the extreme spatial and temporal patterns of abiotic conditions. Improved process understanding is critical not only for enhanced predictive capacity of dryland biogeochemical processes, but also for more accurate predictive understanding of mesic systems where water limitations are becoming increasingly prevalent due to climate change (6).

Decomposition has long captured the interest of dryland ecologists for being an important, but difficult to characterize, biogeochemical process (5, 7). Litter is the primary input to soil organic C, which is the largest terrestrial global pool (8). Due to the vast expanse of drylands, they contribute ~30% of the global soil organic C (2). Interestingly, available data indicate that while roughly 25% of global annual litter fall occurs in these regions, their slower decay results in them accounting for nearly half of the global standing litter pool (*SI Appendix*, Table S1 and *SI Text: Global Litter Pool Synthesis*). Litter can exert a strong control over ecological processes through altering nutrient mineralization and availability (9), enhancing soil moisture, and buffering soil temperatures (10). The importance of these processes is magnified in drylands as litter, soil organic material, and mineral nutrients are

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overall much lower than wetter systems (11, 12). However, characterizing decomposition in dryland regions has vexed researchers for decades, as simple, climate-based decomposition models that work well in other systems typically substantially underpredict dryland decomposition (7, 8). The model-measurement disconnect suggests that abiotic and biotic decomposition drivers that are not prominent in mesic systems may be prominent in drylands.

While moisture limitation is the defining characteristic of drylands, it also drives extreme spatial heterogeneity in vegetation cover, which is a key secondary characteristic of drylands (13). Limited moisture availability restricts plant cover to discrete patches which are interspersed with large stretches (often 1 m or more) of bare ground (Fig. 1). This discontinuous vegetation cover leads to spatial heterogeneity in litter inputs, with litter fall concentrated under and around plants. Heterogeneous litter distribution is further reinforced by transport processes (e.g., wind and water; 13–15) that move litter to "litter retention elements" (objects that resist horizontal litter transport; Fig. 2, 16). These structures range in size from cm (e.g., animal footprints or foraging pits, pinnacled biological soil crust, pebbles), to meters (e.g., boulders, plant canopies, coarse woody debris, water courses), to hundreds of meters (e.g., dry lakebed playas, dune slip faces). Litter accumulating at a litter retention element may create a boundary layer that further resists surface transport, particularly as litter becomes embedded in the soil (9). As a result, litter on a mass per area basis can be orders of magnitude greater in litter retention elements, such as under woody plant canopies, than in intercanopy locations (*SI Appendix*, Fig. S1; 10). Biogeochemical processes in drylands are largely concentrated at litter retention elements, as biotic and abiotic inputs are concentrated or persist in these microsites (11).

We posit that accurate representation of average decomposition at the landscape scale requires integration of both the spatial patterns of litter distribution and the decomposition rates in microsites. Each microsite has distinctive abiotic conditions which strongly influence microsite-specific decomposition rates; however, most studies do not account for abiotic microsite heterogeneity. We hypothesize that the mismatch between where litter accumulates and where experimental studies generally characterize microsite-specific decomposition rates currently compromises our ability to accurately characterize landscape-level dryland decay dynamics. To test this hypothesis, we conducted a literature survey coupled with a meta-analysis and upscaling exercise.

Controls over Dryland Decomposition Rates. Moisture, temperature, and solar radiation are key abiotic factors in modifying decomposition rates, and these factors differ greatly among dryland litter microsites. Climate indirectly controls decomposition by regulating biotic activity in most systems (12), suggesting that extreme spatial and temporal heterogeneity in microclimate may exert control over decay processes. In addition, soil-litter mixing is an important microclimate modifier that influences decomposition (17). The role of these abiotic factors in regulating decomposition has been discussed in detail elsewhere (e.g., refs. 12 and 18–21), so we provide only a brief discussion of the mechanistic controls, focusing on expectations for differences among dryland microsites where litter is likely to accumulate.

Moisture is typically positively related to global decomposition across annual scales, with simple climate variables such as annual actual evapotranspiration predicting decomposition rate in many systems due to the direct link between moisture availability and decomposer activity (12). However, this predictive relationship often breaks down in drylands. Individual studies in such regions have used precipitation inputs as a moisture analog but have found inconsistent results, including positive (22, 23) and no (24, 25) response to enhanced annual precipitation and no response to rainfall pulse size (26, 27). One possibility is that annual precipitation does not reflect biologically available litter moisture at the fine spatial and temporal scales relevant to microbial-driven decomposition

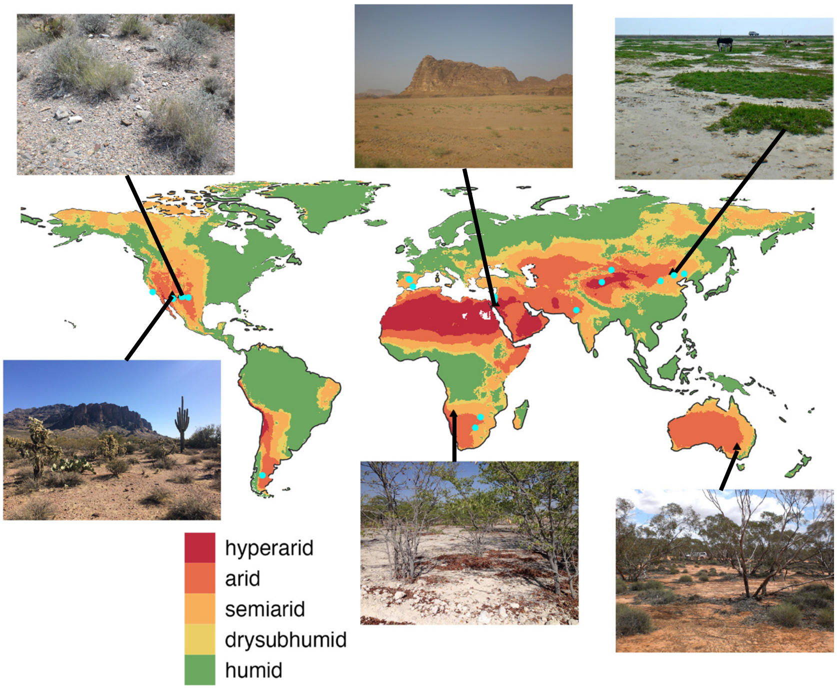

Fig. 1. The global distribution of drylands based on the aridity index. Photos illustrate a range of different vegetation cover. Although vegetation structure varies dramatically, most drylands are characterized by distinct vegetation patches separated by large intercanopy patches. Example drylands are (clockwise from *Upper Left* and designated as black triangles on the map) in New Mexico, USA; Wadi Rum, Jordan; Inner Mongolia, China; New South Wales, Australia; Oshikoto, Namibia; and Arizona, USA. Light blue circles on the map indicate locations for study sites included in the meta-analysis. Note that closely colocated study sites can not be distinguished from one another on this map (see *SI Appendix*, Table S2 for locations).

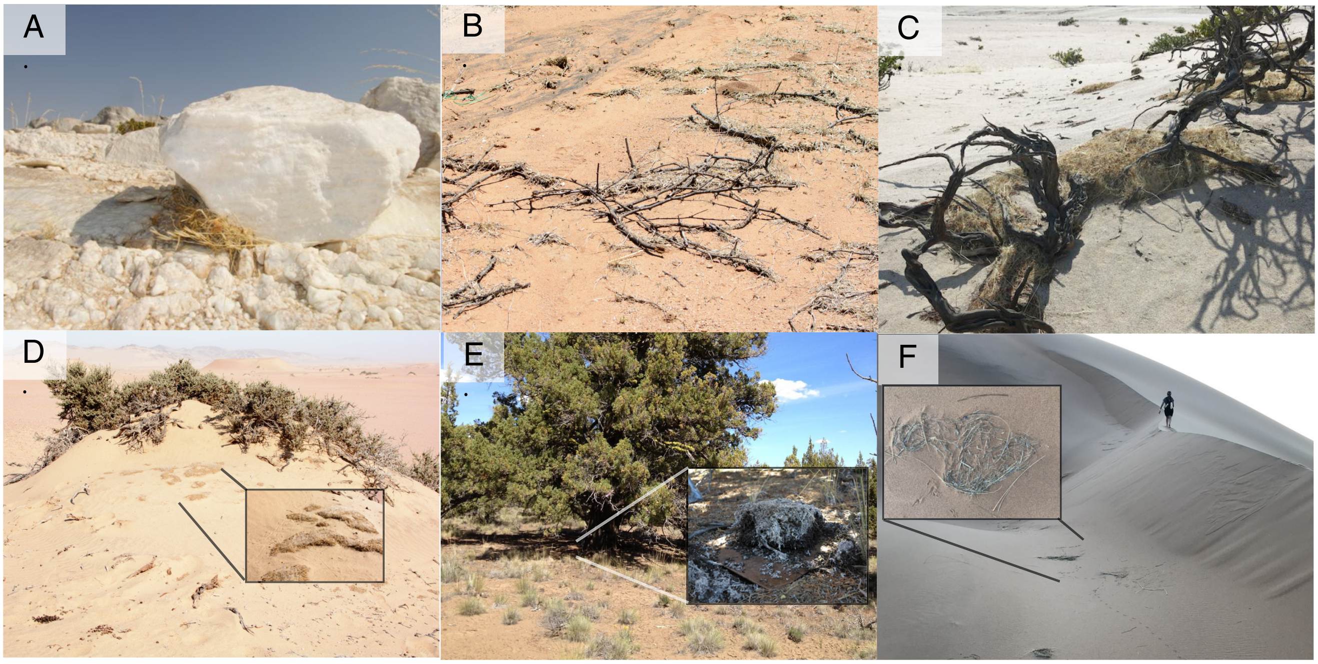

Fig. 2. Litter is captured in litter retention elements of varying size, including (*A*) a rock, (*B*) small woody debris, (*C*) coarse woody debris, (*D*) a shrub canopy and surrounding hummock (*Inset* shows accumulated surface litter), (*E*) a tree canopy (*Inset* shows thick litter layer after extraction), and (*F*) the base of a dune slip face (*Inset* shows surface litter that is being buried).

processes. For example, controlled environment studies simulating dryland conditions indicate that the timing and frequency of precipitation pulses can be more important than total precipitation in affecting biotic decomposition (17, 28). Furthermore, nonrainfall moisture (fog, dew, and adsorption of atmospheric water) can contribute substantially to biotic decomposition (29, 30), underscoring that moisture impacts on decomposition may be decoupled from long-term precipitation. Thus, moisture is likely an important dryland decomposition driver, although careful consideration of litter moisture content at temporal scales relevant to microbial activity is required.

Temperature is positively related to many biogeochemical processes due to its influence on enzyme kinetics. Biotic decomposition might follow this pattern, at least where moisture is not limiting. However, organic compounds differ in their temperature sensitivity to decomposition (31), making it difficult to generalize response rates (32). Few studies have explicitly explored temperature impacts on biotic litter decomposition, and this gap is notably present in drylands where frequent periods of moisture limitation might overwhelm temperature influences. Temperature may have an indirect negative influence on decomposition under conditions when temperature enhances evaporative losses from litter, shortening windows of opportunity for microbial decomposers. In contrast, temperature can cause abiotic degradation of litter ("thermal degradation"), releasing CO_2, CO, CH_4, and H_2, ostensibly via several chemical pathways (33–36). Thermal degradation is limited below 35 °C but increases rapidly at higher temperatures (33, 34). Mesic systems experience these high temperatures infrequently, but temperatures greater than 35 °C are frequent in many drylands, particularly in intercanopy spaces that receive direct solar radiation. Consequently, thermal degradation may be of particular importance to dryland decomposition.

Photodegradation can accelerate litter decomposition, although assessments of its importance in drylands vary widely (reviewed in refs. 19, 20, and 37). Photolysis of lignin and subsequent biotic decay via enzymatic degradation of cellulose may be a primary pathway (38), although there are likely complex interactions between biotic and abiotic drivers (39). System-specific differences in photodegradation may therefore be a function of the organic compounds present in litter as well as the amount, wavebands, and timing of solar radiation (33, 39). Furthermore, laboratory studies suggest that a substantial fraction of photodegradation observed in field studies could be thermal degradation (33, 37). In addition to direct effects of photo-oxidation, solar radiation may affect decomposition more indirectly via photopriming that alters litter quality for subsequent microbial decomposition (40, 41); microbially enhanced photodegradation, the degradation of litter by microbes that enhances future photodegradation (42); or microbial photoinhibition, a detrimental influence of solar radiation on decomposer activity or communities (43, 44). While the balance of these pathways is unknown, high solar radiation exposure is likely to enhance abiotic decomposition.

Soil-litter mixing through erosional processes causes litter to be partially to fully buried by soil, modifying dryland decomposition through several processes. Field studies in diverse dryland locations have found a positive relationship between soil-litter mixing and decomposition rates (e.g., refs. 45 and 46). Laboratory studies indicate that soil-litter mixing can buffer litter from desiccation, extending windows of opportunity for microbial decomposers (17, 47). Soil that covers litter will also buffer litter from temperature extremes. Additionally, soil-litter mixing can enhance colonization by bacterial decomposers (48). It may also enhance surface area available for microbial degradation by physically abrading litter surfaces (21), although this mechanism currently lacks field evidence. In contrast, soil-litter mixing can decrease photodegradation as even a small amount of soil covering litter may negate both direct and indirect mechanisms of photodegradation (37, 49).

Microsite Conditions Vary: Hypothesized Effects on Microsite-Specific Decomposition Rates. Few studies in any biome have parsed out decomposition differences among microsites, but the extreme heterogeneity in abiotic conditions among dryland microsites suggests that accurate up-scaling of decomposition in

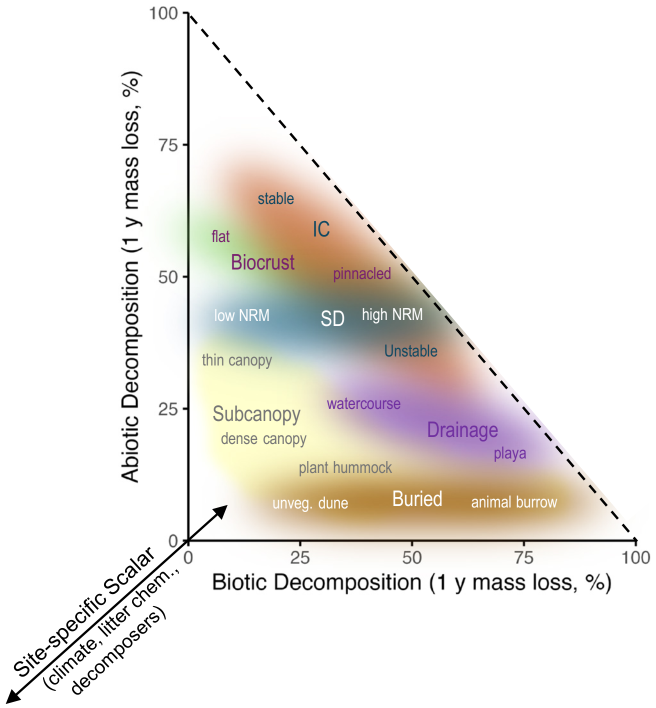

Fig. 3. Hypothesized microsite-specific decomposition rates within a dryland ecosystem. Litter in different microsites (colored clouds) experiences different biotic (*x*-axis) and abiotic (*y*-axis) decomposition drivers. The sum of biotic and abiotic drivers is represented as the decomposition rate (percent mass loss in 1 y). The dashed line represents the maximum possible decomposition rate (100% mass loss in 1 y). Site-specific properties (e.g., climate, litter and soil chemistry, and the decomposer community present) influence overall decomposition rates, represented as a scalar value on the third axis that modifies the decomposition rate (positively or negatively) for the entire site. Biotic decomposition is expected to be greatest in microsites where litter experiences soil-litter mixing, retaining moisture and increasing decomposer organism activity. Abiotic decomposition is expected to be greatest where litter has high solar radiation and temperature exposure, such as single layers of litter on the soil surface. Many of the microsites are represented by large clouds, indicating an expected range of abiotic and biotic drivers. Intercanopy ("IC") is litter lying on the soil surface away from plant canopies. For standing dead ("SD"), biotic decomposition is affected by the amount of nonrainfall moisture ("NRM") from fog, dew, or atmospheric relative humidity. The gap at the top of the abiotic axis reflects that abiotic decomposition alone is not expected to drive very high decomposition rates.

these systems necessitates inclusion of microsite-specific data. Characterizing the differences in dominant biotic and abiotic drivers in key microsites where litter accumulates and decomposes will allow us to better constrain decomposition predictions (Fig. 3). While the importance and distribution will differ among drylands with different vegetation structure, geomorphology, and surface processes, we outline here key microsites for litter decomposition that are common across most drylands. Predicted environmental conditions (moisture, temperature, solar radiation, and soil-litter mixing) for each microsite type and their impacts on decomposition rates are synthesized in Table 1 and described in detail in *SI Appendix, SI Text: Litter Accumulation Microsites: Environmental Conditions and Decomposition Rates*.

Intercanopy spaces are areas in between plant canopies. Intercanopy is the dominant microsite type in most drylands, although frequent transport of litter from these areas means litter pools tend to be low on an areal basis. We hypothesize that average decomposition rates for intercanopy litter will be moderate, with abiotic decomposition from solar radiation and thermal degradation of high importance due to high litter exposure to radiation, particularly in drylands with stable surface soils. We use intercanopy spaces as a comparison when describing decomposition rates in other microsites given the prominence of studies in this microsite.

Standing dead is senesced material that remains attached to a plant, such as quiescent material on perennial bunch grasses. The vertical orientation and distance above the ground will generally reduce temperature and solar radiation, while nonrainfall moisture inputs increase with height above the ground (50–52). We hypothesize that decomposition rates for standing dead will be moderately low, with abiotic decomposition driven by solar radiation and pulses of biotic decomposition in systems where standing dead is wetted by nonrainfall moisture.

Buried litter is completely covered by soil. This burial may occur through soil-litter mixing, litter falling into depressions such as foraging pits, or belowground transport by animals (16). We hypothesize high average decomposition rates for buried litter, with decomposition driven by biotic processes and with inconsequential abiotic decomposition.

Plant subcanopies contain litter that was deposited by plants and retained within the subcanopy or moved into the subcanopy by horizontal transport processes. We hypothesize that decomposition rates beneath plant subcanopies will be low relative to intercanopy microsites, with low to moderate abiotic decomposition from photodegradation and thermal degradation (depending on canopy shading) and moderate biotic decomposition activity.

Small litter retention elements (e.g., rocks, dead wood; Fig. 2*A*) resist litter transport by wind or water, causing litter to accumulate next to or underneath them. Modification of microclimate and decomposition processes are similar to those for plant subcanopies but are affected by litter retention element characteristics (e.g., size, shape, amount of material retained). We hypothesize moderate decomposition rates that are similar to intercanopy rates. Modification of the microclimate will often lead to slight increases in biotic decomposition while abiotic decomposition from solar radiation and photodegradation will be reduced relative to intercanopy.

Soil crusts, including biological soil crusts ("biocrusts") and physical crusts, are dominant features in many drylands that can accumulate litter on rough surfaces. We hypothesize that average decomposition rates in these conditions will be moderate, similar to intercanopy areas, with pinnacled biocrusts slightly depressing abiotic decomposition from solar radiation and photodegradation, while also enhancing biotic decomposition.

Ephemeral watercourses such as dry washes, streams, and rivers accumulate material transported by aeolian or fluvial processes. We hypothesize that average decomposition rates in these conditions will be high relative as occasional flooding will enhance biotic decomposition, counteracting decreases in photodegradation from shading.

Playas accumulate litter transported via overland flow or ephemeral watercourses. Litter in playas is likely to quickly become buried due to depositional processes, so we hypothesize high average decomposition rates and dominance of biotic processes, despite possible slowing by saline conditions.

Study Overview. We tested our microsite-specific decomposition hypotheses (presented above) using meta-analysis of decomposition data from published studies that include contrasting microsites. We focused on leaf litter due to its dominance in litter pools and the literature, using "decomposition" to describe declines in leaf litter mass through time. To explore the consequences of including microsite differences when scaling to the landscape level, we extrapolated landscape-level decomposition rates for several idealized dryland systems by combining microsite-specific decomposition rates with estimates of microsite-specific litter

Table 1. Key decomposition microsites where litter accumulates and decomposes in dryland ecosystems, with a description of environmental conditions and subsequent decomposition rates and dominant drivers in each microsite

Microsite	Moisture	Temperature	Solar radiation	Soil-litter mixing	Decomposition rates	Dominant drivers
Intercanopy spaces (surface exposure between plant canopies)	Low and variable, with rapid dry down after wetting	Very high but variable due to exposure	Very high due to exposure	Moderate, depending on surface stability	Moderate	**Abiotic**: solar radiation and thermal degradation
Standing dead	Low but variable, susceptible to nonrainfall moisture	Moderate, responsive to air temperature	Moderate, depending on orientation	None	Moderately low	**Abiotic**: solar radiation **Biotic**: during moisture pulses
Buried litter	High, soil cover retains moisture	Low, buffered by soil cover	None	High	High	Exclusively **biotic**
Plant subcanopies	Moderate, canopy alters moisture inputs and losses	Low due to canopy shading	Low due to canopy shading	Variable, depending on soil stability	Low	**Biotic** processes dominate
Small litter retention elements (LREs; rocks, dead wood)	Moderate, thick litter layer and LRE structure retain moisture	Moderate, reduced by litter layer and LRE shading	Moderate, reduced by litter layer and LRE shading	Moderately high, soil and litter both accumulate	Moderate	**Abiotic**: reduced relative to intercanopy **Biotic**: enhanced relative to intercanopy
Soil crusts	Moderate, moisture may be retained by biocrust and accumulated litter	Moderately high, some reduction by pinnacled biocrust and accumulated litter	Moderately high, some reduction by pinnacled biocrust	Low	Moderate	**Abiotic**: reduced relative to intercanopy **Biotic**: enhanced relative to intercanopy
Ephemeral watercourses	Moderate, enhanced by irregular flood events	Moderate, shade from canopies and accumulated litter	Low: reduced by canopies & LRE structures and clumps	High	High	**Biotic**: high from flooding & shading **Abiotic**: reduced relative to intercanopy
Playas	High, water inputs from flooding and moisture retention in finely textured soils	Moderate, reduced by flooding or soil-litter mixing	Moderate, reduced by flooding or soil-litter mixing	High due to flooding	High	**Biotic**: pulses follow flooding **Abiotic**: high only for surface exposed litter

Additional details on microsites are available in *SI Appendix, SI Text: Litter accumulation microsites: Environmental Conditions and Decomposition Rates*.

pool sizes and areal extent. We supplemented available literature data with observations from decades of research in the deserts, which were selected for their visually apparent differences in litter distribution. We hypothesize that landscape-level decomposition rates that combine microsite-specific decomposition rates and pool sizes will be faster than estimates based on intercanopy rates and pool sizes.

Results

Most of the 146 dryland decomposition studies that we compiled examined litter decomposition in only one microsite (58%), with the most common microsites open intercanopy (72%) and subcanopy (16%). Microsite could not be determined from reported data in 18% of studies; many of these were contrasts across land-cover treatments or topography. Filtering publications to fit our microsite, climate, and time constraints yielded 23 studies with 64 unique cases that we included in the meta-analysis (Fig. 1 and *SI Appendix*, Table S2). These provided sufficient data to test our hypotheses on intercanopy decomposition rates relative to those of standing dead, buried litter, and litter beneath woody plant canopies using meta-analysis. There was a large range in decomposition rates for the intercanopy across all studies, with mean mass remaining in litter exposed for approximately 1 y (8 to 12 mo) of 62.2% and a range of 20.1 to 92.5%. There were no relationships with annual mean climate variables.

Meta-Analyses for Microsite-Specific Decomposition Rates. When decomposition of litter suspended above the surface (to simulate standing dead) was contrasted with surface litter, there was no difference in effect size (Fig. 4*A*; log response ratio for mass remaining = 0.04, $P = 0.24$). Thus, this did not support our hypothesized low decomposition of standing dead relative to intercanopy litter. However, this lack of effect masks substantial underlying variation in responses for specific litter species and studies, with a similar number of cases where litter decomposition was greater for standing than surface litter, greater for surface than suspended litter, and where there was no difference between these microsites. There was a large range in absolute decomposition rates among suspended litter cases included in the meta-analysis, with mass remaining after 1 y varying from 38.9 to 93.5% (*SI Appendix*, Fig. S2*A*).

Buried litter enhanced decomposition relative to surface litter in most cases (Fig. 4*B*), supporting our hypothesis (log response ratio for mass remaining = 0.24, $P < 0.01$). There was a large range in absolute decomposition rates among buried litter cases, with mass remaining varying from 19.0 to 93.3% (*SI Appendix*, Fig. S2*B*).

Decomposition was generally slower for litter under woody canopies than for intercanopy litter (Fig. 4*C*; log response ratio for mass remaining = −0.13, $P < 0.05$), although there were some cases with greater subcanopy than intercanopy decomposition. Subcanopy mass remaining after 1 y varied from 32.1 to 91.0% (*SI Appendix*, Fig. S2*C*).

Many of the microsites that we identified as important litter accumulation locations had insufficient data for inclusion in the meta-analysis. While repeated observations show that litter accumulates disproportionately next to physical objects (e.g., rocks and dead wood) and among biocrust pinnacles, we did not find any decomposition data from these locations. We also found no data probing decay in ephemeral watercourses and the single study assessing decomposition in a dryland playa did not contrast results with other microsites (53).

Landscape-Level Decomposition Rates–Consideration of Microsites. Our exploration of landscape-level patterns in dryland landscapes suggests that consideration of microsites can substantially impact estimates of landscape-level litter pools and decomposition rates (Fig. 5). Subcanopy microsites dominated the litter pools in both the Colorado Plateau and the Sonoran Desert (Fig. 5 and *C*; 92% and 69%, respectively). In contrast, the Namib Desert was distinct in that subcanopy litter only accounted for 6% of the total pool (Fig. 5*B*). However, at this site buried and standing dead litter (22% and 33%, respectively) are concentrated around the same plant hummocks that constitute the subcanopy pools, making more than 60% of the litter pools concentrated in sparsely distributed plant hummocks. Litter pools were roughly an order of magnitude higher in the Colorado Plateau and Sonoran Desert than the Namib Desert. In all three dryland sites, litter pools were substantially underestimated if extrapolated from intercanopy areas alone, with the greatest underestimate for the Colorado Plateau where the intercanopy accounted for 4% of landscape-level litter. Landscape-level decomposition rates (Fig. 5 *D*–*F*) reflected in part the distribution of litter among microsites, but also the microsite-specific decay rates. Landscape-level decomposition was dominated by subcanopy litter in the Colorado Plateau and Sonoran Desert (73% and 64%, respectively). In contrast, buried litter account for the greatest percentage of landscape-level decomposition in the Namib Desert (70%). Similar to litter pools and supporting our hypothesis, landscape-level decomposition was substantially underestimated if based on intercanopy area alone.

Discussion

Microsite-Specific Decomposition Differences.

Intercanopy litter. The large range in decomposition from intercanopy spaces seen in this study (29 to 92% mass remaining after 1 y) likely reflects the variability in site conditions, climate,

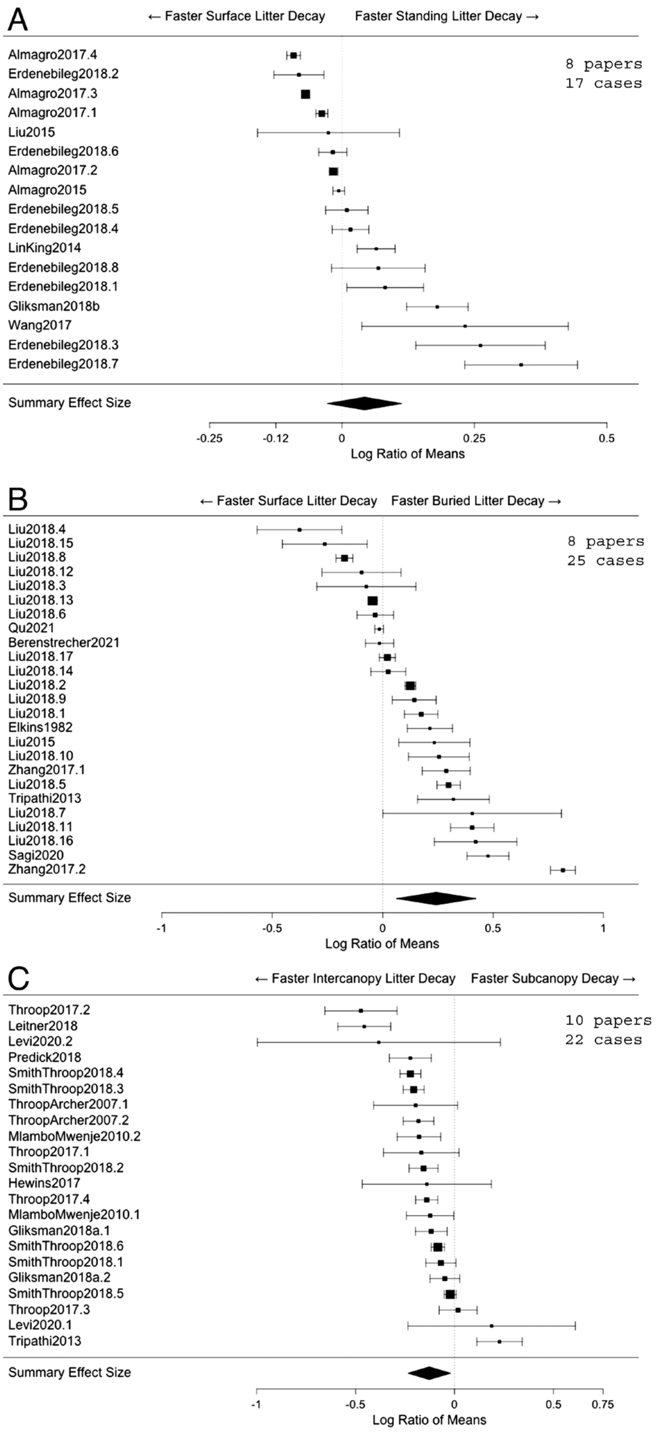

Fig. 4. Caterpillar plots (forest plots with ordered estimates) of log response ratios of litter mass remaining from manipulative studies where litter was decomposed on the soil surface in contrast with (*A*) suspended above the surface, (*B*) buried, or (*C*) under woody plant canopies. For each panel, individual cases (a unique study, litter species, and location combination) are represented by squares and error bars. The zero line represents no difference between surface and contrasting microsite decomposition. Negative log response ratios (to the left of the vertical zero line) indicate greater decay rates on the surface than the microsite contrast while positive log response ratios indicate faster decay in the microsite contrast than on the surface. The size of the square symbol represents model weight in the meta-analysis. The summary response across all cases for each of the three microsite contrasts is illustrated as a diamond at the bottom of each panel. The number of papers and cases with unique species and geographic location combinations are shown for each contrast. Details on the study location, climate, and litter species are available in *SI Appendix*, Table S2.

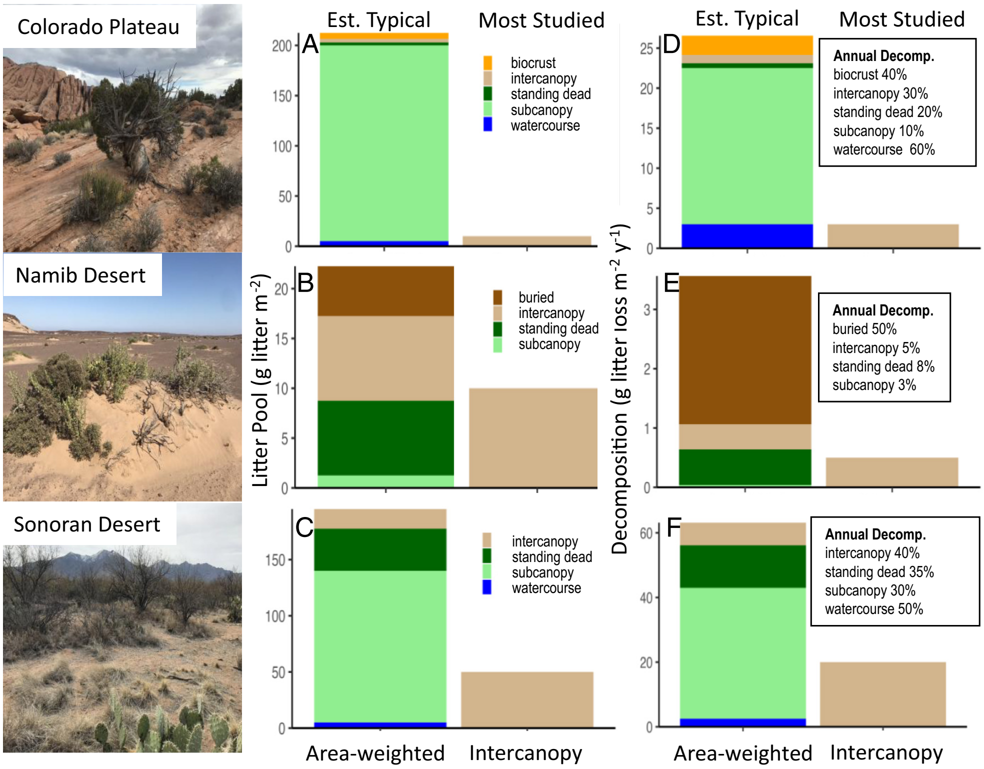

Fig. 5. Estimated litter pools and decomposition rates for three different dryland sites. For litter pools (*A*–*C*), the stacked bars ("Est. Typical") represent area-weighted estimates expected to be typical for how litter is distributed among microsites in drylands. Litter pools were calculated from litter pool estimates for each dominant microsite multiplied by the proportional microsite area. In contrast, the tan bars ("Most Studied") represent the values estimated if litter pools were based entirely on intercanopy data, given the predominant use of this microsite in the decomposition literature. Landscape-level decomposition rates, the mass per area of litter lost to decomposition annually (g litter loss m^{-2} y^{-1}; *D*–*F*), were calculated as the litter pool (*A*–*C*) multiplied by the expected percent of litter decomposed each year (see *Inset* boxes in panels *D*–*F* for microsite-specific decomposition). See *SI Appendix*, Table S3 for data sources and assumptions.

experimental design, and litter characteristics (e.g., litter quality, litter mass:area, litterbag mesh size, etc.) at the different study sites. We only included intercanopy litter with no radiation manipulation in this study, but studies comparing decomposition with full solar radiation exposure relative to litter under filters (blocking some wavebands) consistently show that photodegradation is an important component of intercanopy decomposition. Two meta-analyses attribute ~23% of intercanopy decay to photodegradation (19, 20). However, it is difficult to separate thermal degradation from photodegradation and enhanced temperatures may be responsible for some portion of the reported photodegradation responses (33). Shading by soil or multiple litter layers can completely block photodegradation in intercanopy locations in natural systems (49, 54), and studies set up to explore photodegradation often employ experimental techniques that inadvertently maximize its effects (e.g., single litter layer, soil-litter mixing restricted; 21) or alter other microclimate parameters (e.g., precipitation and temperature; 19). Without explicit manipulation or characterization of abiotic factors present, it is difficult to parse out the relevant driving variable. For example, data comparing decomposition in intercanopy versus subcanopy locations in Arizona, USA, showed higher decomposition in intercanopy areas than under shrub canopies, consistent with photodegradation being the driver. However, when the shrub canopy was removed, low decomposition rates were obtained, showing the driver was, instead, the amount of soil-litter mixing (55). Similarly, intercanopy litter decomposition in a Mediterranean olive grove was attributed to soil-litter mixing, as photodegradation was blocked with filters and a strong positive relationship existed between soil-litter mixing (a function of hillslope location) and decay rates (46). Site-specific conditions such as soil surface stability, solar radiation intensity, and nonrainfall moisture are infrequently reported but have the potential to be important decomposition drivers, as reflected in the large range in reported decomposition rates. Greater consistency in cross-study experimental design, such as reporting litter mass:area ratios in experimental decomposition experiments (21) and characterizing of microsite environmental conditions may ultimately provide key data needed to better resolve intercanopy decomposition patterns and processes.

Standing dead decomposition. Our hypothesis that decay would be moderately low for standing dead (and lower than surface litter) was not supported. However, the meta-analysis also indicated a wide range of response functions (Fig. 4), suggesting that further experimental studies are needed to describe the site and litter-specific decomposition responses for standing dead litter. For example, one of the cases with faster decomposition of standing dead than surface litter was in a Mediterranean climate, where accelerated standing dead decomposition was attributed to nonrainfall moisture. This hypothesized driver was supported by short-term measurements where microbial respiration was positively related to litter moisture content (50). Ecologically meaningful nonrainfall moisture inputs have been documented in drylands throughout the globe (56), with data from sites ranging from hyperarid to mesic, suggesting that standing dead litter is moist from nonrainfall sources for a longer duration annually than from rainfall (29). For example, standing dead wetted by nighttime dew in the Namib Desert was moist (reaching ~20% gravimetric moisture) from ~1900 h to ~0900 h, drying out as air temperature rose and relative humidity dropped (29). However, site-specific climate and structural features will dictate the importance of this moisture source. While several studies have documented that nonrainfall moisture in drylands systems can stimulate standing dead decomposition in terms of measurable respiration, mass loss, and microbial colonization (29, 57, 58), a lack of comparisons with other microsites limits our ability to assess whether these dynamics are unique for standing dead. We expect variability in standing dead decomposition with litter orientation, given the potential for orientation to affect abiotic conditions. For the experimental data that we compiled, most studies suspended litter horizontally above the soil surface, which may increase the role of photodegradation. Horizontal orientation of suspended litter may limit its applicability as a simulation of standing dead, particularly for grasses, which account for a large portion of persistent standing dead in many drylands. There were insufficient studies with vertical litter orientation to quantitatively assess whether orientation impacted decomposition. Finally, one paper in the meta-analysis illustrates the potential importance of litter type in influencing results, in that different species from this single study covered much of the span between the highest and lowest difference between surface and standing litter in the entire meta-analysis (59).

Buried litter. Our hypothesized high decomposition of buried litter was supported by the meta-analysis results, with decomposition rates likely increased by buffered temperature and moisture regimes that enhance biotic decomposition. Favorable environmental conditions for buried litter decay have been tracked in a few studies: in a cold desert system in China, litter buried at 10 cm had less diurnal variation in temperature and, on average, greater and more stable relative humidity than did surface litter (60). Differences in litter temperature and moisture may directly enhance decomposer abundance or activity. For example, decomposition of litter from an introduced leguminous tree (*Colophospermum mopane*) in an arid grassland in India was greater for buried than surface litter, with enhanced decay associated with increased faunal abundance and nutrient availability (61). If enhanced decomposition of buried litter is associated with more favorable conditions for decay, it is likely that the relative impact of burial on decomposition will differ with environmental variability in burial depth, space, and time. Burial enhancement of decay of *C. mopane* was greater at shallow than deeper depths (3 to 7 and 8 to 12 cm, respectively), with faunal abundances and nutrients also declining with depth (61). The temporal variability of burial is illustrated with a decomposition study in North America's Chihuahuan Desert that used different initial litterbag deployment dates. While decomposition was faster for buried than surface litter across the study, there was greater mass loss in surface litterbags when litter was deployed during the wet summer months, as termites colonized the surface litterbags (62). Species-specific litter traits may also influence litter burial outcomes. One study included in the meta-analysis reported data from 17 species, accounting for the majority of our cases (60). This study reported overall faster decomposition in buried than surface litter, but individual species responses included positive to negative effects of burial on decomposition (Fig. 4*B*). In that study, decomposition rates were positively related to litter specific leaf area (surface area per unit mass) for both surface and buried litter; it is not clear whether specific leaf area affected the decomposition rate of buried litter relative to surface litter. It is interesting to note that this single study with a large number of cases (60) took place in a desert with unstable, sandy soil surfaces. Decomposition rates were quite high for all species and conditions, with mean mass loss across species of 52% for surface litter and 56% for buried litter over a 1-y period. A challenge to interpreting the meta-analysis results is that we restricted studies to those using experimental litter burial, and these burial treatments may not mimic conditions experienced by naturally buried litter. For example, bandicoot foraging pits in Australia (~7 cm deep) have greater soil moisture content than undisturbed soils, potentially speeding decomposition of fine litter that accumulates in these pits (63). Similarly, microclimate differences appear to be the driver of litter losing twice as much mass when buried in artificial isopod burrows as surface litter (64). However, mass loss was greater still in natural isopod burrows than artificial ones, perhaps the function of a difference in nutrients or the decomposer community (64, 65). This pattern was also present in buried leaf litter in fungal-infested termite galleries, which decayed up to four times faster than that in termite-free areas (66). These data collectively support the idea that buried litter had rapid decay dominated by biotic processes, with greatest decay likely in sites such as animal burrows where environmental conditions and decomposer organisms are most favorable for decay.

Plant subcanopy litter. Results from the meta-analysis supported our hypothesis that litter decomposition is typically faster in intercanopy relative to subcanopy microsites. Intercanopy decomposition may be dominated by abiotic processes, whereas differences in site and canopy types may result in a range of microsite conditions. Lower subcanopy decomposition rates were expected due to canopy-induced reductions in temperature, moisture, solar radiation, and soil-litter mixing. However, it is challenging to tease apart which driver(s) or interactions among drivers are responsible for reduced decomposition, as all woody canopies are likely to modify multiple decomposition drivers. For example, litter decomposition in a Sonoran Desert grassland was reduced in shrub subcanopy locations relative to intercanopy locations, as would be expected if photodegradation was a driver (67). However, UV-B filters in this study did not depress decay in either intercanopy or subcanopy microsites. Reduced subcanopy decay could be due to any possible combination of changes in subcanopy temperature, moisture, or soil-litter mixing, and it could be affected by other wavebands of solar radiation (67). In other examples, slow subcanopy decomposition was linked to decreased soil-litter mixing at sites in the southwestern United States where shrub canopies facilitate dense grass growth or litter layer development. Manipulative studies of woody canopy cover were needed to separate out direct impacts of the canopies from those mediated by factors that influence soil-litter mixing (55, 68). This raises the important caveat in interpreting woody plant canopy impacts on subcanopy decomposition of the range in size and structure of canopies, with canopy differences potentially strongly affecting abiotic conditions and subsequent litter decomposition. For example, woody plant size strongly affected *C. mopane* leaf litter decomposition (intercanopy > under small canopy > under large canopy) in a Zimbabwean semiarid savanna (69). While most studies found slower subcanopy decomposition, there were exceptions that suggest different drivers may be at play in some sites. Greater subcanopy decomposition in the case of the nitrogen-fixing plant *C. mopane* in a nonnative habitat was attributed to greater nutrient availability and decomposer activity supported by high-nitrogen litter (61). In contrast, the absence of canopy impact on decomposition in a coppice dune system in the Chihuahuan Desert was attributed to high decomposition through soil-litter mixing, regardless of location relative to canopies (70).

Small litter retention elements (e.g., rocks, dead wood). While casual observations suggest that litter can accumulate disproportionately next to physical objects, we are not aware of quantitative data that explore decomposition patterns in these locations. This is an important area for future study.

Biological and physical soil crusts. We are not aware of studies measuring decomposition rates for litter lodged within biocrust pinnacles. However, an experimental warming study in the Colorado Plateau (USA) found that degradation of soil crusts from warming decreases soil stability, thus increasing soil-litter mixing. In this case, soil-litter mixing enhanced decomposition relative to intact biocrusts in the control plots, although moisture reduction from warming counteracted these effects (71). Given the extensive area covered by crusts and their widespread degradation (72), impacts of crust on litter decomposition is an area ripe for future study.

Ephemeral watercourses. We found no comparative data examining decay rate differences between ephemeral watercourses and other microsites. Flooding of ephemeral watercourses can lead to pulses of rapid mass loss (73), with colonization by decomposers and aquatic macroinvertebrates occurring during flood events (74). Wetting and drying cycles from flood events also influence litter chemical changes during decomposition, with rapid loss of dissolved organic carbon (DOC) following initial wet-up and smaller losses with subsequent wet-ups (75). Abiotic decomposition processes have also been documented in ephemeral watercourses, with exposure of litter to UV in dry floodplains influencing the DOC chemistry during later flooding (76). Future efforts to characterize litter dynamics in ephemeral watercourses will fill a critical need, particularly if they consider the movement dynamics of litter into and through watercourses as well as decomposition rates.

Playas. We are aware of only one decomposition study in a dryland playa, where decomposition of grass litter was rapid in litterbags submerged during seasonal flooding (roughly 60% mass loss in 6 wk; 53). Substantial mass loss occurred from leaching, with evidence for some microbial decay. High salinity and ephemeral inundation resulted in little macrofaunal activity (53). High soil organic carbon in playa soils in the northern Chihuahuan Desert was positively associated with vegetation cover and area of the surrounding watershed (77), suggesting that litter and/or dissolved organic matter inputs are substantial in playas. Future assessment of litter inputs into playas and their decomposition dynamics will be important for understanding C and nutrient dynamics in internally drained drylands.

Landscape-Level Decomposition Rates–Consideration of Microsites. Our synthesis suggests that microsite-specific differences in decomposition rates can substantially impact landscape-level estimates (Fig. 5) in the three selected drylands. Litter distribution among microsites differs with vegetation and surface transport dynamics in these three drylands. For example, the Namib Desert dune system has highly erosive winds. This results in 22% of the litter being buried by sand, while this is a relatively minor pool in the other two drylands. The importance of perennial grass cover differs widely among drylands, and high grass cover contributed to large standing dead pools in the Namib and Sonoran Deserts (34% and 19%, respectively), as well as increasing the number of litter retention elements. As estimated values for litter pools based on microsite area-weighted are much higher than those obtained from using only intercanopy estimates, the critical importance of using microsite-level data for estimating landscape decomposition rates is underscored. A critical paucity of data exists at present on litter pools in general (78, 79) and this is magnified in dryland regions, given both limited available data and challenges to accurately measuring dryland litter pools.

Using microsite-specific decomposition rates also substantially shifted the picture of where most decomposition in a given system was occurring. For example, in the Namib Desert the highest microsite-specific decomposition rates occurred in buried litter (70%) despite this microsite accounting for only 22% of the landscape litter pool. In contrast, the Colorado Plateau watercourse microsites had disproportionately high decomposition losses. Not surprisingly, our estimate of area-weighted landscape-level decomposition rates showed a substantial difference (3.5 to 63 g litter loss m^{-2} per year) among the contrasting desert types we examined.

Our most important finding was that in all cases, landscape-level decomposition losses were many times greater when calculated using an area-weighted approach rather than using intercanopy data only. While the estimates of litter pool size and decomposition rates are based on both data and observation, and thus represent an educated guess, they serve to illustrate the crucial importance of considering microsite pools and conditions when estimating C and nutrient cycling dynamics in dryland settings. Future detailed characterization of decomposition that embraces the complex distribution and transport patterns among microsites is critical for moving our understanding of biogeochemical cycling in these systems forward.

Conclusions and Synthesis. Results from dryland decomposition models frequently underestimate directly measured rates. Our meta-analysis suggests that the almost-exclusive use of rates obtained from intercanopy studies misrepresents dryland decomposition rates. Our study shows an accurate portrayal of decomposition rates for a given location requires considering rates from all the dominant microsite types. Many of these often-ignored microsites, despite being more spatially limited than the intercanopy, have such high rates of decomposition their inclusion substantially raises the landscape-level decomposition rate. Thus, including diverse microsites in decomposition studies will likely resolve much of the mismatch between models and observations. Our findings have important implications for improving global C and nutrient models (78, 80, 81), as drylands contribute substantially to global values (2, 82). Environmental changes such as climate change and land use (e.g., livestock grazing, settlements) will reshape microsite distribution and function in drylands, underscoring the importance of including consideration of these microsites in biogeochemical studies and modeling synthesis efforts.

Methods

Meta-Analysis of Microsite-Specific Decomposition Rates. We systematically searched Web of Science (www.webofknowledge.com) to compile a comprehensive list of dryland leaf litter decomposition studies using all possible combinations of a dryland climate description (dryland, desert, arid, semiarid, hyperarid, mediterranean) and a description of decomposition (decompos*, litter, degrad*; where * is a wildcard). We also added papers not captured by the formal literature search that were included in the *aridec* database (83), known to us from reading the literature, or referenced in papers captured by the literature search. We excluded papers with intensive land use (e.g., tilling) or in constructed environments or growth chambers. We screened this list to include studies that contrasted surface leaf litter decomposition in intercanopy open areas with decomposition in one or more of the possible microsite contrasts to test our hypotheses: standing dead, buried, beneath woody plant canopies, small litter retention elements, soil crusts, ephemeral watercourses, or playas. Given that most dryland decomposition studies to date have quantified loss of surface leaf litter in spaces among plant canopies, we consider the intercanopy locations the default microsite for comparisons. We included studies only when leaf litter from the same species was used in the contrasting microsites, litter was contained in litterbags or some similar structure (e.g., litter cages), solar radiation was not manipulated (data from control treatments in UV studies were included if other criteria were satisfied), data were reported as mass remaining (or mass loss, in which case we converted the data to mass remaining for consistency) at one or more times since exposure (papers that reported only the decay constant, *k,* were excluded), and the samples size and SD or SE were reported. We acquired mass remaining or mass loss data either from published tables or by estimating values from figures using WebPlotDigitizer (84). We compiled ancillary information on vegetation type, microsite characteristics, and litter mass:area of litterbags when reported. While litter quality can be an important predictor of decomposition (85), we did not include any litter quality metrics in our analysis due to insufficient comparable data. We obtained modeled annual mean climate data (1970 to

2000) for each site as potential evapotranspiration and aridity index (AI) from the Global Aridity Index and Potential Evapotranspiration Database v.3 (86) and temperature and precipitation from WorldClim 2.1 (87). We categorized climate for each site based on AI (<0.03 = hyperarid, 0.03–0.2 = arid, 0.2–0.5 = semiarid, 0.5–0.65 = dry subhumid). Studies with AI > 0.65 were excluded.

We carried out meta-analyses using the *metafor* package (88) in R (89), calculating effect sizes from litter mass remaining as log response ratios in which we contrasted mass remaining for surface litter in open microsites with that of the previously defined microsite contrasts. Due to insufficient data for many of our defined microsites, we were able to conduct meta-analyses only for standing dead (typically simulated by suspending litter above the ground), buried litter, and woody plant subcanopy litter. Many of the studies presented data from more than one litter species, study location, or season. We maintained each of these separate "cases" and calculated effect sizes for each. We included in the meta-analyses only the single collection time per study that was closest to 12 mo but between 8 and 16 mo. Studies shorter than 8 mo were excluded. We modeled the net effect size of the three microsite contrasts using the rma.va function in *metafor*. As we assumed that cases were not entirely independent (e.g., the same location and experimental design particularities would lead to greater similarity between cases within than across studies), we treated study as a random variable in the meta-analyses.

Landscape-Level Decomposition Rates. We tested our hypothesis that landscape-level decomposition rates that combine weighted (based on areal extent) microsite-specific decomposition rates and pool sizes will be faster than estimates based on intercanopy rates and pool sizes by estimating landscape-level decomposition rates for three dryland sites based on microsite-specific litter pools and decomposition rate estimates, using data and observations. The three dryland sites represent a hot desert with a relatively flat, stable surface (Sonoran Desert), a hot desert with an unstable surface (dune field in the Namib Desert), and a cold desert with a rolling to pinnacled stable surface (Colorado Plateau). For each site, we first identified 4 to 5 dominant microsites. For each microsite, we estimated the standing litter pool (g litter m^{-2}) and the proportion of site area covered by that microsite. We multiplied these values to obtain a site-level litter pool estimate that was area-weighted by microsite. We contrasted these area-weighted litter pool estimates with the litter pool estimates from that assuming 100% cover by intercanopy microsites, as these are the sites most frequently used for decomposition studies. We estimated microsite-specific decomposition (percent litter lost via decomposition per year) for each microsite by site combination and calculated landscape-level decomposition based on the area-weighted litter pools and microsite-specific decomposition rates. As with the litter pool estimates, we contrasted landscape-level decomposition rates that were calculated using area-weighted microsite values with those calculated only from intercanopy microsite values. For all estimates, we used available data where possible and filled in additional values as plausible based on predictions for microsite-specific decomposition from our meta-analysis and our own experience in these systems (see *SI Appendix*, Table S3 for details on data sources and assumptions).

Data, Materials, and Software Availability. Previously published data were used for this work (*SI Appendix*, Table S1).

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