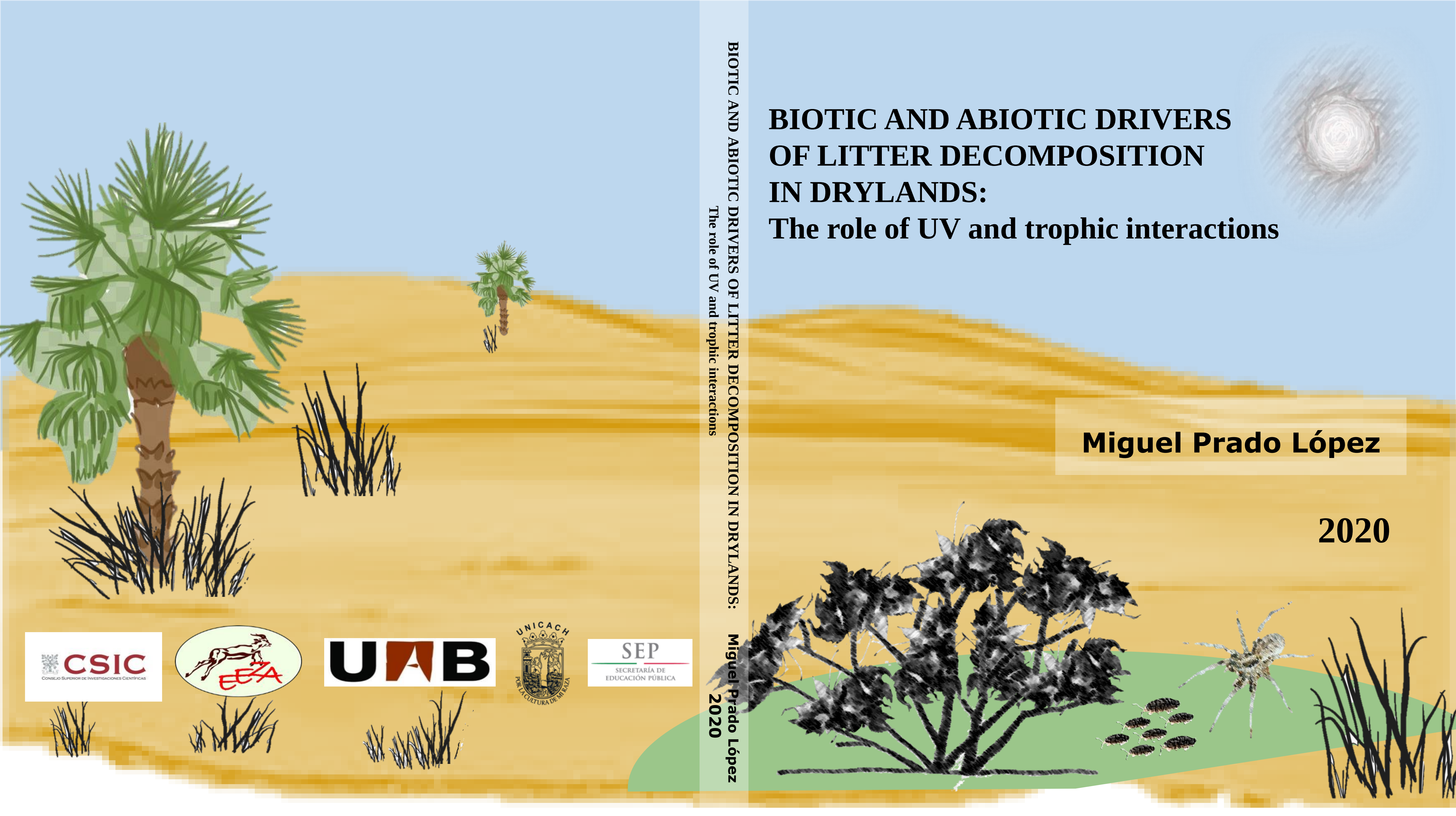

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The role of UV and trophic interactions
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# BIOTIC AND ABIOTIC DRIVERS OF LITTER DECOMPOSITION IN DRYLANDS:

## The role of UV and trophic interactions

PhD Thesis

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# Abstract

Decomposition returns to the soil more than 50% of primary productivity and provides the main source of energy and nutrients to complex detritus-based soil food webs. In terrestrial ecosystems, decomposition is hierarquically governed by climate, litter quality and soil biota. However, in drylands decomposition seem to be governed by complex abiotic/biotic interactions that are largely unknown. The main objective of this thesis was to study the interactions of these abiotic and biotic factors that control decomposition in a semi-arid ecosystem. As a first objective I assessed the effects of UV radiation and microbial activity in the early stage of decomposition, and explore the legacy effects of these two components on a later stage of decomposition involving detritivores (isopods) (**chapter 2**). In a laboratory experiment UV radiation accounted for a small proportion (<3%) of the total litter decomposition and no photopriming effects were observed. Contrary to UV radiation, microorganisms had a paramount role during decomposition through legacy effects on detritivores, as we found substantial cumulative effects of microbes and detritivores adding up to 42% of total decomposition (**chapter 2**). The latter promoted the expression of synergistic effects in litter mixtures (**chapter 2 and 3**) and worked as a link between predator and litter decomposition (**chapter 3**). In addition, the removal of microorganisms by biocides reverted litter mixture synergistic effects and gave rise to antagonisms among litter species (**chapter 2**). In summary, UV radiation had a minor effect as compared to microbes in their legacy effects on detritivore-driven decomposition. The aim of **chapter 3** was to evaluate the multiple effects of predators on decomposition via indirect consumptive and non-consumptive effects, and via ecological engineering effects, and how they may generate synergies with litter mixtures (**chapter 3**). Despite the high impact of predators on the detritivores (both on mortality and on behavior), multiple synergistic predator engineering ecosystem effects with the identity and diversity of the litter, prevailed over predator top-down control, making predators to enhance rather than inhibit decomposition. These results suggest that the traces of predator activity (e.g. excreta) provide with some extra nutrients that can boost microbial activity and ultimately benefit secondary decomposers and accelerate decomposition. In **chapter 4** I assessed the role of fertility islands on decomposition of leaf litter mixtures in drylands. Decomposition under shrub canopy consistently showed antagonistic effects and slower decomposition differently depending on the

identity of the litter species. On the contrary, decomposition away from shrubs resulted in mostly additive effects, with only a mild synergy in one of the species. Unexpectedly, no diversity (richness) effect was found. As we also found far more mesofauna in decomposition mesocosms under shrubs, the results suggest that mainly biotic-driven decomposition operates under shrubs and abiotic-driven decomposition operates away from shrubs. The information provided by this thesis may help understanding how litter decomposes in drylands, where it may remain either on the plant or on the ground, and to understand the interaction between abiotic and biotic factors, which have effects difficult to disentangle when predicting decomposition in these ecosystems.

# Resum

La descomposició retorna al sòl més del 50% de la producció primària i aporta la font principal d'energia i nutrients a la complexa xarxa tròfica del sòl, basada en detritus. En ecosistemes terrestres la descomposició està dirigida de manera jeràrquica pel clima, la qualitat de la fullaraca i la biota del sòl. Tanmateix, en zones àrides la descomposició sembla dirigida per complexes interaccions bio-abiòtiques que són prou desconegudes. L'objectiu principal d'aquesta tesi va estar estudiar aquestes interacciones en un ecosistema semi-àrid. Com a primer objectiu es va estudiar els efectes de la radiació ultraviolada (UV) en l'activitat dels microbis en les primeres etapes de la descomposició, i es van explorar els efectes de legat d'aquests dos components en un estadi posterior de descomposició que involucrava els detritívors (isòpodes) (**capítol 2**). En un experiment de laboratori la radiació UV només va explicar una minsa proporció (<3%) del total de la descomposició de la fullaraca i no es van observar efectes de foto-facilitació. Al contrari de la radiació UV, la microbiota semblava tenir un efecte principal en la descomposició a través d'efectes legats als detritívors, atès que es van trobar efectes acumulats de la microbiota i els detritívors, arribant al 42% del total de la descomposició (**capítol 2**). A més aquests dos components varen originar efectes sinèrgics en barreges de fullaraca (**capítols 2 i 3**) i varen funcionar d'enllaç entre els depredadors i la descomposició de la fullaraca. A més, l'eliminació dels microorganismes amb biocides va revertir els efectes sinèrgics de les barreges de fullaraca resultant en efectes antagònics entre les espècies involucrades en la fullaraca (**capítol 2**). En resum, la radiació UV va tenir un efecte minoritari comparat amb els microbis en els seus efectes de legat sobre la descomposició mitjançant detritívors. L'objectiu del **capítol 3** va ser avaluar els efectes múltiples dels depredadors en la descomposició mitjançant efectes de consumició i de no-consumició, i en particular mitjançant efectes d'enginyeria de l'ecosistema i com aquests poden generar sinèrgies entre les barreges de fullaraca (**capítol 3**). Malgrat el fort efecte dels depredadors sobre els detritívors (tan en mortalitat com en comportament), els efectes de control descendent (top-down) varen ser indetectables, essent substituïts per efectes múltiples d'enginyeria ecològica per part dels depredadors, mostrant sinèrgies amb la identitat i la diversitat de la fullaraca, accelerant, més que no pas inhibint, la descomposició. Aquests resultats suggereixen que les restes d'activitat dels depredadors (p. ex. productes d'excreció) aporten

nutrients extres que augmenten l'activitat microbiana redundant en el benefici dels descomponedors secundaris i finalment en la descomposició. En el **capítol 4** es va avaluar el paper de les illes de fertilitat en la descomposició de barreges de fullaraca en un ecosistema semi-àrid. La descomposició sota la copa dels arbusts va mostrar efectes antagonistes entre espècies de fullaraca i va alentir la descomposició de manera diferent depenent de la identitat de l'espècie de fullaraca. Contràriament, la descomposició fora dels arbusts va resultar en efectes additius, amb tan sols una sinèrgia dèbil en una de les espècies. Malgrat el que s'esperava, no es van trobar efectes de la riquesa d'espècies de planta conformant les barreges de fullaraca. Atès que es van trobar abundàncies més elevades de mesofauna en els mesocosms ubicats sota dels arbusts, es suggereix que la descomposició biòtica predomina a sota dels arbusts, mentre que fora predominaria la descomposició basada en factors abiòtics. La informació aportada per aquesta tesi pot ajudar a entendre com es descomposa la fullaraca en zones àrides, així com entendre millor la interacció entre components biòtics i abiòtics, atès que tenen efectes difícils de diferenciar per tal de predir les taxes de descomposició en aquests ecosistemes.

# Resumen

La descomposición retorna al suelo más del 50% de la productividad primaria y provee del principal recurso de energía y nutrientes para la compleja red alimenticia del suelo. En ecosistemas terrestres, la descomposición está jerárquicamente regulada por el clima, la calidad de la hojarasca y la biota del suelo. Sin embargo, en ecosistemas semiáridos, la descomposición parece estar gobernada por complejas interacciones bióticas y abióticas que no son bien entendidas. El principal objetivo de esta tesis es estudiar las interacciones que regulan la descomposición en ecosistemas semiárdios. Como primer objetivo evalué el efecto de la radiación UV y la actividad microbiana en etapas tempranas de la descomposición y exploré los efectos de estos dos componentes en etapas de descomposición avanzada que involucran a detritívoros (isópodos) (**Capítulo 2**). En un experimento de laboratorio, la radiación UV causó únicamente una pequeña proporción (3%) de la descomposición total y no se encontraron efectos de foto-facilitación. Por lo contrario, los microorganismos tuvieron un papel destacable en durante la descomposición a través de efectos sucesivos sobre los detritívoros, dado que encontramos sustanciales efectos aditivos de microorganismos y detritívoros sumando un 42% de la descomposición total (**Capítulo 2**). Los microorganismos también promovieron la expresión de sinergias en las mezclas de hojas (C**apítulo 2 y 3**) y actuaron como enlace entre depredadores y la descomposición de hojarasca (**Capítulo 3**). Además, la eliminación de microorganismos a través de biosidas revirtió los efectos sinérgicos en la mezcla de hojas y disparó los antagonismos entre las especies (**Capítulo 2**). En resumen, la radiación UV tuvo un efecto menor comparado con el efecto de los microorganismos y sus efectos sucesorios en la descomposición dirigida por detritívoros. El principal objetivo del **capítulo 3** fue evaluar los múltiple efectos de los depredadores en la descomposición a través de efectos indirectos por consumo y efectos de no consumo, así a través de los efectos de los depredadores como ingenieros del ecosistema y cómo estos pueden generar sinergias durante la descomposición de mezclas de hojas (**Capítulo 3)**. A pesar del alto impacto de los depredadores sobre los detritívoros (tanto en mortalidad como en comportamiento), prevalecieron múltiples efectos de los depredadores como ingenieros del ecosistema en sinergia con la identidad y diversidad de hojas sobre los efectos descendentes, haciendo que los depredadores mejoraran la descomposición al contrario de inhibirla. Estos resultados sugieren que

los restos de la actividad de los depredadores (excretas) proveen de nutrientes adicionales que pueden fomentar la actividad microbiana y finalmente beneficiar a los descomponedores secundarios y acelerar la descomposición. En el capítulo 4 se evaluó el papel de las islas de fertilidad durante la descomposición de mezclas de hojas en ecosistemas semiáridos. La descomposición bajo el dosel de los arbustos fue consistentemente baja y mostró primordialmente efectos antagónicos dependiendo de la identidad de las hojas. Por lo contrario, la descomposición fuera del dosel resultó mayormente en efectos aditivos con escazas sinergias en una de las especies. Contrario a lo esperado, el gradiente de diversidad en la mezcla de hojas no tuvo efectos significativos. Debido a que encontramos mayor abundancia de fauna bajo el dosel, se sugiere que la descomposición funciona principalmente por factores bióticos bajo el dosel y abióticos fuera. La información provista por esta tesis podría ayudar al entendimiento de cómo la hojarasca se descompone en ecosistemas semiáridos, donde puede descomponerse en la planta o en el suelo. Esta tesis también ofrece propuestas sobre el entendimiento en la interacción entre factores bióticos y abióticos que tienen efectos difíciles de descifrar cuando se predice la descomposición en este tipo de ecosistemas.

# Chapter 1. Introduction

Drylands represent 41% of the Earth's surface (Solé, 2007) and provide ecosystem services that support the livelihood of more than 38% of the world's population (Kéfi *et al.*, 2007). Decomposition in drylands, which is a key ecosystem process tightly related to nutrient availability, primary productivity, nitrogen and phosphorous cycling, and carbon sequestration (Brussaard, 1997; De Deyn, *et al.*, 2008; Maestre *et al.*, 2012). In fact, it has been estimated that 27% of the soil organic C on Earth is immobilized in drylands (Safriel, *et al.*, 2005). In the present context of global environment change, decomposition is a key process strongly threatened by the loss of diversity and land use change. This ecosystem process also needs to be studied more deeply in drylands because current decomposition models substantially underpredict mass loss rates in these ecosystems compared to the models in mesic ecosystems, suggesting that additional drivers need to be considered (Austin, 2011; King, *et al*, 2012; Throop & Archer, 2009). Hence, the better understanding of this ecosystem process is critical in order to propose mitigation strategies to sustain ecosystem productivity and the provisioning of ecosystem services (Ramón-Vallejo *et al.*, 2012).

## 1.1 Decomposition in a context of drylands

Drylands are mainly distributed in North and South America, northern and southern of Africa, central Asia and Australia (Feng & Fu, 2013). In Europe, these ecosystems expand across almost 65,000,000 ha along the Mediterranean Sea, being Spain the country with the largest surface (Dregne, 2002). Drylands encompass arid, semi-arid, and dry sub humid climates occupied by biomes such as desert, grassland and savanna woodlands (hereafter "drylands") (Feng & Fu, 2013; Reynolds *et al.*, 2007) mainly characterized by stressful conditions including water scarcity (Ramón-Vallejo *et al.*, 2012), low rainfall and strong seasonality (Hulme, 1996); high temperatures and high intensity of UV radiation (Austin & Vivanco, 2006; Reynolds *et al.*, 2007); low soil fertility with small amounts of litter, organic matter, mineral nutrient pools and low aggregate strength (Throop & Archer, 2009); large spatial variability and patchy distribution of resources (Barnes *et al.*, 2015; Rey *et al.*, 2011).

The main threats for ecosystem stability in drylands are anthropogenic disturbances such as agriculture intensification, overgrazing, mining and urban sprawls (Allen, 1995) that contribute to desertification through loss of plant cover, increases of soil compaction and loss of soil fertility, soil water availability and biodiversity (Keller & Goldstein, 1998). Additionally, global warming effects foster changes in precipitation patterns, increase the frequency of extreme climate events, and in Mediterranean climates with marked seasonality wetter winters and drier summers (Alessandri *et al*., 2014); increment of the drought periods, mean air temperature and evapotranspiration rates (Feng & Fu, 2013), aggravation of fire regime (Smanis *et al*., 2012), and increment in solar radiation due to the decrease of cloudiness (Herman, 2010). Such threats make drylands one of the most vulnerable ecosystems and foster the intensity and expansion of desertification (Carpenter *et al*., 2009; Maestre *et al*., 2012; Verstraete, 1986) to the extent that recent projections suggest that by the end of the century, drylands may occupy more than 50% of the total land surface (Feng & Fu, 2013; Huang, *et al*., 2015), increasing the population affected by water scarcity and jeopardizing the number and quality of ecosystem services (Feng & Fu, 2013; Maestre *et al*., 2012).

This thesis tackles the abiotic and biotic drivers of decomposition in drylands and their statistical interactions, in a context biodiversity loss and global warming. We define decomposition in a broad sense which is the major determinant of carbon and nutrient cycling and the main source of energy and nutrients for complex detritus-based food webs (Abelho, 2016) and focus on UV radiation, its effects through photodegradation and its interaction with biotic factors such as microorganisms and detritivores; a process termed photopriming; and also the largely unexplored role of soil predators indirectly affecting decomposition. Lastly, we will address the role of leaf litter mixtures and the role of shrub understories on decomposition in drylands.

## 1.2 What drives decomposition in drylands abiotic or biotic factors, or both?

Decomposition in drylands is a key process for biogeochemical cycles (Delgado-Baquerizo *et al*., 2013) and the global annual flux of carbon (Stringer *et al*., 2012). It is the main source of energy and nutrients for complex detritus-based soil food webs because it returns  to the soil more than 50% of primary productivity (Wardle *et al*., 2004). Also, it constitutes a valuable ecosystem service by sustaining soil biotic diversity, nutrient availability, water retention capacity and soil physical structure

(Brussaard, 1997; García-Palacios, et al., 2016; Hättenschwiler *et al*., 2005; Patrick *et al*., 2008).

Decomposition in terrestrial ecosystems is globally controlled by climate; then by litter quality and by soil organisms (Hättenschwiler, *et al*., 2005; Lavelle *et al*., 2006). However, drylands decomposition models substantially underpredict decomposition rates compared to models in mesic ecosystems (Austin, 2011; King, *et al*, 2012; Throop & Archer, 2009), the latter depending mostly on climatic variables. These forecasting failures suggest that decomposition in drylands may be driven by different factors that are not yet well understood (Adair, *et al*., 2017; Kemp, *et al*, 2003; Moorhead & Reynolds, 1991; Parton *et al*., 2007).

Currently we know that decomposition in drylands is mainly driven by factors such as water scarcity (Rey *et al*., 2011), temperature (Lee *et al*., 2014; Lee, *et al*., 2012) and UV radiation (Brandt, *et al*., 2010; King *et al*., 2012) and by soil-litter mixing (Lin, *et al*., 2015). Additionally, litter in drylands is commonly rich in microbial inhibiting compounds such as lignin, cutin, cellulose and tanins which mitigate microbial activity and make litter extremely resistant to decomposition (Gallardo & Merino, 1993). These constraining conditions for decomposition lead to litter remaining in the soil for decades, being probably the reason why arid ecosystems retain 27% of the soil organic C (Safriel, *et al*., 2005).

Another aspect to consider in drylands is the long-term exposure of litter as standing death material, remaining on the plant before reaching the soil surface. During this process, UV radiation and microorganisms, likely adapted to adverse conditions, induce decomposition in unique circumstances, rarely documented in mesic ecosystems, and not well documented in drylands (Almagro, *et al*., 2015). Combined, all of the above factors determine litter decomposition both standing and on the ground (Austin & Vivanco, 2006).

## 1.3 UV radiation as the primary abiotic factor during decomposition in drylands

In the past 50 years ultraviolet radiation have received considerable attention as the main abiotic factor of litter decomposition in drylands (Austin & Vivanco, 2006; Brandt, *et al*., 2010; Brandt, *et al*., 2007; Day,*et al*., 2007; Pauli, 1964). However, the assessment of UV radiation effects on decomposition has resulted in contradictory results. While some studies found that UV radiation increases decomposition (Austin *et al*., 2016; King *et al*., 2012), others found negative effects (Paul & Gwynn-Jones, 2003; Zepp, *et al*, 1998) and others no effects (Yanni, *et al*, 2015). These inconsistences highlight the largely unknown mechanisms through which UV radiation impact on decomposition, and the consequences of the UV statistical interaction with some other factors. These include microorganisms adapted to dryland conditions (Austin & Vivanco, 2006; Baker *et al*., 2015; King *et al*., 2012; Pancotto *et al*., 2005; Zepp, *et al*., 2007), litter chemistry (Austin & Ballaré, 2010; Day, *et al*, 2015), plant species identity and plant functional traits (Day, *et al*., 2015; Pan *et al*., 2015). For example, it has been reported that UV radiation mainly impact plant species with higher leaf area and on species that decompose quickly under shade (Pan *et al*., 2015). UV radiation effects may also change across spatial scales due to moisture and temperature variability (Almagro *et al*., 2016; King *et al*., 2012; Song, *et al*., 2013; Wang *et al*., 2015). For instance, UV radiation effects are stronger under xeric conditions (Almagro *et al*., 2016; Brandt *et al*., 2007; Smith, *et al*, 2010) and weaker in moist environments (Smith, *et al*., 2010).

The best documented mechanism of UV radiation on litter decomposition is the so called photodegradation (Lee, et al., 2012), which is the molecular fragmentation of complex molecules such as lignin, cellulose, hemicellulose and aromatic compounds caused by the incidence of UV light (García-Palacios, *et al*., 2016; King *et al*., 2012). However some inconsistent results suggest an interaction with microorganisms not yet well understood (Bing *et al*., 2018; Chen *et al*., 2016). For example, some studies show that litter rich in complex molecules is easily depolymerized by photodegradation (Adair, P*et al*., 2017; Austin & Ballaré, 2010; Austin & Vivanco, 2006; Baker, *et al*., 2015; Huang & Li, 2017), while others suggest that the decomposition of these compounds is mostly driven by microbial activity (Brandt, *et al*., 2010; Brandt *et al*., 2007; King *et al*., 2012; Lin, *et al*, 2018; Lin, *et al*., 2015).

Photodegradation impacts mainly litter with higher C:N and lignin/N (Bing, *et al*., 2018; Brandt *et al*., 2007; King *et al*., 2012). In early stages of decomposition and in leaves after re-wetting, photodegradation decreases N immobilization (Verhoef *et al*., 2000), facilitating microbial access to litter N (Foereid, *et al*., 2010; Predick *et al*., 2018; Wang *et al*., 2015).

Photodegradation is especially relevant for understanding carbon loss of standing litter (Wang *et al*., 2017), as a substantial amount of carbon is lost directly to the atmosphere without cycling through soil pools (Austin & Vivanco, 2006; Brandt, *et al*., 2009; King *et al*., 2012). Hence, accounting for the impact of photodegradation on standing litter is critical for accurately model carbon cycling in drylands (Wang *et al*., 2017). However it is important to include the interaction of abiotic and biotic factors since considering solely UV radiation on predictions of C losses will likely overestimate the importance of photodegradation (Barnes, *et al*., 2012).

## 1.4 Photodegradation and microorganisms: a key interaction

Microorganisms are the most important biotic factor to turn organic matter into mineral nutrients available for plants (Throop & Archer, 2009). Since in drylands microbial activity act simultaneously with photodegradation (Wang, *et al*., 2015), it is important to take in to account this interaction to better predict decomposition in drylands. However, the assessment of this interaction is unclear, suggesting hidden mechanisms that are necessary to understand (Wang *et al*., 2015). The positive effects of UV radiation on microbial activity (hereafter “photopriming”) are the result of changes induced by photodegradation on litter chemistry, including N release and the breakage of complex carbon molecules (Foereid *et al*., 2010; Huang *et al*., 2017; Ma, *et al*., 2012; Predick *et al*., 2018). This molecular simplification facilitates microbial accessibility to lignin and labile carbon compounds (Foereid, *et al*., 2010; Gallo, *et al*., 2006; Henry, *et al*., 2008; Lin & King, 2014; Wang, *et al*., 2015), which is particularly feasible for microbial communities adapted to drylands (Foereid *et al*., 2010; Gallo *et al*., 2006; Henry *et al*., 2008; Lin & King, 2014).

The occurrence of photopriming effects is related to the decomposition stage of the litter (Song, *et al*., 2013), but most importantly photopriming is related to the temporal scale such as daily dark-light cycles (Brandt, *et al*., 2009; Yanni, *et al*., 2015) and long-term seasonality such as dry/wet periods (Gliksman *et al*., 2016; Lin, *et al*., 2018). Drying and rewetting cycles promote the formation of small soluble molecules readily available for microorganisms (Berg, *et al*., 2003; Gliksman *et al*., 2016; Uselman, *et al*., 2011); hence, in the absence of precipitation, the absorption of dew and water vapor enables microbial degradation. Photodegradation during dry periods modifies litter chemistry and stimulates mass loss through chemical reactions, while microbial activity is inhibited (Gliksman *et al*., 2016). In contrast, during wet periods, when UV radiation is lower, microbial activity increases because of the accessibility to chemical compounds  made available during summer (Baker, *et al*., 2015). Moreover, alternative dark-light exposure stimulate microbial activity more intensely in standing litter compared with soil surface litter (Wang *et al*., 2017). Photopriming on standing litter is thus the most important effect of UV radiation on decomposition in drylands (Foereid, *et al*., 2010).

Besides the well-recognized positive effects of photodegradation, UV radiation may also induce negative impacts on decomposition as has been observed on the structure, growth and activity of microbial communities, affecting mostly fungal abundance (Baker, *et al*., 2015; Zhang & Wang, 2015), and the activity of several extracellular enzymes important for decomposition (Baker, *et al*., 2015). UV radiation also impacts negatively microbial DNA and stimulates the release of free radicals that damage microorganisms (Baker *et al*., 2015; Hughes *et al*., 2003; Johnson, 2003; Rohwer *et al*., 2000). Moreover, photodegradation induces changes in litter quality that may negatively impact microbial activity, such as enhancing the release of secondary metabolites (flavonoids, tannins and lignin) that strongly inhibit the growth of microorganisms (Brandt, *et al*., 2009; Duguay & Klironomos, 2000; Gehrke *et al*., 1995; Moody, *et al*., 1999; Pancotto *et al*., 2003; Rozema *et al*., 1997; Verhoef *et al*., 2000; Wang, *et al*., 2015).

## 1.5 Soil fauna: more than shredding litter

Soil animals are an important biotic driver of decomposition (Brussaard, *et al.*, 2007; Lavelle, *et al.*, 1992). However, their role in drylands may be underestimated if considered in isolation from other biotic and abiotic factors. The main role of macro-detritivores in decomposition seems to be their improvement of microbial activity by improving substrates by the shredding of litter, and via the deposition of faeces; the enrichment of microbiota by the detritivore own gut microbial community seems to be important (Hättenschwiler & Gasser, 2005; Tiunov, 2009). Macro-detritivores also enhance the physical stability of soil, soil porosity and water retention (Brussaard, 1997). The combination of all of the above effects translate into the substantial increase of primary productivity, fertility and nutrient cycling, thus contributing to the provisioning of main ecosystem services (Moreira, *et al.*, 2012).

While the role of detritivores in decomposition is relatively well known, the effect of predatory macrofauna (e.g., centipedes and arachnids) in drylands is largely unknown (Estes *et al.*, 2011; Goncharov & Tiunov, 2014; Kajak, 1995), and the few empirical studies exploring the role of predators in drylands decomposition have resulted in either negative (i.e., depress soil metabolism by $CO_2$ flux; Sitvarin & Rypstra, 2014) or non-significant effects. In addition, there is no consensus on the processes involved in the role of predatory macro-arthropods in decomposition (Kajak, 1995; Wu, *et al.*, 2011).

## 1.6 More than predation in litter decomposition: the multiple effects of soil predators

Soil predators can cascade on decomposition via consumptive (CE) or non-consumptive effects (NCE; Sitvarin & Rypstra, 2014). Consumptive effects may negatively affect decomposition (Schmitz, *et al.*, 2010) through decreases in detritivores population densities leading to a decrease in decomposition rates (Buchkowski, 2016; Hawlena *et al.*, 2012; Lawrence & Wise, 2000, 2004; Preisser *et al.*, 2016). However, in three-level trophic networks deritivores decreases affect positively decomposition because it may lead to a an increase in microorganism activity, increasing decomposition rates (Crowther *et al.*, 2012; Kajak, 1995;

Lawrence & Wise, 2004; Lensing & Wise, 2006; Melguizo-Ruiz *et al*., 2019; Ngai & Srivastava, 2006).

Non-consumptive effects appear when predators affect decomposition via two non-mutually exclusive mechanisms; for instance, fear of predation or ecological engineering effects. Fear of predation emerges when prey respond to predatory cues (visual, chemical or tactile) that warn the prey of predation risk. The cues that trigger fear of predation are diverse such as carcasses, egested faeces or excreta, but can also can come from conspecific prey as debris, carcasses of dead or injured conspecifics, that may even release necromones (Yao *et al*., 2009). Fear of predation may cascade down on decomposition via stress-induced changes in the diet, changes in foraging patterns or foraging microhabitat, changes in prey metabolism (i.e., the demand for, and the release of particular nutrients; Schmitz, *et al*., 2010) or changes in general prey activity (Schmitz & Barton, 2014; Sitvarin, *et al*., 2016). Overall, the few studies conducted to date suggest that fear of predation slow down decomposition and decrease soil respiration and nitrogen content (Hawlena *et al*., 2012; Sitvarin & Rypstra, 2014).

Ecological engineering effects may affect decomposition when predators induce changes in the physical or chemical environment (Sanders & van Veen, 2011) as in terrestrial and aquatic food webs that supply high quality resources (Lawton & Jones, 1993; Majdi, *et al*., 2014; Schmitz, *et al*., 2010) via metabolism or byproducts of predation activity (Hawlena & Schmitz, 2010). This animal-originated resources are readily taken up by microorganisms and detritivores (Guenet, *et al*., 2010; Schmitz, *et al*., 2010), especially those highly dependent on microorganisms and debris, such as isopods, that feed on plant detritus but also on fungi covering decaying leaf litter, or faeces and carcasses of other invertebrates (Crowther, *et al*., 2012; Hornung, *et al*., 1998; Zimmer, *et al*., 2005). Hence, ecological engineering effects may mainly lead to positive effects on decomposition (Guenet, *et al*., 2010; Schmitz *et al*., 2010) and substantially alter the flow of energy in soil food webs (Hawlena & Schmitz, 2010).

Both fear of predation and ecological engineering effects may strongly depend on the natural heterogeneity and patch distribution of resources in drylands (Ettema & Wardle, 2002) where fertility islands promote accumulation of litter from different species (Huete & Jackson, 1987; Pugnaire, *et al*., 1996) and create complex structures as leaf litter mixtures. In the face of predation risk, detritivores seek shelter (Sitvarin *et al*., 2016) in structures that may serve as habitats that interfere with predator-prey interactions via the reduce encounter rates (Janssen, *et al*., 2007). Such structures , in addition to minimizing predation risk, facilitate litter consumption by detritivores, and may compensate both CE and NCEs (Kalinkat, Brose, & Rall, 2013). As other soil keystone structures (Melguizo-Ruiz, 2016), litter mixtures can be relevant driving the configuration of soil communities and nutrient distribution across the landscape (Hawlena & Zaguri, 2016; Schmitz, *et al*., 2010).

A growing body of evidence suggests that NCEs spread more intensely through lower trophic levels and have a stronger impact on ecosystems functioning than CEs (Preisser & Bolnick, 2008; Stephan, *et al*., 2017). However, the overall mechanisms of CEs and NCEs are largely unknown (Preisser *et al*. 2005) and the lack of information is scant in drylands where abiotic factors and the patchy distribution of resources would have a major impact on animal performance, and consequently on ecosystem functioning (Ballaré, 2014; Inh, *et al*., 2013; Rechner & Poehling, 2014). In addition, global change especially threatens predators, since higher trophic levels are less diverse, less abundant, and are more sensitive to environmental disturbances (Duffy, 2002; Schneider & Brose, 2013; Melguizo-Ruiz *et al*. 2019). For all these reasons, the role of assemblages of spiders and other large predators must be included in decomposition models based on detritus food webs (Lesny, 1995) and further research on the role of predators on decomposition is required (Buchkowski, 2016; Hawlena & Zaguri, 2016).

## 1.7 Leaf litter mixtures: top-down or bottom-up control?

As stated above, fertility islands play a fundamental role in the patchy distribution of nutrients in drylands, where wind and water flows redistribute litter and lead to accumulation in depositional areas, related to the micro topography and plant distribution (Barnes *et al*., 2015; Schlesinger *et al*., 1990). In islands, litter from different species mix, in a process with important consequences for nutrient cycling. Cumulative evidence shows that decomposition of leaf litter mixtures may trigger non-additive effects, such as synergies and antagonisms that impact decomposition in a disruptive way, also known as leaf litter mixture effects (Gartner & Cardon, 2004). Additive effects appear when litter of a particular species decomposes at the same rate in monospecific and mixed with other species. In contrast, non-additive effects implies that decomposition of a particular species decompose faster (synergies) or slower (antagonisms) when mixed with other species (Hunter, *et al.*, 2003; Santonja, *et al.*, 2015). The mechanisms to explain leaf litter mixture effects are strongly related to the diversity of functional traits (Viketoft *et al.*, 2009) rather than to species richness (Gessner *et al.*, 2010). These variety of physical-chemical litter characteristics lead to several process that impact on decomposition rates such as nutrient transfer by leaching from high quality to poor quality leaves (Heal, Anderson, & Swift, 1997). Litter diversity in mixtures also provides a large range of nutrients to soil organisms which enhance their decomposition activity (Gartner & Cardon, 2004; Hättenschwiler, *et al.*, 2005b; Schuster & Dukes, 2014). Finally the complexity of the structure of mixtures produces micro-environmental conditions favorable for micro and macro decomposers (Gartner & Cardon, 2004; Hättenschwiler, *et al.*, 2005; Schuster & Dukes, 2014), which, as stated above can even decrease predation risk.

Decomposition in leaf litter mixtures may be regulated by bottom-up and top-down effects. Bottom-up effects in litter mixtures are driven by fluxes of energy from litter to the upper levels in the soil food web, providing not only structural protection against predation (Doblas-Miranda, *et al.*, 2009), but also a diversity of basal resources valuable for detritivores (Hättenschwiler & Gasser, 2005). Furthermore, top-down effects in litter mixtures are driven by soil decomposers that change the quality of litter, mostly through the degradation of recalcitrant litter (Gessner *et al.*, 2010). Hence, soil fauna may foster synergies in leaf litter mixtures rather than antagonisms (De Oliveira *et al.*, 2010). However, the effects of predators on leaf litter mixtures are largely unknown (Schmitz *et al.*, 2010; Wagg *et al.*, 2014).

The study of litter mixtures has been conducted almost exclusively in mesic ecosystems, and as a consequence the assessment of photodegradation has been mostly addressed in monocultures (Almagro, *et al.*, 2015; Almagro, *et al.*, 2016; Martínez-Yrízar, *et al.*, 2007; Verhoef *et al.*, 2000). Thus, the extent to which photodegradation, high temperatures, and water limitation in arid lands may affect the additive and non-additive effects of mixtures is little known (Birkhofer *et al.*, 2011; García-Palacios *et al.*, 2016; Hooper & Vitousek, 1997; Wardle *et al.*, 1997).

There are several reasons to expect a photodegradation affects litter mixtures. First, photodegradation depends on plant species identity which is likely linked to contrasting chemical properties and differences in plant functional traits  (Bing *et al.*, 2018; King *et al.*, 2012). Second, twigs and woody plants –dominant in arid environments-- are more photo-sensible than herbaceous litter (Day, *et al.*, 2007; Song, *et al.*, 2013). Finally, position of the litter substrate significantly regulates the contribution of photodegradation (Lin & King, 2014); i.e. thin-layered litter decomposes faster under UV radiation than thick-layered litter (Bing,*et al.*, 2018). Hence, the inclusion of woody plant material in the assessment of decomposition of leaf litter mixtures, besides making the litter mixture experiments more realistic, may shed light on largely unexplored abiotic-biotic interaction in drylands.

## 1.8 Fertility Islands from Ziziphus lotus: oasis in a sea of sand

As stated earlier, decomposition in drylands is disproportionately influenced by photodegradation (Austin & Vivanco, 2006), as well as by the physical abrasion and burial by soil (Barnes, *et al.*, 2012). All these abiotic factors can be modulated by the so-called "fertility islands" conformed by dominant perennial plants that facilitate the accumulation of litter (Throop. & Archer, 2007) and modify the micro environmental conditions (Pugnaire, *et al.*, 2004, 2011) such as promoting an increase of soil moisture and a reduction of soil temperature, evapotranspiration and the intensity of solar radiation (Hobbie, 1992; Moro *et al.* 1997; Safriel, *et al.*, 2005; Throop & Archer, 2009). Despite improved micro-environmental conditions under shrub canopies that enhance microbial activity (Zhang & Zak, 2010), decomposition below shrubs is generally slow (Gliksman, *et al.*, 2018; Predick *et al.*, 2018), an effect that persists even after canopy removal, which suggests that decomposition is driven by legacy effects on soil (Throop & Archer, 2009).

In contrast, decomposition away from shrubs (e.g., in bare soil) is higher, revealing the relevant role of abiotic factors such as photodegradation (Throop & Archer, 2009) and soil abrasion (Hewins, *et al*, 2013; Throop. & Archer, 2007). Abrasion may in turn affect colonization by microorganisms,  further promoting leaching and fragmentation (Levi *et al*., 2009; Moorhead & Reynolds, 1991; Throop & Archer, 2009; Uselman, *et al*., 2011).

In our site of study in SE Spain, *Ziziphus lotus* is an endangered deciduous shrub which may be locally dominant and able to create fertility islands, is present in active sand dunes where it is a typical facilitator of other dominant shrubs (Tirado Fernández, 2003; Tirado & Pugnaire, 2005). The microenvironment under the canopy of *Ziziphus* is characterized by lower temperature and higher air humidity. These shrubs promote a massive accumulation of sand, organic matter, nitrogen and phosphorous below their canopy (Tirado, 2009). When it comes to  decomposition, however, it may be a constraining factor, particularly because leaves of this species have strong inhibitory capacity for bacterial growing (Gram-positive), due to the high quantity of alkaloids and antioxidants flavonoids (Li *et al*., 2018; Naili, *et al*., 2010). Fertility island based on *Ziziphus* may be fundamental for ecosystem functioning, because they are nutrient-limited with extreme climatic conditions (Pugnaire, *et al*, 2004; Tirado & Pugnaire, 2005). Hence, the scattered, patchy distribution of *Ziziphus* and the enhancing of nutrient availability and microclimatic conditions under the canopy make this system ideal to explore the response of decomposition under and away from the shrub canopy (Barnes *et al*., 2015).

## 1.9 References

Abelho, M. (2016). Litter traits and decomposer complexity set the stage for a global decomposition model. *Functional Ecology*,30,674-675. doi:10.1111/1365-2435.12640

Adair, E. C., Parton, W. J., King, J. Y., Brandt, L. A., & Lin, Y. (2017). Accounting for photodegradation dramatically improves prediction of carbon losses in dryland systems. *Ecosphere*, *8*(7), e01892. doi:10.1002/ecs2.1892

Alessandri, A., De Felice, M., Zeng, N., Mariotti, A., Pan, Y., Cherchi, A., Artale, V. (2015). Robust assessment of the expansion and retreat of Mediterranean climate in the 21st century. *Scientific Reports*, *4*(1), 7211. doi:10.1038/srep07211

Allen, E. B. (1995). Wildland Shrub and Arid Land Restoration. In *Restoration Ecology: Limits and Possibilities in Arid and Semiarid Lands* (p. 7).

Almagro, M., Maestre, F. T., Martínez-López, J., Valencia, E., & Rey, A. (2015). Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. *Soil Biology and Biochemistry*, *90*, 214–223. doi:10.1016/j.soilbio.2015.08.006

Almagro, M., Martínez-López, J., Maestre, F. T., & Rey, A. (2017). The contribution of photodegradation to litter decomposition in semiarid mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. *Ecosystems*, *20*(3), 527–542. doi:10.1007/s10021-016-0036-5

Austin, A. T. (2011). Has water limited our imagination for aridland biogeochemistry? *Trends in Ecology & Evolution*, *26*(5), 229–235. doi:10.1016/j.tree.2011.02.003

Austin, A. T., & Ballare, C. L. (2010). Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, *107*(10), 4618–4622. doi:10.1073/pnas.0909396107

Austin, A. T., Méndez, M. S., & Ballaré, C. L. (2016). Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(16), 4392–7.

doi:10.1073/pnas.1516157113

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, *442*(7102), 555–558. doi:10.1038/nature05038

Baker, N. R., & Allison, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology, 96*(7), 1994–2003. doi:10.1890/14-1482.1

Ballaré, C. L. (2014). Light regulation of plant defense. *Annual Review of Plant Biology*, *65*(1), 335–63. doi:10.1146/annurev-arplant-050213-040145

Barnes, P. W., Throop, H. L., Archer, S. R., Breshears, D. D., Mcculley, R. L., & Tobler, M. A. (2015). Sunlight and soil–litter mixing: drivers of litter decomposition in drylands. In U. Lüttge & W. Beyschlag (Eds.), *Progress in Botany* (Vol. 76, pp. 273–302). Cham: Springer International Publishing. doi:10.1007/978-3-319-08807-5

Barnes, P. W., Throop, H. L., Hewins, D. B., Abbene, M. L., & Archer, S. R. (2012). Soil coverage reduces photodegradation and promotes the development of soil-microbial films on dryland leaf litter. *Ecosystems*, *15*(2), 311–321. doi:10.1007/s10021-011-9511-1

Barthel, W., & Markwardt, F. (1975). Aggregation of blood platelets by adrenaline and its uptake. *Biochemical Pharmacology*, *24*(20), 1903–1904. doi:10.1016/0006-2952(75)90415-3

Berg, B., McClaugherty, C., & Ekbohm, G. (2003). *Plant litter, decomposition, humus formation, carbon sequestration*. Berlin: Springer-Verlag.

Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., & Wolters, V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biology and Biochemistry*, *43*(10), 2200–2207. doi:10.1016/j.soilbio.2011.07.008

Brandt, L. A., Bohnet, C., & King, J. Y. (2009a). Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research: Biogeosciences*, *114*(G02004), 1–13. doi:10.1029/2008JG000772

Brandt, L. A., Bohnet, C., & King, J. Y. (2009b). Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research: Biogeosciences*, *114*(G2), 1–13. doi:10.1029/2008JG000772

Brandt, L. A., King, J. Y., Hobbie, S. E., Milchunas, D. G., & Sinsabaugh, R. L. (2010). The Role of Photodegradation in Surface Litter Decomposition Across a Grassland Ecosystem Precipitation Gradient. *Ecosystems*, *13*(5), 765–781. doi:10.1007/s10021-010-9353-2

Brandt, L. A., King, J. Y., & Milchunas, D. G. (2007). Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. *Global Change Biology*, *13*(10), 2193–2205. doi:10.1111/j.1365-2486.2007.01428.x

Brussaard, L. (1997). Biodiversity and ecosystem functioning in soil. *Ambio*, *26*(8), 563–570. Retrieved from http://www.jstor.org/stable/4314670

Brussaard, Lijbert. (1997). Biodiversity and Ecosystem Functioning in Soil. *Ambio*, *26*(8), 563–570.

Brussaard, Lijbert, Pulleman, M. M., Oudraogo, lise, Mando, A., & Six, J. (2007). Soil fauna and soil function in the fabric of the food web. *Pedobiologia*, *50*(6), 447–462. doi:10.1016/j.pedobi.2006.10.007

Buchkowski, R. W. (2016). Top-down consumptive and trait-mediated control do affect soil food webs: It's time for a new model. *Soil Biology and Biochemistry*, *102*, 29–32. doi:10.1016/j.soilbio.2016.06.033

Carpenter, S. R., Mooney, H. a, Agard, J., Capistrano, D., DeFries, R. S., Diaz, S., … Whyte, A. (2009). Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences*, *106*(5), 1305–1312. doi:10.1073/pnas.0808772106

Chen, M., Parton, W. J., Adair, E. C., Asao, S., Hartman, M. D., & Gao, W. (2016). Simulation of the effects of photodecay on long-term litter decay using DayCent. *Ecosphere*, *7*(12), e01631. doi:10.1002/ecs2.1631

Cheung, J. Y., Tillotson, D. L., Yelamarty, R. V, & Scaduto, R. C. (1989). Cytosolic free calcium concentration in individual cardiac myocytes in primary culture. *The American Journal of Physiology*, *256*(6 Pt 1), C1120-30. doi:10.1152/ajpcell.1989.256.6.C1120

Crowther, T. W., Boddy, L., & Hefin Jones, T. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. *The ISME Journal*, *6*(11), 1992–2001. doi:10.1038/ismej.2012.53

Day, T. A., Guénon, R., & Ruhland, C. T. (2015). Photodegradation of plant litter in the Sonoran Desert varies by litter type and age. *Soil Biology and Biochemistry*, *89*, 109–122. doi:10.1016/j.soilbio.2015.06.029

Day, T. A., Zhang, E. T., & Ruhland, C. T. (2007). Exposure to solar UV-B radiation accelerates mass and lignin loss of Larrea tridentata litter in the Sonoran Desert. *Plant Ecology*, *193*(2), 185–194. doi:10.1007/s11258-006-9257-6

De Deyn, G. B., Cornelissen, J. H. C., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, *11*(5), 516–531. doi:10.1111/j.1461-0248.2008.01164.x

De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, *24*(4), 937–946. doi:10.1111/j.1365-2435.2010.01694.x

Delgado-Baquerizo, M., Maestre, F. T., Gallardo, A., Bowker, M. a, Wallenstein, M. D., Quero, J. L., Zaady, E. (2013). Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, *502*(7473), 672–6. doi:10.1038/nature12670

Đinh, S. T., Gális, I., & Baldwin, I. (2013). UVB radiation and 17-hydroxygeranyllinalool diterpene glycosides provide durable resistance against mirid ( Tupiocoris notatus ) attack in field-grown Nicotiana attenuata plants. *Plant, Cell & Environment*, *36*(3), 590–606. doi:10.1111/j.1365-3040.2012.02598.x

Doblas-Miranda, E., Sánchez-Piñero, F., & González-Megías, A. (2009). Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem. *Applied Soil Ecology*, *41*(3), 329–335. doi:10.1016/j.apsoil.2008.12.008

Dregne, H. E. (2002). Land Degradation in the Drylands. *Arid Land Research and Management*, *16*(2), 99–132. doi:10.1080/153249802317304422

Duffy, J. E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, *99*(2), 201–219. doi:10.1034/j.1600-0706.2002.990201.x

Duguay, K. J., & Klironomos, J. N. (2000). Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi. *Applied Soil Ecology*, *14*(2), 157–164. doi:10.1016/S0929-1393(00)00049-4

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, *333*(6040), 301–6. doi:10.1126/science.1205106

Feng, S., & Fu, Q. (2013). Expansion of global drylands under a warming climate. *Atmospheric Chemistry and Physics*, *13*(19), 10081–10094. doi:10.5194/acp-13-10081-2013

Foereid, B., Bellarby, J., Meier-Augenstein, W., & Kemp, H. (2010a). Does light exposure make plant litter more degradable? *Plant and Soil*, *333*(1), 275–285. doi:10.1007/s11104-010-0342-1

Foereid, B., Bellarby, J., Meier-Augenstein, W., & Kemp, H. (2010b). Does light exposure make plant litter more degradable? *Plant and Soil*, *333*(1–2), 275–285. doi:10.1007/s11104-010-0342-1

Gallardo, A., & Merino, J. (1993). Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality. *Ecology*. doi:10.2307/1939510

Gallo, M. E., Sinsabaugh, R. L., & Cabaniss, S. E. (2006). The role of ultraviolet radiation in litter decomposition in arid ecosystems. *Applied Soil Ecology*, *34*(1), 82–91. doi:10.1016/j.apsoil.2005.12.006

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, *19*(5), 554–563. doi:10.1111/ele.12590

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, *104*(2), 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gehrke, C., Johanson, U., Callaghan, T. V., Chadwick, D., & Robinson, C. H. (1995). The Impact of Enhanced Ultraviolet-B Radiation on Litter Quality and Decomposition Processes in Vaccinium Leaves from the Subarctic. *Oikos*, *72*(2), 213. doi:10.2307/3546223

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, *25*(6), 372–80. doi:10.1016/j.tree.2010.01.010

Gliksman, D., Haenel, S., Osem, Y., Yakir, D., Zangy, E., Preisler, Y., & Grünzweig, J. M. (2018). Litter decomposition in Mediterranean pine forests is enhanced by reduced canopy cover. *Plant and Soil*, *422*(1–2), 317–329. doi:10.1007/s11104-017-3366-y

Gliksman, D., Rey, A., Seligmann, R., Dumbur, R., Sperling, O., Navon, Y., … Grünzweig, J. M. (2017). Biotic degradation at night, abiotic degradation at day: positive feedbacks on litter decomposition in drylands. *Global Change Biology*, *23*(4), 1564–1574. doi:10.1111/gcb.13465

Goncharov, A. A., & Tiunov, A. V. (2014). Trophic chains in the soil. *Biology Bulletin Reviews*, *4*(5), 393–403. doi:10.1134/S207908641405003X

Guenet, B., Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, *91*(10), 2850–61. doi:10.1890/09-1968.1

Hattenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, *102*(5), 1519–1524. doi:10.1073/pnas.0404977102

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Hawlena, D., Strickland, M. S., Bradford, M. A., & Schmitz, O. J. (2012). Fear of predation slows plant-litter decomposition. *Science, 336*(June), 1434–1438.

Hawlena, Dror, & Schmitz, O. J. (2010a). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences*, *107*(35), 15503–15507. doi:10.1073/pnas.1009300107

Hawlena, Dror, & Schmitz, O. J. (2010b). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist*, *176*(5), 537–56. doi:10.1086/656495

Hawlena, Dror, & Zaguri, M. (2016). Fear and below-ground food-webs. *Soil Biology and Biochemistry*, *102*, 26–28. doi:10.1016/j.soilbio.2016.06.019

Heal, O. W., Anderson, J. M., & Swift, M. J. (1997). Plant litter quality and decomposition: an historical overview. In C. G. & K. E. Giller (Eds.), *Driven By nature: Plant litter quality and decomposition* (pp. 3–32). Wallingford, Inglaterra: CAB International.

Henry, H. A. L., Brizgys, K., & Field, C. B. (2008). Litter Decomposition in a California Annual Grassland: Interactions Between Photodegradation and Litter Layer Thickness. *Ecosystems*, *11*(4), 545–554. doi:10.1007/s10021-008-9141-4

Herman, J. R. (2010). Global increase in UV irradiance during the past 30 years (1979–2008) estimated from satellite data. *Journal of Geophysical Research*, *115*(D4), D04203. doi:10.1029/2009JD012219

Hewins, D. B., Archer, S. R., Okin, G. S., McCulley, R. L., & Throop, H. L. (2013). Soil–Litter Mixing Accelerates Decomposition in a Chihuahuan Desert Grassland. *Ecosystems*, *16*(2), 183–195. doi:10.1007/s10021-012-9604-5

Hobbie, S. E. (1992). Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution*, *7*(10), 336–9. doi:10.1016/0169-5347(92)90126-V

Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*. doi:10.1126/science.277.5330.1302

Hornung, E., Farkas, S., & Fischer, E. (1998). Tests on the Isopod Porcellio scaber. In *Handbook of soil invertebrate toxicity tests* (pp. 208–226).

Huang, G., & Li, Y. (2017). Photodegradation effects are related to precipitation amount, precipitation frequency and litter traits in a desert ecosystem. *Soil Biology and Biochemistry, 115*(December), 383–392. doi:10.1016/j.soilbio.2017.08.034

Huang, G., Zhao, H., & Li, Y. (2017). Litter decomposition in hyper-arid deserts: Photodegradation is still important. *Science of The Total Environment, 601–602*, 784–792. doi:10.1016/j.scitotenv.2017.05.213

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*(2), 166–171. doi:10.1038/nclimate2837

Huete, A. R., & Jackson, R. D. (1987). Suitability of spectral indices for evaluating vegetation characteristics on arid rangelands. *Remote Sensing of Environment, 23*(2), 213–232. doi:10.1016/0034-4257(87)90038-1

Hughes, K. a, Lawley, B., & Newsham, K. K. (2003). Solar UV-B Radiation Inhibits the Growth of Antarctic Terrestrial Fungi. *Applied and Environmental Microbiology, 69*(3), 1488–1491. doi:10.1128/AEM.69.3.1488

Hunter, M. D., Adl, S., Pringle, C. M., & Coleman, D. C. (2003). Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia*, *47*(2), 101–115. doi:10.1078/0031-4056-00174

Janssen, A., Sabelis, M. W., Magalhaes, S., Montserrat, M., & van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology*, *88*(11), 2713–2719. doi:10.1890/06-1408.1

Jesenšek, M. (1996). Recent climatic change in the world’s drylands. *Geophysical Research Letters, 23*(1), 61–64. doi:10.5817/SL2016-2-9

Johnson, D. (2003). Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. *Research in Microbiology*, *154*(5), 315–20. doi:10.1016/S0923-2508(03)00078-0

Kajak, A. (1995). The role of soil predators in decomposition processes. *European Journal of Entomology*.

Kalinkat, G., Brose, U., & Rall, B. C. (2013). Habitat structure alters top-down control in litter communities. *Oecologia*, *172*(3), 877–887. doi:10.1007/s00442-012-2530-6

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & de Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, *449*(7159), 213–217. doi:10.1038/nature06111

Keller, A. A., & Goldstein, R. A. (1998). Impact of Carbon Storage Through Restoration of Drylands on the Global Carbon Cycle. *Environmental Management*, *22*(5), 757–766. doi:10.1007/s002679900145

Kemp, P. R., Reynolds, J. F., Virginia, R. a., & Whitford, W. G. (2003). Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. *Journal of Arid Environments*, *53*(1), 21–39. doi:10.1006/jare.2002.1025

Kennedy, J. (1994). The archaeological recovery of smallpox victims in Hawaii: scientific investigation or public health threat? *Perspectives in Biology and Medicine*, *37*(4), 499–509. doi:10.1353/pbm.1994.0004

King, J. Y., Brandt, L. A., & Adair, E. C. (2012). Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. *Biogeochemistry*, *111*(1–3), 57–81. doi:10.1007/s10533-012-9737-9

Lavelle, P., Blanchart, E., Martin, a., Spain, a. V., & Martin, S. (1992). Impact of Soil Fauna on the properties of Soils in the Humid Tropics. *Myths and Science of Soils of the Tropics. SSSA Spe- Cial Publication No. 29.*, (29), 29.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., … Rossi, J.-P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, *42*(SUPPL. 1), S3–S15. doi:10.1016/j.ejsobi.2006.10.002

Lavelle, Patrick, Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A Hierarchical Model for Decomposition in Terrestrial Ecosystems: Application to Soils of the Humid Tropics. *Biotropica*, *25*(2), 130. doi:10.2307/2389178

Lawrence, K. L., & Wise, D. H. (2000). Spider predation on forest-floor Collembola and evidence for indirect effect on decomposition. *Pedobiologia*, *44,* 33–39.

Lawrence, K. L., & Wise, D. H. (2004). Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, *48*(2), 149–157. doi:10.1016/j.pedobi.2003.11.001

Lawton, J. H., & Jones, C. G. (1993). Linking species and ecosystem perspectives. *Trends in Ecology & Evolution*, *8*(9), 311–313. doi:10.1016/0169-5347(93)90236-I

Lee, H., Fitzgerald, J., Hewins, D. B., McCulley, R. L., Archer, S. R., Rahn, T., & Throop, H. L. (2014). Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment. *Soil Biology and Biochemistry*, *72*, 123–132. doi:10.1016/j.soilbio.2014.01.027

Lee, H., Rahn, T., & Throop, H. (2012). An accounting of C-based trace gas release during abiotic plant litter degradation. *Global Change Biology*, *18*(3), 1185–1195. doi:10.1111/j.1365-2486.2011.02579.x

Lensing, J. R., & Wise, D. H. (2006). Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences*, *103*(42), 15502–15505. doi:10.1073/pnas.0607064103

Levi, E., Archer, S., Rasmussen, C., Throop, H., Hewins, D., & Cover, L. (2009). *Soil-litter mixing accelerates decomposition and facilitates soil aggregation in a shrub-invaded Sonoran Desert grassland*.

Li, Y., Chen, X., Veen, G. F. C., Eisenhauer, N., Liang, Y., Zhou, X., … Ma, K. (2018). Negative effects of litter richness on root decomposition in the presence of detritivores. *Functional Ecology*, *32*(4), 1079–1090. doi:10.1111/1365-2435.13057

Lin, Y., Karlen, S. D., Ralph, J., & King, J. Y. (2018). Short-term facilitation of microbial litter decomposition by ultraviolet radiation. *Science of The Total Environment*, *615*, 838–848. doi:10.1016/j.scitotenv.2017.09.239

Lin, Y., & King, J. Y. (2014). Effects of UV Exposure and Litter Position on Decomposition in a California Grassland. *Ecosystems*, *17*(1), 158–168. doi:10.1007/s10021-013-9712-x

Lin, Y., King, J. Y., Karlen, S. D., & Ralph, J. (2015). Using 2D NMR spectroscopy to assess effects of UV radiation on cell wall chemistry during litter decomposition. *Biogeochemistry*, *125*(3), 427–436. doi:10.1007/s10533-015-0132-1

Lin, Y., Scarlett, R. D., & King, J. Y. (2015). Effects of UV photodegradation on subsequent microbial decomposition of Bromus diandrus litter. *Plant and Soil*, *395*(1–2), 263–271. doi:10.1007/s11104-015-2551-0

Ma, S., Baldocchi, D. D., Hatala, J. A., Detto, M., & Curiel Yuste, J. (2012). Are rain-induced ecosystem respiration pulses enhanced by legacies of antecedent photodegradation in semi-arid environments? *Agricultural and Forest Meteorology*, *154–155*, 203–213. doi:10.1016/j.agrformet.2011.11.007

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Zaady, E. (2012). Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. *Science*, *335*(6065), 214–218. doi:10.1126/science.1215442

Majdi, N., Boiché, A., Traunspurger, W., & Lecerf, A. (2014). Predator effects on a detritus-based food web are primarily mediated by non-trophic interactions. *The Journal of Animal Ecology*, *83*(4), 953–62. doi:10.1111/1365-2656.12189

Mao, B., Zhao, L., Zhao, Q., & Zeng, D. (2018). Effects of ultraviolet (UV) radiation and litter layer thickness on litter decomposition of two tree species in a semi-arid site of Northeast China. *Journal of Arid Land*, *10*(3), 416–428. doi:10.1007/s40333-018-0054-6

Martínez-Yrízar, A., Núñez, S., & Búrquez, A. (2007). Leaf litter decomposition in a southern Sonoran Desert ecosystem, northwestern Mexico: Effects of habitat and litter quality. *Acta Oecologica*, *32*(3), 291–300. doi:10.1016/j.actao.2007.05.010

Melguizo-Ruiz, N. (2016). *Determinantes ecológicos de la red trófica del suelo de los hayedos: disponibilidad hídrica, regulación por grandes depredadores y estructuras clave en la hojarasca*.

Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., … Moya-Laraño, J. (2019). Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. *Journal of Animal Ecology*, (January), 1365-2656.13101. doi:10.1111/1365-2656.13101

Moody, S. A., Newsham, K. K., Ayres, P. G., & Paul, N. D. (1999). Variation in the responses of litter and phylloplane fungi to UV-B radiation (290–315 nm). *Mycological Research*, *103*(11), 1469–1477. doi:10.1017/S0953756299008783

Moreira, F. M., Huising, E. J., & Bignell, D. E. (2012). *A handbook of tropical soil biology: sampling and characterization of below-ground biodiversity*. Routledge.

Naili, M. B., Alghazeer, R. O., Saleh, N. A., & Al-Najjar, A. Y. (2010). Evaluation of antibacterial and antioxidant activities of Artemisia campestris (Astraceae) and Ziziphus lotus (Rhamnacea). *Arabian Journal of Chemistry*, *3*(2), 79–84. doi:10.1016/j.arabjc.2010.02.002

Ngai, J. T., & Srivastava, D. S. (2006). Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. *Science*, *314*(5801), 963–963. doi:10.1126/science.1132598

Pan, X., Song, Y.-B., Liu, G.-F., Hu, Y.-K., Ye, X.-H., Cornwell, W. K., … Cornelissen, J. H. C. (2015). Functional traits drive the contribution of solar radiation to leaf litter decomposition among multiple arid-zone species. *Scientific Reports*, *5*(1), 13217. doi:10.1038/srep13217

Pancotto, V.A., Sala, O. E., Robson, T. M., Caldwell, M. M., Scopel, A. L., & Aires, B. (2005). Direct and indirect effects of solar ultraviolet-B radiation on long-term decomposition. *Global Change Biology*, *11*(11), 1982–1989. doi:10.1111/j.1365-2486.2005.01027.x

Pancotto, Veronica A., Sala, O. E., Cabello, M., Lopez, N. I., Matthew Robson, T., Ballare, C. L., Scopel, A. L. (2003). Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community. *Global Change Biology*, *9*(10), 1465–1474. doi:10.1046/j.1365-2486.2003.00667.x

Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., … Fasth, B. (2007). Global-Scale Similarities in Nitrogen Release Patterns During Long-Term Decomposition. *Science*, *315*(5810), 361–364. doi:10.1126/science.1134853

Paul, N. D., & Gwynn-Jones, D. (2003). Ecological roles of solar UV radiation: towards an integrated approach. *Trends in Ecology & Evolution*, *18*(1), 48–55. doi:10.1016/S0169-5347(02)00014-9

Pauli, F. (1964). Soil Fertility Problem in Arid and Semi-Arid Lands. *Nature*, *204*(4965), 1286–1288. doi:10.1038/2041286a0

Predick, K. I., Archer, S. R., Aguillon, S. M., Keller, D. A., Throop, H. L., & Barnes, P. W. (2018). UV-B radiation and shrub canopy effects on surface litter decomposition in a shrub-invaded dry grassland. *Journal of Arid Environments*, *157*(July), 13–21. doi:10.1016/j.jaridenv.2018.06.007

Preisser, E. L., & Bolnick, D. I. (2008). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PloS One*, *3*(6), e2465. doi:10.1371/journal.pone.0002465

Preisser, E. L., Bolnick, D. I., & Benard, M. E. (2016). Scared to Death ? The Effects of Intimidation and Consumption in Predator-Prey Interactions. *Ecology*, *86*(2), 501–509.

Price, C. M., & Pettijohn, D. E. (1986). Biodiversity and litter decomposition in terrestrial ecosystems. *Experimental Cell Research*, *166*(2), 295–311. doi:10.1016/0014-4827(86)90478-7

Pugnaire, F. I., Armas, C., & Maestre, F. T. (2011). Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function. *Journal of Arid Environments*, *75*(12), 1310–1320.

doi:10.1016/j.jaridenv.2011.01.016

Ramón Vallejo, V., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., & Vilagrosa, A. (2012). Perspectives in dryland restoration: approaches for climate change adaptation. *New Forests*, *43*(5–6), 561–579. doi:10.1007/s11056-012-9325-9

Rechner, O., & Poehling, H.-M. (2014). UV exposure induces resistance against herbivorous insects in broccoli. *Journal of Plant Diseases and Protection*, *121*(3), 125–132. doi:10.1007/BF03356500

Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., & Raimundo, J. (2011). Impact of land degradation on soil respiration in a steppe (Stipa tenacissima L.) semi-arid ecosystem in the SE of Spain. *Soil Biology and Biochemistry*, *43*(2), 393–403. doi:10.1016/j.soilbio.2010.11.007

Reyes Reyes, M. V., Iñíguez, M. A., Hevia, M., Hildebrand, J. A., & Melcón, M. L. (2015). Description and clustering of echolocation signals of Commerson's dolphins ( Cephalorhynchus commersonii ) in Bahía San Julián, Argentina. *The Journal of the Acoustical Society of America*, *138*(4), 2046–2053. doi:10.1121/1.4929899

Reynolds, J. F., Smith, D. M. S., Lambin, E. F., Turner, B. L., Mortimore, M., Batterbury, S. P. J., … Walker, B. (2007). Global desertification: building a science for dryland development. *Science (New York, N.Y.)*, *316*(5826), 847–51. doi:10.1126/science.1131634

Rohwer, F., Segall, A., Steward, G., Seguritan, V., Breitbart, M., Wolven, F., & Farooq Azam, F. (2000). The complete genomic sequence of the marine phage Roseophage SIO1 shares homology with nonmarine phages. *Limnology and Oceanography*, *45*(2), 408–418. doi:10.4319/lo.2000.45.2.0408

Rozema, J., Tosserams, M., Nelissen, H. J. M., Heerwaarden, L. Van, Broekman, R. a, & Flierman, N. (1997). Stratospheric ozone reduction and ecosystem processes: enhanced UV-B radiation affects chemical quality and decomposition of leaves of the dune grassland species Calamagrostis epigeios. *Plant Ecology*, *128*, 285–294. doi:10.1023/A:1009723210062

Sanders, D., & van Veen, F. J. F. (2011). Ecosystem engineering and predation: the multi-trophic impact of two ant species. *Journal of Animal Ecology*, *80*(3), 569–576. doi:10.1111/j.1365-2656.2010.01796.x

Santonja, M., Fernandez, C., Gauquelin, T., & Baldy, V. (2015). Climate change effects on litter decomposition: intensive drought leads to a strong decrease of litter mixture interactions. *Plant and Soil*, *393*(1–2), 69–82. doi:10.1007/s11104-015-2471-z

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science (New York, N.Y.)*, *247*(4946), 1043–8. doi:10.1126/science.247.4946.1043

Schmitz, O. J., & Barton, B. T. (2014). Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control. *Biological Control*, *75*, 87–96. doi:10.1016/j.biocontrol.2013.10.001

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. doi:10.1111/j.1461-0248.2010.01511.x

Schneider, F. D., & Brose, U. (2013). Beyond diversity: how nested predator effects control ecosystem functions. *The Journal of Animal Ecology*, *82*(1), 64–71. doi:10.1111/1365-2656.12010

Schuster, M. J., & Dukes, J. S. (2014). Non-additive effects of invasive tree litter shift seasonal N release: a potential invasion feedback. *Oikos*, *123*(9), 1101–1111. doi:10.1111/oik.01078

Sitvarin, M. I., & Rypstra, A. L. (2014). Fear of predation alters soil carbon dioxide flux and nitrogen content. *Biology Letters*, *10*(6), 20140366. doi:10.1098/rsbl.2014.0366

Sitvarin, M. I., Rypstra, A. L., & Harwood, J. D. (2016). Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*, *125*(8), 1057–1068. doi:10.1111/oik.03190

Smith, W. K., Gao, W., Steltzer, H., Wallenstein, M. D., & Tree, R. (2010). Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Global Change Biology*, *16*(1), 484–495. doi:10.1111/j.1365-2486.2009.01973.x

Solé, R. (2007). Scaling laws in the drier. *Nature*, *449*(7159), 151–153. doi:10.1038/449151a

Song, X., Peng, C., Jiang, H., Zhu, Q., & Wang, W. (2013). Direct and indirect effects of UV-B exposure on litter decomposition: a meta-analysis. *PloS One*, *8*(6), e68858. doi:10.1371/journal.pone.0068858

Song, X., Zhang, H., Jiang, H., Donaldson, L. A., & Wang, H. (2013). Influence of elevated UV-B radiation on leaf litter chemistry and subsequent decomposition in humid subtropical China. *Journal of Soils and Sediments*, *13*(5), 846–853. doi:10.1007/s11368-013-0661-y

Stephan, J. G., Stenberg, J. A., & Björkman, C. (2017). Consumptive and nonconsumptive effect ratios depend on interaction between plant quality and hunting behavior of omnivorous predators. *Ecology and Evolution*, *7*(7), 2327–2339. doi:10.1002/ece3.2828

Stringer, L. C., Dougill, A. J., Thomas, A. D., Spracklen, D. V., Chesterman, S., Speranza, C. I., … Kopolo, G. (2012). Challenges and opportunities in linking carbon sequestration, livelihoods and ecosystem service provision in drylands. *Environmental Science & Policy*, *19–20*, 121–135. doi:10.1016/j.envsci.2012.02.004

Tan, A. W., & Nuttall, F. Q. (1975). Characteristics of the dephosphorylated form of phosphorylase purified from rat liver and measurement of its activity in crude liver preparations. *Biochimica et Biophysica Acta*, *410*(1), 45–60. doi:10.1016/0005-2744(75)90206-5

Throop., & Archer, S. R. (2007). Interrelationships Among Shrub Encroachment, Land Management, and Litter Decomposition in a Semidesert Grassland. *Ecological Applications*, *17*(6), 1809–1823.

Throop, H. L., & Archer, S. R. (2009). *Resolving the Dryland Decomposition*

*Conundrum: Some New Perspectives on Potential Drivers*. (U. Lüttge, W. Beyschlag, B. Büdel, & D. Francis, Eds.), *Progress in Botany* (Vol. 70). Berlin, Heidelberg: Springer Berlin Heidelberg. doi:10.1007/978-3-540-68421-3

Tirado Fernández, R. (2003). *Interacciones Positivas entre plantas: Mecanismos y consecuencias.*

Tirado, R. (2009). Matorrales arborescentes con Ziziphus. In  y M. R. y M. Ministerio de Medio Ambiente (Ed.), *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España.*

Tirado, R., & Pugnaire, F. I. (2005). Community structure and positive interactions in constraining environments. *Oikos*, *111*(3), 437–444. doi:10.1111/j.1600-0706.2005.14094.x

Tiunov, A. V. (2009). Particle size alters litter diversity effects on decomposition. *Soil Biology and Biochemistry*, *41*(1), 176–178. doi:10.1016/j.soilbio.2008.09.017

Uselman, S. M., Snyder, K. A., Blank, R. R., & Jones, T. J. (2011). UVB exposure does not accelerate rates of litter decomposition in a semi-arid riparian ecosystem. *Soil Biology and Biochemistry*, *43*(6), 1254–1265. doi:10.1016/j.soilbio.2011.02.016

Verhoef, H. A., Verspagen, J. M. H., & Zoomer, H. R. (2000). Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. *Biology and Fertility of Soils*, *31*(5), 366–371. doi:10.1007/s003749900181

Verstraete, M. M. (1986). Defining desertification: A review. *Climatic Change*, *9*(1–2), 5–18. doi:10.1007/BF00140520

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M. P., Petchey, O., Palmborg, C., & Huss-Danell, K. (2009). Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology*, *90*(1), 90–9. doi:10.1890/08-0382.1

Wagg, C., Bender, S. F., Widmer, F., & van der Heijden, M. G. A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality.

*Proceedings of the National Academy of Sciences of the United States of America*, *111*(14), 5266–70. doi:10.1073/pnas.1320054111

Wang, J., Liu, L., Wang, X., & Chen, Y. (2015). The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. *Global Change Biology*, *21*(5), 2095–104. doi:10.1111/gcb.12812

Wang, J., Liu, L., Wang, X., Yang, S., Zhang, B., Li, P., … Liu, W. (2017). High night-time humidity and dissolved organic carbon content support rapid decomposition of standing litter in a semi-arid landscape. *Functional Ecology*, *31*(8), 1659–1668. doi:10.1111/1365-2435.12854

Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and Plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, *79*(2), 247–258.

Wardle, D. a, Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science (New York, N.Y.)*, *304*(5677), 1629–33. doi:10.1126/science.1094875

Wu, X., Duffy, J. E., Reich, P. B., & Sun, S. (2011). A brown-world cascade in the dung decomposer food web of an alpine meadow: effects of predator interactions and warming. *Ecological Monographs*, *81*(2), 313–328. doi:10.1890/10-0808.1

Yanni, S. F., Suddick, E. C., & Six, J. (2015). Photodegradation effects on CO2 emissions from litter and SOM and photo-facilitation of microbial decomposition in a California grassland. *Soil Biology and Biochemistry*, *91*, 40–49. doi:10.1016/j.soilbio.2015.08.021

Yao, M., Rosenfeld, J., Attridge, S., Sidhu, S., Aksenov, V., & Rollo, C. D. (2009). The Ancient Chemistry of Avoiding Risks of Predation and Disease. *Evolutionary Biology*, *36*(3), 267–281. doi:10.1007/s11692-009-9069-4

Yasui, T., Sumita, T., & Tsunogae, S. (2004). Stability of myofibrillar EDTA-ATPase in rabbit psoas fiber bundles. *Journal of Agricultural and Food Chemistry*, *23*(6), 1163–8. doi:10.1021/jf60202a030

Zepp, R. G., Callaghan, T. V., & Erickson, D. J. (1998). Effects of enhanced solar ultraviolet radiation on biogeochemical cycles. *Journal of Photochemistry and Photobiology B: Biology*, *46*(1–3), 69–82. doi:10.1016/S1011-1344(98)00186-9

Zepp, R. G., Erickson, D. J., Paul, N. D., & Sulzberger, B. (2007). Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochemical & Photobiological Sciences : Official Journal of the European Photochemistry Association and the European Society for Photobiology*, *6*(3), 286–300. doi:10.1039/b700021a

Zhang, Q., & Zak, J. C. (2010). Effects of Gap Size on Litter Decomposition and Microbial Activity in a Subtropical Forest. *America*, *76*(7), 2196–2204.

Zhang, X., & Wang, W. (2015). Control of climate and litter quality on leaf litter decomposition in different climatic zones. *Journal of Plant Research*, *128*(5), 791–802. doi:10.1007/s10265-015-0743-6

Zimmer, M., Kautz, G., & Topp, W. (2005). Do woodlice and earthworms interact synergistically in leaf litter decomposition? *Functional Ecology*, *19*(1), 7–16. doi:10.1111/j.0269-8463.2005.00926.x

## 1.10 Objectives

In this thesis we address the abiotic and biotic factors that contribute to litter decomposition in order to contribute to the understanding of this complex process in the scarcely studied context of drylands. We directly manipulated UV radiation as the main abiotic factor, whereas as biotic drivers we manipulated microorganisms, detritivores and predators, and the effects of litter mixtures. We also considered multiple drivers at once (temperature, moisture, abrasion, UV) by testing decomposition under and away of *Z. lotus* shrubs.

All the assessments of decomposition were based on leaf litter mixtures as complex substrate, where multiple abiotic and biotic interactions occur, including interception of UV radiation, the creation of complex microenvironment conditions that provides a diversity of nutrients for microbial activity and detritivore performance and finally regulate predator prey interactions. The aims of this thesis are:

1. To quantify the effects of UV radiation and microbial activity and its interaction in two stages of decomposition, and to explore the legacy effects of these interactions during the early stage on a later stage of decomposition involving detritivores (Chapter 1).
2. To evaluate the multiple effects of predators on decomposition via indirect consumptive and non-consumptive effects, and via ecological engineering effects, and how they may generate synergies with litter mixtures (Chapter 2).
3. To assess the role of fertility islands on decomposition of leaf litter mixtures in drylands (Chapter 3).

## 1.11 Details of procedures and tests by chapter

In the **first chapter** we conducted a two-stage laboratory experiment in which we assessed the direct (photodegradation) and indirect (photopriming) effects of UV radiation on the mass loss of three common species in drylands in SE Spain (*Chamaerops humilis, Retama sphaerocarpa* and *Stipa tenacissima*). Using monospecific litter and leaf litter mixtures we tested the impact of photodegradation alone and the positive or negative impact of UV radiation on decomposition driven by microorganisms, during the first stage of decomposition, and on decomposition driven by detritivores and their performance in a second stage. In the **second chapter,** we designed a laboratory patch-choice experiment, which allowed exploring the effects of a large soil predator on litter mass loss. We focused on consumptive and non-consumptive effects of spiders on detritivores and additionally, we explored the ecosystem engineering effects of predators on leaf litter mixture decomposition. Finally, in the **third chapter,** in a field experiment we assessed the role of *Ziziphus lotus* fertility islands on litter decomposition under shrub canopy and in gaps, and analyzed its effects on decomposition of leaf litter mixtures and monospecific litter.

# Chapter 2. Microbes, not photodegradation, affect detritivore-driven and litter mixture decomposition

Prado López, M., Moya-Laraño, J., Pugnaire, F.I. Microbes, not photodegradation,
affect detritivore-driven and litter mixture decomposition.
Submitted to *Functional Ecology*

## 2.1 Abstract

1. Litter decomposition is a key ecosystem process driven by photodegradation in drylands. However, how photodegradation may interact with the different biotic components such as microbes, detritivores and plant diversity is still largely unknown.
2. In a laboratory experiment using biotic components from a dryland ecosystem from South-East Spain, we assessed the extent to which photodegradation and microbial activity contribute to litter decomposition and tested the combined effects of these factors on the performance of isopods, a major detritivore guild in this ecosystem. We also tested these effects on litter mixtures. We hypothesized that photodegradation would enhance microbial activity, and that both factors, either additively and synergistically, would accelerate decomposition by detritivores. Also, we predicted that the three factors above would enhance the synergistic effects of litter decomposition in mixtures.
3. The experiment was conducted in two stages that aimed at assessing the priming effects of UV radiation and microbial activity on mixtures and monospecific litter, and the legacy effects on detritivore activity. In the first stage, litter was exposed to UV radiation for 7 months. To tell apart UV radiation from microbial effects, we sterilized half the litter using biocides. In the second stage, we added isopods for 80 days to assess the legacy effects of our manipulations on further litter decomposition.
4. UV radiation accounted for a small proportion (<3%) of the total litter decomposition, and was equivalent to that of microbes alone. We did not find cumulative effects of UV radiation and microbial activity, and thus no photopriming effects could be concluded. However, microbes had important legacy effects on detritivores as we found substantial cumulative effects of microbes and detritivores adding up to 42% of total decomposition. In addition, microbial removal reverted litter mixture synergistic effects.
5. UV radiation had a minor effect as compared to microbes in their legacy effects on detritivore-driven decomposition. Since microbes are also involved in synergistic effects in mixtures and we also found litter species-identity effects, we suggest that biodiversity is much more important driving

decomposition in drylands than previously thought, providing new insights on how biotic factors affect dryland ecosystem processes.

**Keywords:** Carbon cycling; Decomposition; Drylands; Functional traits; Isopoda; Photopriming; Plant diversity; Soil Microbial Community

## 2.2 Introduction

Litter decomposition is a critical ecosystem process linked to nutrient cycling, soil fertility and global carbon balance (Bünemann *et al.*, 2018; Verduzco *et al.*, 2018). In high-irradiance environments such as drylands, decomposition is initially driven by photodegradation caused by UV-B (280–315 nm) and UV-A (315–400 nm). In drylands, standing dead biomass is often exposed to UV radiation, leading to a substantial fraction of carbon being lost directly to the atmosphere as $CO_2$ without cycling through soil pools (Austin and Vivanco, 2006). In addition to UV, microorganisms have a main role in decomposition (Almagro *et al.*, 2016; Wang *et al.*, 2017) although the impact of photodegradation on microbial activity is not well understood and negative and positive effects have been reported. For example, photodegradation facilitates microorganisms access to litter through a process termed photopriming (Baker, Allison, and Frey, 2015); i.e., the depolymerisation of complex carbon molecules such as lignin, cellulose, hemicellulose, and aromatic compounds that may restrict microbial activity (Baker, *et al.*, 2015; García-Palacios, *et al.*, 2016; King *et al.*, 2012). However, UV radiation may also have direct, negative consequences for microbial activity through DNA alterations that affect microbial community structure and negatively impact decomposition (Lin, Scarlett, and King, 2015).

UV radiation may also affect detritivores, although these effects have been rarely assessed (Coyle *et al.*, 2017) and may be underreported (Austin and Ballaré, 2010; Manzoni, *et al.*, 2008). The performance of isopods, one of the most abundant detritivore guilds in Spain drylands, is governed both by the presence of plant secondary compounds, such as tannins and flavonoids (Boelter, Quadros and Araujo, 2009; Hassall, *et al.*, 2006), and by microbial communities colonizing the substrate, as they feed on both (Zimmer, Kautz and Topp, 2005). Since UV radiation affects litter chemical composition and the structure of the microbial community, we propose that photodegradation should have important consequences for detritivore performance and overall litter decomposition (Boelter, *et al.*, 2009; Hassall, *et al.*, 2006). Photodegradation has been addressed mostly on monospecific litter samples (Almagro *et al.*, 2015, 2016), ignoring the fact that litter from different species usually mix in plant patches. Litter mixtures may modify decomposition rates through additive or non-additive effects (Castro-Díez, Alonso and Romero-Blanco, 2019; Gartner and Cardon, 2004). However, we do not know whether photodegradation may differentially affect litter mixtures nor how UV light interacts with the effects of high temperatures and water shortage in dry systems (Birkhofer *et al.*, 2011; García-Palacios *et al.*, 2016; Hooper and Vitousek, 1997; Wardle, Bonner and Nicholson, 1997). Most research on litter mixtures has been conducted in mesic ecosystems where the effect of photodegradation has been largely overlooked (Martínez-Yrízar, Núñez, and Búrquez, 2007; Verhoef, Verspagen and Zoomer, 2000). Furthermore, the synergistic effects of litter mixtures have been shown to be more pronounced when detritivores are involved in the decomposition process (De Oliveira, Hättenschwiler and Handa, 2010; Hattenschwiler and Gasser, 2005).

In a laboratory experiment we manipulated UV radiation, microbial communities, leaf litter composition and presence of detritivores to test whether litter decomposition would increase as a result of the combined effects of UV radiation and microbial activity (photopriming) (Wang, Wang and Chen, 2015). We predicted that litter mixtures would enhance the effects of photodegradation and microbial activity on mass loss as they create a favorable, more structured microenvironment (Gartner and Cardon, 2004; Hättenschwiler and Gasser, 2005). Finally, we hypothesized that the impact of photodegradation on litter chemical composition and growth of microbial communities would contribute to enhance detritivore performance, particularly in litter mixtures.

Under controlled conditions, we conducted and experiment in two stages. In the first stage we exposed leaf litter to UV radiation and biocides using either monospecific litter of each of 3 plant species or a mixture of the three of them. After estimations of mass loss, we presented litter to isopods in order to assess the consequences of UV radiation and microbial activity on isopod performance and their contribution to litter decomposition. The purpose of stage 1 was to mimic the high heat, high UV, and low water availability conditions outside the rainy season, and the purpose of stage 2 was to mimic the effects of soil fauna during the colder and wetter months of winter, when detritivores are more active. We predicted that a) decomposition would increase as a result of the combination of UV radiation and microbial activity (photopriming effects); b) photopriming effects would be more important in litter mixtures than in monospecific litter; c) photopriming effects would enhance isopod performance in later decomposition stages; d) Regardless of UV radiation, microbial effects would also increase litter decomposition; and e) all of the above enhancing effects would be more pronounced in litter mixtures.

## 2.3 Materials and Methods

### 2.3.1 Site and species selection

We collected fresh litter of three different plant species from three different functional types in which litter starts decomposing while still standing on the plant. We selected *Chamaerops humilis* L., a dwarf palm; *Retama sphaerocarpa* L. (Boiss), a leguminous shrub, and *Stipa tenacissima* L., a tussock-grass species. *Stipa* and *Retama* litter was collected in the Tabernas basin (37°02’ N, 2°24’ W) and *Chamaerops* litter in Cabo de Gata-Nijar Natural Park (36°43’ N, 2°11’ W) both in Almeria, Spain. After collection, plant material was oven-dried at 60°C for 72 h and then trimmed to 10 cm-long segments (10 x 1 cm in *Chamaerops*). A subsample of each litter sample was obtained to assess differences in physical and chemical composition. Carbon (C) and nitrogen (N) content were determined using a C/N analyzer (LECO Truspec, St. Joseph, MI, USA). Water holding capacity (WHC) and specific leaf area (SLA) were assessed according to Pérez-Harguindeguy *et al*. (2013). The selected species show substantial differences in the measured traits (Table 1).

Table 1. Chemical and physical characteristics of *Chamaerops humilis*, *Retama sphaerocarpa* and *Stipa tenacissima* litter collected in Almeria province, SE Spain. Values are Mean ± 1 SE (n = 3). Values in a column with the same superscript letter are not significantly different (Tukey-test).

| | **C (mg / g$^{-1}$)** | **N (mg / g$^{-1}$)** | **WHC (%)** | **C/N (mg / g$^{-1}$)** | **SLA (cm$^{2}$/g$^{-1}$)** |
|---|---|---|---|---|---|
| ***C. humilis*** | 47.6 ± 0.03$^{b}$ | 1.65 ± 0.01$^{c}$ | 115.41 ± 2.35$^{c}$ | 37.13 ± 0.95$^{b}$ | 51.67 ± 2.87$^{c}$ |
| ***R. sphaerocarpa*** | 48.19 ± 0.02$^{c}$ | 1.89 ± 0.01$^{b}$ | 85.14 ± 2.48$^{b}$ | 27.24 ± 0.07$^{a}$ | 26.59 ± 0.43$^{a}$ |
| ***S. tenacissima*** | 46.5 ± 0.01$^{a}$ | 0.57 ± 0.001$^{a}$ | 64.61 ± 1.02$^{a}$ | 90.58 ± 0.33$^{c}$ | 38.43 ± 1.62$^{b}$ |

In the second stage we used *Porcellio ornatus* (L.) (Isopoda: Porcelionidae), a detritivore highly abundant and widespread in the area. Adult individuals were hand-collected and kept in plastic containers for one week prior to the beginning of the experiment, being fed plant material (*Avena* sp.) from the place they were collected and supplied with water.

### 2.3.2 First stage of decomposition

The first stage started in May 2017 and ended in December 2017. We used 20 x 20 cm plastic trays filled with 3 g (dry mass) of litter of each species in monospecific samples, and 1 g of each species in mixtures. The material was oven-dried (48 h at 60ºC) before weighing. We will refer to monospecific treatments by the plant genus (*Stipa, Retama* and *Chamaerops*) and to the 3-species mix as mixture. We had four levels concerning plant diversity (three monospecific levels plus the mixture); two UV levels (+ and -) and two of biocide (+ and -), with 17 replicates, yielding a total of 272 trays. We used UV lamps (325–400 nm wavelengths) to irradiate litter and withe light lamps (400–700 nm) as control. The UV radiation used in this experiment accounted for 7 kJ/day, the mean daily UV irradiance reported for the study site during summer (Almagro *et al*., 2015). Trays were randomly distributed in a flat platform 20 cm below the lamps for 200 days of continuous exposition. Due to logistic constraints, the UV-irradiation treatment was located in a room and the control treatment in another. The control room remained at 28.43±0.06$^{o}$C and 65-70% air humidity throughout the duration of the experiment and the UV chamber was at 29.24±0.02$^{o}$C and 65-70% humidity. Decomposition was estimated by physically and carefully separating samples by species identity in the mixture samples, oven-drying them (48 h at 60ºC) and weighing them to the nearest 0.001g. This procedure allowed us to include species identity as an additional factor analysis.

### 2.3.3 Microbial inhibition

To tell apart irradiance-induced biomass loss from microbial decomposition, we used biocides to minimize microbial loads (Rutledge, *et al*., 2010). We sprayed half the litter samples before UV exposition with Captan® (N-trichloromethyl-thio-tetrahydroftalimide), a common fungicide (Badalucco, *et al*., 1994; Johnson *et al*., 2005), and the wide-spectrum antibiotic dihidrostreptomycin (Feckler, Goedkoop, Zubrod, Schulz, and Bundschuh, 2016). Both were selected because they had been used frequently in similar studies and did not show effects on isopod performance (Ihnen and Zimmer, 2008). These products were diluted 1:3 (v/v) in distilled water and sprayed once a month with 3 ml of product, while control treatments received 3 ml of distilled water. Applications were repeated every month because the product effects only last about 50 days (Chen, Edwards and Subler, 2001).

The experiment was carried out under dry conditions to maximize UV radiation effects since it is known that they are enhanced under water shortage (Almagro *et al.*, 2015; Bradford, *et al.*, 2015), while microbial degradation is noticeable even in dry conditions (Day, Guenon, and Ruhland, 2015). Therefore, no water other than the used for biocide application was supplied. At the end of the first stage we took three replicates per treatment (i.e., 24 samples) for water holding capacity analyses, and the remaining replicates were used for the second stage of the experiment.

### 2.3.4 Second stage

The second stage was carried out between December 2017 and March 2018. Samples from each of the first-stage treatments (i.e., UV-irradiated and control, either sterilized or not) were divided into two groups, one with isopods and one without (control), each with 7 replicates, yielding a total of 224 microcosms. Litter from each stage 1 samples was placed in a 18 x 11 cm plastic microcosm over a 2.5 cm layer of culturing substrate (calcium sulphate with activated charcoal) to keep humidity levels steady and soak up animal waste (OECD, 2016). Each microcosm received five large isopods (>1 cm long; average fresh mass 0.82mg ± 0.13 SE, n = 40), while control treatments received none. Dead isopods were recorded, removed and replaced every week to keep numbers steady. Microcosms were located in a chamber with 16:8 h light:dark cycles for 80 days, with temperature similar to the mean annual registered in Cabo de Gata-Nijar Natural Park (20±2°C) and 60% air relative humidity, and were additionally sprayed 5 ml of distilled water each week in order to keep a moist substrate and mimic winter conditions. Before offering it to isopods, all litter was carefully washed with distilled water to remove biocide residues and blotted dry with paper towels. After 80 days we finished stage 2 and the remaining litter was oven-dried at 60°C for 72 h, litter mixtures were sorted by plant species, and mass loss per species assessed by weighing.

## 2.4 Statistical analyses

All analyses were performed using R 3.6.1 (R Core Team, 2019). Litter mass loss was calculated as the percentage of the difference between initial and final dry mass: i.e.; [(initial-final)/initial]*100. Litter diversity effects, considered as additive or non-additive (synergic or antagonistic), were estimated by calculating the net diversity effect (NDE), a difference/sum ratio based on the RII index (Armas, Ordiales and Pugnaire, 2004), for which we used the recorded mass loss of a species in the mixture (M) and in monospecific treatments (S).

$$NDE = (M - S) / (M + S)$$

NDE is positive when a species decomposes more in mixtures than in monospecific samples, and *vice versa*.

We determined the effects of UV (Irradiated *vs* Control), microbial activity (Sterilized *vs* Unsterilized), species composition (Monospecific *vs* Mixtures), and isopod activity (Presence *vs* Absence) on litter loss using General Linear Models. In all these models we used backward elimination starting with third order interactions and eliminating non-significant terms, keeping only the final model with all significant terms. When necessary (e.g., to check for differences among plant species), we ran Tukey post-hoc tests using the functions in library "emmeans" version 1.4.3. (Lenth 2019). Biomass loss data were boxcox-transformed to account for normality deviations of residuals among treatments. Data was back-transformed using the "make.tran" function in "emmeans". The function "eff_size" was also used to compare Cohen's effect sizes when necessary.

## 2.5 Results

### 2.5.1 Stage 1

After 200 days of UV exposition, we found that the combined effects of UV radiation and microbial activity were similar to the contribution of UV radiation alone (i.e., with biocides) in reducing litter mass (mean ± SD, 3.5 ± 0.31 g vs 3.8 ± 0.2 g, respectively) and also similar to the effects of microorganisms alone (i.e., without UV or biocides; 3.3 ± 0.2 g). The lowest mass loss was recorded in treatments where microbial activity was reduced by biocides and received no UV radiation (1.83 ± 0.2

g). Microbial activity drove decomposition of UV-exposed samples, as suggested by the significant interaction of UV with Biocides ($F_{1,\ 334} = 5.09$, $p < 0.05$; Table 1S). When biocides were applied, decomposition was higher in UV than in control treatments, indicating that UV alone has an important effect on decomposition regardless of its effect on the microbiota ($Z = 4.2$, $p < 0.0001$; Fig. 1). However, during the first stage UV radiation accounted overall for less than 3% of the total decomposition process.

Litter mixtures showed higher mass loss than monospecific samples (Fig. 2), and UV irradiation increased mass loss in monospecific samples ($Z = 4.4$, $p < 0.001$), but not in mixtures ($Z = 0.90$, $p = 0.36$; interaction UV x Mixtures; $F_{1,\ 334} = 6.34$, $p <0.05$; Table 1S; Fig.2). Finally, UV radiation did not cause differences in decomposition among species ($F_{2,\ 332} = 2.33$, $p = 0.098$; Fig. 3).

Figure 1. Litter mass loss (%) under UV radiation (UV+) and white light exposition (UV-) with and without biocides. Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars show statistical differences (*** = $P < 0.001$). $\alpha = 0.05$ level (lsm pairwise-tests).

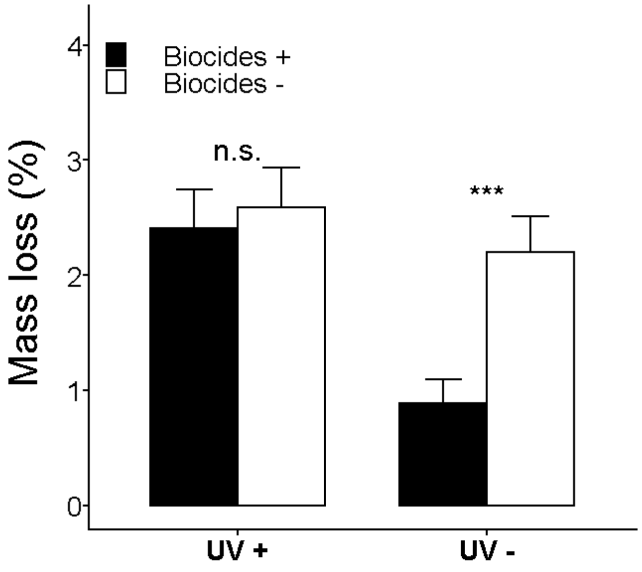


Figure 2. Litter mass loss (%) in monospecific and in mixtures under UV radiation (UV+) and white light (UV-). Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars show statistical differences (*** = $P < 0.001$). $\alpha = 0.05$ level (lsm pairwise-tests).

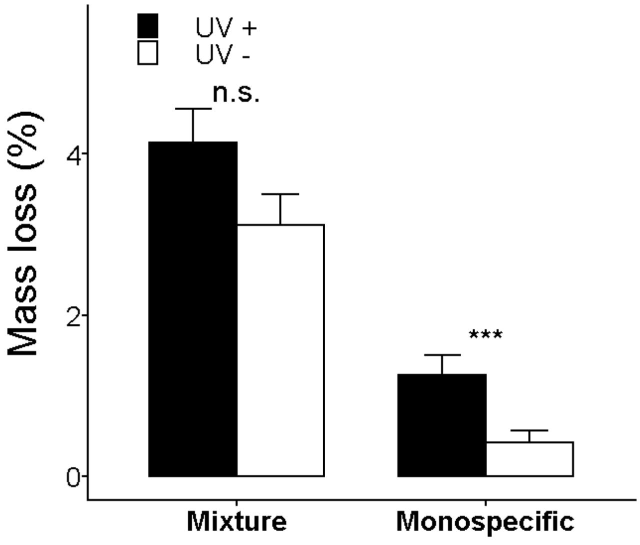
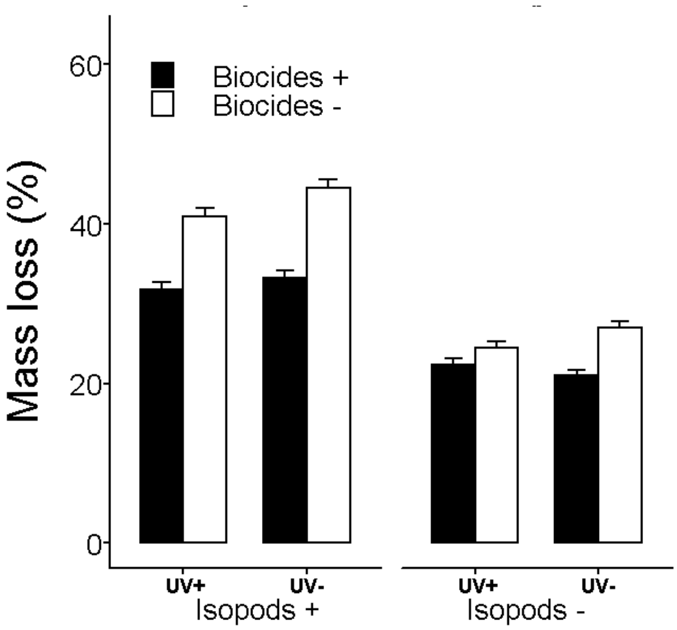


Figure 3. Litter mass loss (%) under UV radiation (UV+) and (UV-), with and without biocides and with and without isopods. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).



## 2.5.2 Stage 2

After 80 days of decomposition in the second stage, decomposition with or without isopods decreased with the use of biocides (Fig. 4). However, a strong significant Biocide *vs* Isopod interaction ($F_{1,\ 318}$ = 14.23, p < 0.001; Table 1S) indicated strong legacy effects of microbes on isopod-driven decomposition as Cohen's effect size for biocide presence/absence was ca. 2X as large when isopods were present (-1.61[-1.91,-1.31]) than when they were absent (-0.79[-1.092,-0.48]).

Isopods increased decomposition rate across all plant species, being *Chamaerops* the species where isopods had the strongest effect on mass loss (Fig. 5). Finally, the significant interaction between Mixtures *vs* Biocides *vs* Species Identity ($F_{2,\ 318}$ = 3.819, p < 0.05; Table 1S) showed that either in mixture or monospecific, *Retama* and *Stipa* had no differences in decomposition between sterilized and unsterilized litter. In contrast, *Chamaerops* decomposed more in mixtures relatively to monocultures in sterilized (Z = -5.56; P < 0.0001; Fig. 6) but no in unsterilized treatments (Z = -0.92;P = 0.35).

Figure 4. Litter mass loss (%) after 80 days of exposition to isopods. Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars indicate statistical differences (*** = P < 0.001). α = 0.05 level (lsm pairwise-tests).

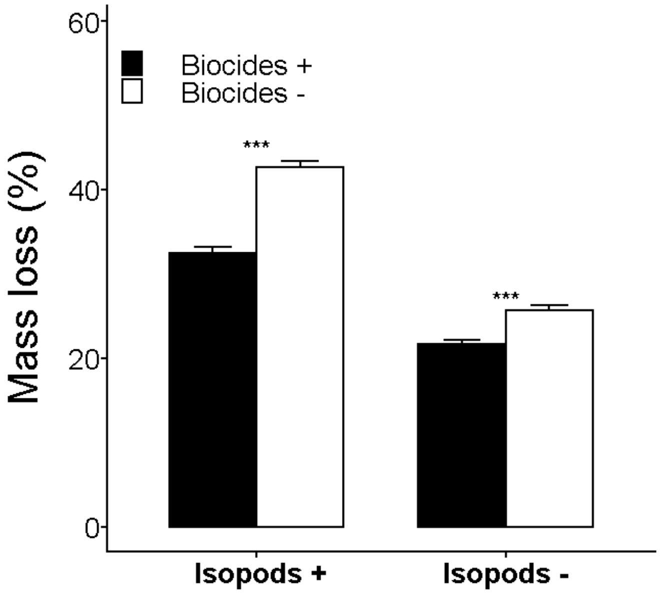


Figure 5. Effects of 80 days of isopods exposition (stage 2). Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars indicate statistical differences (*** = P < 0.001). α = 0.05 level (lsm pairwise-tests).

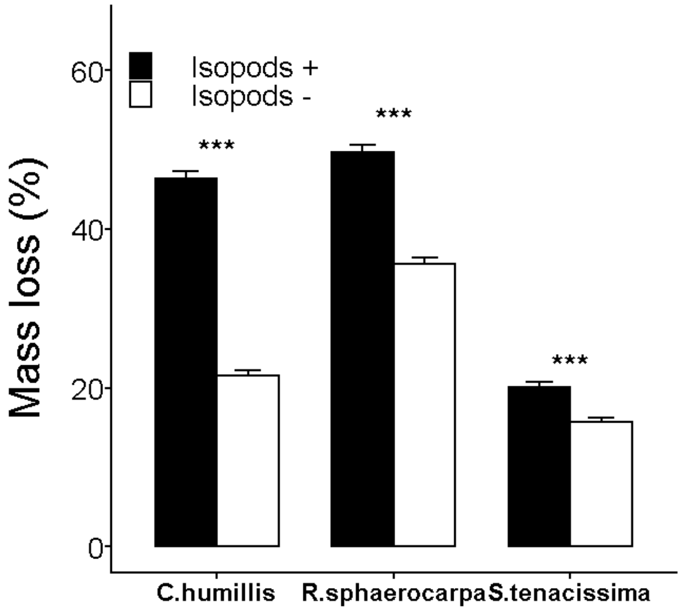
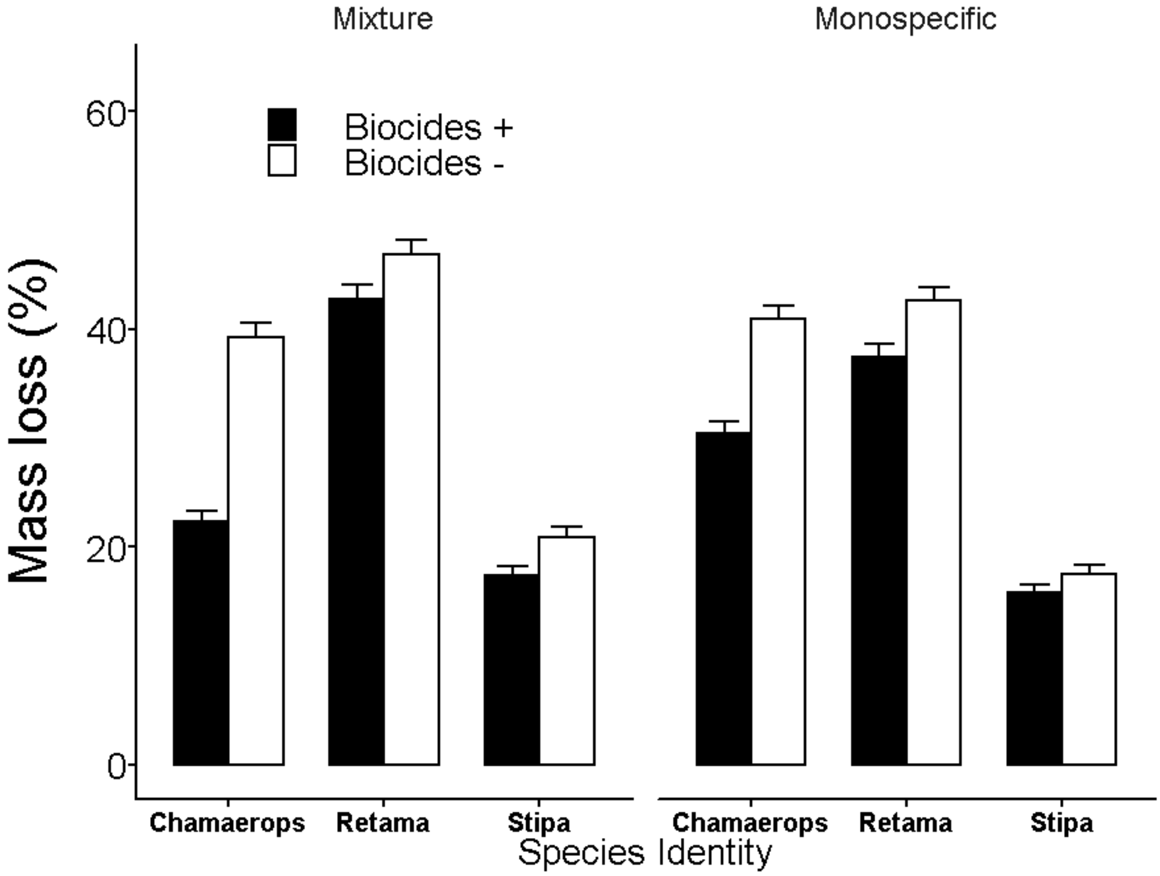


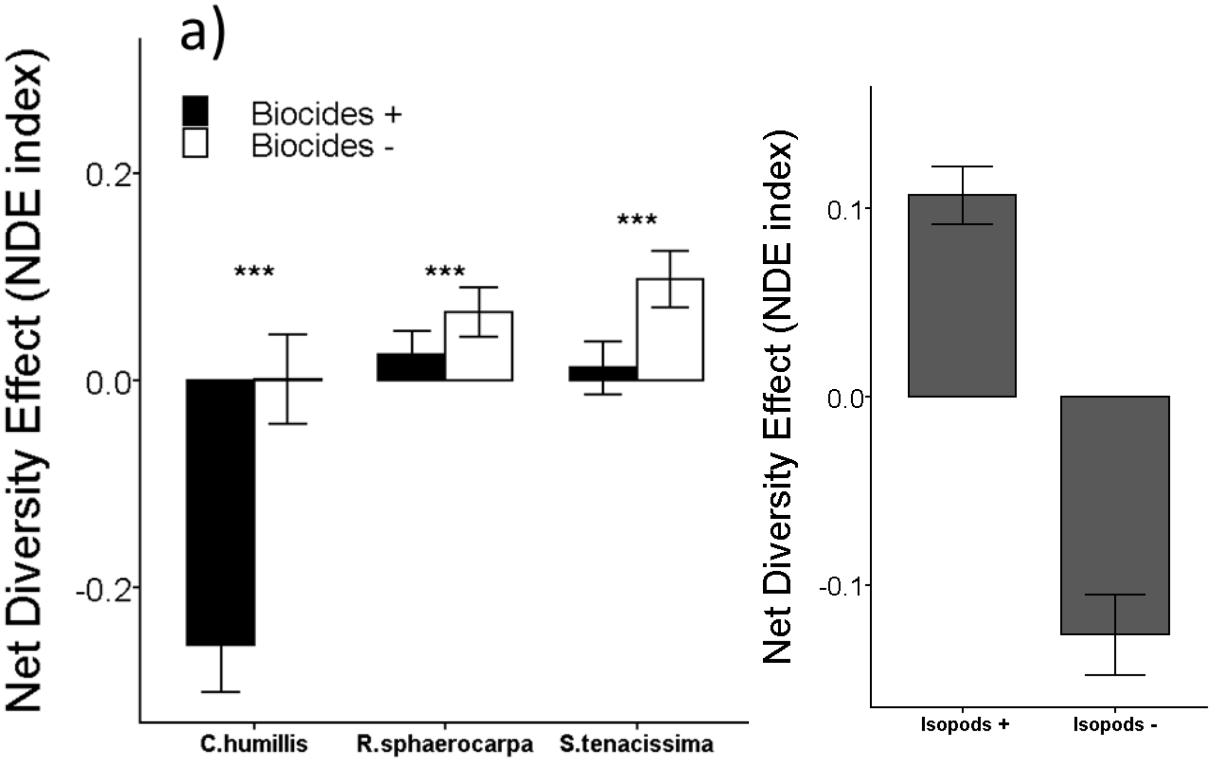
Figure 6. Biomass loss (%) of the different species and mixture after 80 days of exposition to isopods. Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars indicate statistical differences (*** = P < 0.001). α = 0.05 level (lsm pairwise-tests).



### 2.5.3 Antagonisms and synergies from mixtures

In the first stage of the experiment, decomposition of litter mixtures resulted only in additive effects (no differences between monospecific *vs* mixtures), regardless of UV or biocide exposition (Table 2S). In contrast, during the second stage there were both synergies (i.e., higher decomposition rates in mixtures than in monospecific) and antagonisms (i.e., lower decomposition rates in mixtures than in monospecific) triggered by the presence of isopods and by the use of biocides. Isopods substantially led to synergisms, whereas treatments without isopods led to antagonisms (Fig. 7). Moreover, a significant interaction between Biocides *vs* Species Identity ($F_{2,\ 57}$ = 11.76, p< 0.001), revealed that unsterilized litter resulted in synergisms or null effects for the three leaf litter species. By contrast, litter exposed to biocides showed null mixture effects in *Retama* and *Stipa*, while in *Chamaerops* there was an intense antagonism (Fig. 7).

Figure 7. Net diversity effect (NDE index) during the second stage of the experiment for a) plant species identity, and b) for isopod presence/absence. Positive values mean additive effects (synergies) and negative non-additive effects (antagonisms). Bars indicate GLM model predicted means and SE after back transformation (from boxcox). Stars indicate statistical differences (*** = P < 0.001). α = 0.05 level (lsm pairwise-tests).



## 2.6 Discussion

Most previous reports on decomposition in drylands focused on the influence of UV radiation on monospecific litter or on the effects of micoorganisms, overlooking the importance of litter mixtures and detritivores, and their potential synergies with micoorganisms. Here we show that photodegradation may have been previously overestimated by not considering mixture effects or the separate effects of microorganisms. Indeed, the influence of UV radiation is significantly smaller in mixtures than in monospecific litter. These fact may explain previous discrepancies between modeled and observed decomposition rates in drylands (Brandt, King and Milchunas, 2007; Day, Zhang and Ruhland, 2007; Foereid, *et al*., 2011; Zepp, *et al*., 2007).

Decomposition in the second stage was much higher than on stage 1 (compare magnitude of the y-axis in Figs. 1-2 to that in Figs. 4-6), even if isopods where not present on the mesocosms. This higher rate occurred whether due to the new conditions of higher water availability, no UV exposure and milder temperatures; or merely due to the fact that the decomposition process was more advanced. Our data support previous reports suggesting that UV radiation effects may be independent from biotic effects (Brandt, *et al*., 2010). These results may be relevant to understand how litter decomposes in drylands, where it may remain either on the plant or on the ground, and to understand the interaction between abiotic and biotic factors, which have effects difficult to disentangle when predicting decomposition in drylands.

### 2.6.1 Lack of evidence for photopriming effects

Since UV radiation seems to facilitate microbial decomposition (Baker, and Allison, 2015; García-Palacios, *et al*., 2016; King *et al*., 2012), we expected that UV radiation would increase litter decomposition by affecting microorganisms in the first stage of our experiment and by affecting isopods in the second stage. Our results show that UV radiation significantly increased decomposition regardless of microbial activity, and that when UV radiation was present, the effect of microorganisms was negligible (i.e., decomposition with UV radiation was equally high whether microbial were present or not) suggesting a simultaneous effect of UV radiation beyond that of microorganisms, as previously reported by Johnson (2003) and Almagro et al. (2016). Our results do not show that photodegradation is more important for decomposition than microbial activity, as did Austin and Vivanco (2006), but rather that decomposition by UV equaled that of microorganisms. We also failed to find synergistic effects between microbiota and UV radiation. Thus, overall in the first stage of the experiment we did not find evidence of photopriming effects. Furthermore, the first stage of decomposition accounting only of as much as 3% of overall decomposition.

The first part of our experiment evidenced that on the early stages of decomposition microorganisms and UV radiation play a significant albeit small role on standing litter decomposition (Gliksman, *et al*., 2018). We may have missed, however, the precise effects of UV radiation, since litter used in our experiment had already been exposed to photodegradation when collected. Also, the relatively short time of UV exposition may have played a role, as photodegradation effects may take longer time periods to appear (see below). Nevertheless, we found that plant physical properties changed after UV exposition and, for instance, WHC increased substantially after exposure to UV (Table 3S), suggesting that after UV light, water holding capacity could play an important role, strongly affecting decomposition. This point should be tested with further research in the future.

Overall, isopods increased decomposition, regardless of UV exposition. However, we did not find any evidence of photopriming effects on detritivores. Moreover, UV radiation had a negative effect on microbial activity as reported also by Lin *et al*. (2015); i.e., without isopods, unsterilized litter lost less mass in irradiated than in non-irradiated treatments, likely because UV radiation also had sterilizing effects. In contrast, treatments with isopods showed higher decomposition in unsterilized than in sterilized litter, regardless of UV exposition, suggesting that isopods could somehow compensate the negative effects of photodegradation on microbiota. These compensatory effects of isopods could be explained by several mechanisms such as the direct consumption of litter, the facilitation of microbial decomposition by breaking the litter substrate (Jia *et al*., 2014), or the stimulation of microbial activity through the addition of microorganisms by isopods excreta (Zimmer and Topp, 1997).

Overall isopods and microbial activity had a strong cumulative effect on litter decomposition with effect size of microbial legacy (biocides having being use in stage 1) being twice as large when isopods were present as compared as when they were absent. Isopods significantly increased decomposition of unsterilized litter, especially in *Chamaerops*, and this species-specific effect suggests that different microbes in different plant species may interact with detritivores and impact decomposition in different, largely unknown ways.

The lack of photopriming effects may be explained by the fact that photodegradation becomes evident only after several months, when litter chemistry changes and increases biodegradability; i.e., after 12–24 months (Wang *et al*., 2017).  Additionally, photopriming effects may disappear by the continuous UV exposition in our experiment. It has been reported that the use of dark-light cycles significantly improves microbial activity and enhance photopriming effects (Gliksman *et al*., 2016; Lin *et al*., 2018). The continuous UV exposition in our experiment might have restricted microbial activity.

Plant species identity resulted in a main driver of litter decomposition. Overall, the three species had higher decomposition rates in unsterilized treatments. However, differences in decomposition between unsterilized and sterilized samples were much higher in *Chamaerops* than in *Retama* and *Stipa.* This could be due to the different C/N, SLA and WHC values of *Chamaerops* (Table 1, 3S). Litter traits have been reported as important drivers of biotic decomposition (De Oliveira, *et al*., 2010) and our results suggest that abiotic-originated changes in litter would be a potential driver for subsequent biotic decomposition in drylands.

### 2.6.2 Microbes but not UV radiation affects litter mixtures

We hypothesized that in stage 1 litter mixtures would have higher decomposition rates than monospecific litter after UV exposure. However, and contrary to our expectations, UV radiation did not increase decomposition rates in mixtures, and although there is a trend, the effect was much stronger in monospecific treatments (Fig. 2). This suggests that decomposition in mixtures (which was higher than in monospecific replicates) was influenced by factors other than photodegradation that compensated for its effect. Thus, plant diversity does not only increase decomposition rates, but also buffer UV effects. The higher decomposition on mixtures agrees with the well documented process in mesic ecosystems but seldom explored in drylands (Castro-Díez *et al*., 2019; García-Palacios, et al., 2015; Hättenschwiler, et al., 2005). Differences could be explained by the structural complexity provided by mixtures, which increases diversity of micro environmental conditions and nutrients, buffering microorganisms against the effects of UV radiation (Gartner and Cardon, 2004; Hättenschwiler, *et al*., 2005; Schuster and Dukes, 2014).

Beyond UV radiation, non-additivity was evident in the second part of the experiment, and basically depended on biotic drivers. We found antagonistic or synergistic effects based on the microbiota (biocides) which depended on the identity of the species involved. It is of substantial interest the fact that when microbiota is not present, decomposition in *C. humilis* is strongly negatively affected by the presence of the other plant species, suggesting that microbiota functions as a buffer ensuring *C. humilis* decomposition in mixtures. The switch from antagonism to synergism observed from the absence or presence of detritivores respectively is in line with the enhancing of mixture effects from detritivores observed in previous studies (De Oliveira *et al.*, 2010; Hattenschwiler and Gasser, 2005). Considering that most decomposition experiments in drylands were conducted with monospecific litter, we highlight the need to include leaf litter mixtures because plant clusters are the prevalent spatial distribution in drylands (Tirado and Pugnaire, 2005) and the accumulation of leaf litter mixtures is the most likely scenario (Bardgett and Van Der Putten, 2014). This is relevant in the context of global environmental change where loss of diversity may modify mixture interactions and potentially increases of UV radiation lead to changes in nutrient cycles.

In summary, decomposition of leaf litter mixtures seems to be controlled mainly by biotic drivers, which may have an impact on the fate of carbon stored in soil organic pools, as $CO_2$ release would be faster than that of monospecific litter. Understanding decomposition in mixtures and monospecific litter in drylands and their interaction with both micro and macrobiota, is a major issue in a context of global environment change that implies an increase in UV radiation (Herman, 2010) and loss of plant diversity (Allen, 1995). The role of these complex biotic interactions should be considered in global models of carbon dynamics.

## 2.7 Acknowledgements

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## 2.8 References

Allen, E. B. (1995). Wildland Shrub and Arid Land Restoration. In *Restoration Ecology: Limits and Possibilities in Arid and Semiarid Lands* (p. 7).

Almagro, M., Maestre, F. T., Martínez-López, J., Valencia, E., & Rey, A. (2015). Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. *Soil Biology and Biochemistry*, *90*, 214–223. doi:10.1016/j.soilbio.2015.08.006

Almagro, M., Martínez-López, J., Maestre, F. T., & Rey, A. (2017). The contribution of photodegradation to litter decomposition in semiarid mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. *Ecosystems*, *20*(3), 527–542. doi:10.1007/s10021-016-0036-5

Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*(10), 2682–2686. doi:10.1890/03-0650

Austin, A. T., & Ballare, C. L. (2010). Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, *107*(10), 4618–4622. doi:10.1073/pnas.0909396107

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, *442*(7102), 555–558. doi:10.1038/nature05038

Badalucco, L., Pomaré, F., Grego, S., Landi, L., & Nannipieri, P. (1994). Activity and degradation of streptomycin and cycloheximide in soil. *Biology and Fertility of Soils*, *18*(4), 334–340. doi:10.1007/BF00570637

Baker, N. R., & Allison, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology*, *96*(7), 1994–2003. doi:10.1890/14-1482.1

Baker, N. R., Allison, S. D., & Frey, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology*, *96*(7), 1994–2003. doi:10.1890/14-1482.1

Bardgett, R. D., & Van Der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature 515*, *505*(7528), 505–511. doi:10.1038/nature13855

Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., & Wolters, V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biology and Biochemistry*, *43*(10), 2200–2207. doi:10.1016/j.soilbio.2011.07.008

Boelter, J., Quadros, A., & Araujo, P. (2009). The feeding rates and preferences of a neotropical terrestrial isopod (Oniscidea). *Nauplius*, *17*(2), 107–113. Retrieved from http://crustacea.org.br/artigos/900_20_05_boelter,_quadros,_araujo.pdf

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., & Wood, S. A. (2015). Understanding the dominant controls on litter decomposition. *Journal of Ecology*, *104*(1), 229–238. doi:10.1111/1365-2745.12507

Brandt, L. A., King, J. Y., & Milchunas, D. G. (2007). Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. *Global Change Biology*, *13*(10), 2193–2205. doi:10.1111/j.1365-2486.2007.01428.x

Bünemann, E. K., Bongiorno, G., Bai, Z., Creamer, R. E., De Deyn, G., de Goede, R., … Brussaard, L. (2018). Soil quality – A critical review. *Soil Biology and Biochemistry*, *120*(January), 105–125. doi:10.1016/j.soilbio.2018.01.030

Castro-Díez, P., Alonso, Á., & Romero-Blanco, A. (2019). Effects of litter mixing on litter decomposition and soil properties along simulated invasion gradients of non-native trees. *Plant and Soil*, *442*(1–2), 79–96. doi:10.1007/s11104-019-04160-4

Chen, S. K., Edwards, C. A., & Subler, S. (2001). A microcosm approach for evaluating the effects of the fungicides benomyl and captan on soil ecological processes and plant growth. *Applied Soil Ecology*, *18*(1), 69–82. doi:10.1016/S0929-1393(01)00135-4

Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., … Callaham, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, *110*, 116–133. doi:10.1016/j.soilbio.2017.03.008

Day, T. A., Guénon, R., & Ruhland, C. T. (2015). Photodegradation of plant litter in the Sonoran Desert varies by litter type and age. *Soil Biology and Biochemistry*, *89*, 109–122. doi:10.1016/j.soilbio.2015.06.029

Day, T. A., Zhang, E. T., & Ruhland, C. T. (2007). Exposure to solar UV-B radiation accelerates mass and lignin loss of Larrea tridentata litter in the Sonoran Desert. *Plant Ecology*, *193*(2), 185–194. doi:10.1007/s11258-006-9257-6

De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, *24*(4), 937–946. doi:10.1111/j.1365-2435.2010.01694.x

Feckler, A., Goedkoop, W., Zubrod, J. P., Schulz, R., & Bundschuh, M. (2016). Exposure pathway-dependent effects of the fungicide epoxiconazole on a decomposer-detritivore system. *Science of The Total Environment*. doi:10.1016/j.scitotenv.2016.07.088

Foereid, B., Rivero, M. J., Primo, O., & Ortiz, I. (2011). Modelling photodegradation in the global carbon cycle. *Soil Biology and Biochemistry*, *43*(6), 1383–1386. doi:10.1016/j.soilbio.2011.03.004

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hättenschwiler, S. (2015). The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, (November), 1–11. doi:10.1111/1365-2435.12589

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, *19*(5), 554–563. doi:10.1111/ele.12590

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, *104*(2), 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D.

H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, *25*(6), 372–80. doi:10.1016/j.tree.2010.01.010

Gliksman, D., Navon, Y., Dumbur, R., Haenel, S., & Grünzweig, J. M. (2018). Higher rates of decomposition in standing vs. surface litter in a Mediterranean ecosystem during the dry and the wet seasons. *Plant and Soil*, 1–13. doi:10.1007/s11104-018-3696-4

Gliksman, D., Rey, A., Seligmann, R., Dumbur, R., Sperling, O., Navon, Y., … Grünzweig, J. M. (2017). Biotic degradation at night, abiotic degradation at day: positive feedbacks on litter decomposition in drylands. *Global Change Biology*, *23*(4), 1564–1574. doi:10.1111/gcb.13465

Hassall, M., Adl, S., Berg, M., Griffiths, B., & Scheu, S. (2006). Soil fauna–microbe interactions: towards a conceptual framework for research. *European Journal of Soil Biology*, *42*, S54–S60. doi:10.1016/j.ejsobi.2006.07.007

Hattenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, *102*(5), 1519–1524. doi:10.1073/pnas.0404977102

Herman, J. R. (2010). Global increase in UV irradiance during the past 30 years (1979–2008) estimated from satellite data. *Journal of Geophysical Research*, *115*(D4), D04203. doi:10.1029/2009JD012219

Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*. doi:10.1126/science.277.5330.1302

Ihnen, K., & Zimmer, M. (2008). Selective consumption and digestion of litter microbes by Porcellio scaber (Isopoda: Oniscidea). *Pedobiologia*, *51*(5–6), 335–342. doi:10.1016/j.pedobi.2007.06.001

Jia, Y., Lv, Y., Kong, X., Jia, X., Tian, K., & Du, J. (2014). Insight into the indirect function of isopods in litter decomposition in mixed subtropical forests in China Insight into the indirect function of isopods in litter decomposition in mixed subtropical forests in China. *Applied Soil Ecology*, *86*(November), 174–181. doi:10.1016/j.apsoil.2014.10.015

Johnson, D. (2003). Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. *Research in Microbiology*, *154*(5), 315–20. doi:10.1016/S0923-2508(03)00078-0

Johnson, D., Krsek, M., Wellington, E. M. H., Stott, A. W., Cole, L., Bardgett, R. D., … Leake, J. R. (2005). Soil invertebrates disrupt carbon flow through fungal networks. *Science (New York, N.Y.)*, *309*(5737), 1047. doi:10.1126/science.1114769

King, J. Y., Brandt, L. A., & Adair, E. C. (2012). Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. *Biogeochemistry*, *111*(1–3), 57–81. doi:10.1007/s10533-012-9737-9

Lin, Y., Karlen, S. D., Ralph, J., & King, J. Y. (2018). Short-term facilitation of microbial litter decomposition by ultraviolet radiation. *Science of The Total Environment*, *615*, 838–848. doi:10.1016/j.scitotenv.2017.09.239

Lin, Y., Scarlett, R. D., & King, J. Y. (2015). Effects of UV photodegradation on subsequent microbial decomposition of Bromus diandrus litter. *Plant and Soil*, *395*(1–2), 263–271. doi:10.1007/s11104-015-2551-0

Manzoni, S., Jackson, R. B., Trofymow, J. a, & Porporato, A. (2008). The global stoichiometry of litter nitrogen mineralization. *Science (New York, N.Y.)*, *321*(5889), 684–686. doi:10.1126/science.1159792

Martínez-Yrízar, A., Núñez, S., & Búrquez, A. (2007). Leaf litter decomposition in a southern Sonoran Desert ecosystem, northwestern Mexico: Effects of habitat and litter quality. *Acta Oecologica*, *32*(3), 291–300. doi:10.1016/j.actao.2007.05.010

Norby, R. J., & Cotrufo, M. F. (1998). A question of litter quality. *Nature*, *396*(November), 12–13. doi:10.1038/23812

Ocde, O. (2016). Test No. 232: Collembolan Reproduction Test in Soil, (July). doi:10.1787/9789264264601-en

Pérez-Harguindeguy, N., & Díaz, S. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of …*, *61*, 167–

234. doi:http://dx.doi.org/10.1071/BT12225

Price, C. M., & Pettijohn, D. E. (1986). Biodiversity and litter decomposition in terrestrial ecosystems. *Experimental Cell Research*, *166*(2), 295–311. doi:10.1016/0014-4827(86)90478-7

Reyes Reyes, M. V., Iñíguez, M. A., Hevia, M., Hildebrand, J. A., & Melcón, M. L. (2015). Description and clustering of echolocation signals of Commerson's dolphins ( Cephalorhynchus commersonii ) in Bahía San Julián, Argentina. *The Journal of the Acoustical Society of America*, *138*(4), 2046–2053. doi:10.1121/1.4929899

Rutledge, S., Campbell, D. I., Baldocchi, D., & Schipper, L. A. (2010). Photodegradation leads to increased carbon dioxide losses from terrestrial organic matter. *Global Change Biology*, *16*(11), 3065–3074. doi:10.1111/j.1365-2486.2009.02149.x

Schade, G. W., & Crutzen, P. J. (1999). CO emissions from degrading plant matter. *Tellus, Series B: Chemical and Physical Meteorology*, *51*(5), 909–918. doi:10.1034/j.1600-0889.1999.t01-4-00004.x

Schuster, M. J., & Dukes, J. S. (2014). Non-additive effects of invasive tree litter shift seasonal N release: a potential invasion feedback. *Oikos*, *123*(9), 1101–1111. doi:10.1111/oik.01078

Team, R. C. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Tirado, R., & Pugnaire, F. I. (2005). Community structure and positive interactions in constraining environments. *Oikos*, *111*(3), 437–444. doi:10.1111/j.1600-0706.2005.14094.x

Verduzco, V. S., Vivoni, E. R., Yépez, E. A., Rodríguez, J. C., Watts, C. J., Tarin, T., … Ivanov, V. Y. (2018). Climate Change Impacts on Net Ecosystem Productivity in a Subtropical Shrubland of Northwestern México. *Journal of Geophysical Research: Biogeosciences*, *123*(2), 688–711. doi:10.1002/2017JG004361

Verhoef, H. A., Verspagen, J. M. H., & Zoomer, H. R. (2000). Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. *Biology and Fertility of Soils*, *31*(5), 366–371. doi:10.1007/s003749900181

Wang, J., Liu, L., Wang, X., & Chen, Y. (2015). The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. *Global Change Biology*, *21*(5), 2095–104. doi:10.1111/gcb.12812

Wang, J., Liu, L., Wang, X., Yang, S., Zhang, B., Li, P., … Liu, W. (2017). High night-time humidity and dissolved organic carbon content support rapid decomposition of standing litter in a semi-arid landscape. *Functional Ecology*, *31*(8), 1659–1668. doi:10.1111/1365-2435.12854

Wang, J., Yang, S., Zhang, B., Liu, W., Deng, M., Chen, S., & Liu, L. (2017). Temporal dynamics of ultraviolet radiation impacts on litter decomposition in a semi-arid ecosystem. *Plant and Soil*, *419*(1–2), 71–81. doi:10.1007/s11104-017-3290-1

Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and Plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, *79*(2), 247–258.

Zepp, R. G., Erickson, D. J., Paul, N. D., & Sulzberger, B. (2007). Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochemical & Photobiological Sciences : Official Journal of the European Photochemistry Association and the European Society for Photobiology*, *6*(3), 286–300. doi:10.1039/b700021a

Zimmer, M., Kautz, G., & Topp, W. (2005). Do woodlice and earthworms interact synergistically in leaf litter decomposition? *Functional Ecology*, *19*(1), 7–16. doi:10.1111/j.0269-8463.2005.00926.x

Zimmer, M., & Topp, W. (1997). Does leaf litter quality influence population parameters of the common woodlouse, Porcellio scaber (Crustacea: Isopoda)? *Biology and Fertility of Soils*, *24*(4), 435–441. doi:10.1007/s003740050269

## 2.9 Supplementary material

Table 1S. General linear model results (F-values) of litter decomposition in stage 1 (after 200 days of exposition to UV) and stage 2 (after 80 days of isopod exposition).

| | **Source** | **Sum Sq** | **Df** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|
| **Stage 1** | **UV (UV)** | 0.748 | 1 | 4.094 | **0.043** |
| | **Biocides (B)** | 0.390 | 1 | 2.135 | 0.144 |
| | **Species identity (ID)** | 0.947 | 2 | 2.592 | 0.076 |
| | **Mixtures (M)** | 2.996 | 1 | 16.396 | < 0.001 |
| | **UV x B** | 0.930 | 1 | 5.090 | **0.024** |
| | **UV x M** | 1.160 | 1 | 6.345 | **0.012** |
| | **Residuals** | 61.035 | 334 | | |
| **Stage 2** | **UV (UV)** | 6.75 | 1 | 5.198 | **0.023** |
| | **Biocides (B)** | 174.95 | 1 | 134.677 | < 0.001 |
| | **Species identity (ID)** | 371.52 | 2 | 143.000 | < 0.001 |
| | **Mixtures (M)** | 40.86 | 1 | 31.453 | < 0.001 |
| | **Isopods (I)** | 379.38 | 1 | 292.044 | < 0.001 |
| | **B x ID** | 62.65 | 2 | 24.114 | < 0.001 |
| | **B x M** | 14.51 | 1 | 11.172 | < 0.001 |
| | **B x I** | 18.49 | 1 | 14.230 | < 0.001 |
| | **ID x M** | 55.01 | 2 | 21.174 | < 0.001 |
| | **ID x I** | 191.71 | 2 | 73.789 | < 0.001 |
| | **B x ID x M** | 9.92 | 2 | 3.819 | **0.022** |
| | **Residuals** | 413.09 | 318 | | |

Table 2S. General linear model on leaf litter mixtures mass loss.

| | Source | Sum Sq | Df | F value | Pr(>F) |
|---|---|---|---|---|---|
| **Stage 1** | **UV (UV)** | 0.007 | 1 | 0.014 | 0.903 |
| | **Biocides (B)** | 1.856 | 1 | 3.805 | 0.052 |
| | **Species identity (ID)** | 0.933 | 2 | 0.956 | 0.386 |
| | **Residuals** | 79.507 | 163 | | |
| **Stage 2** | **UV (UV)** | 0.022 | 1 | 1.790 | 0.221 |
| | **Biocides (B)** | 0.955 | 1 | 74.982 | < 0.001 |
| | **Species identity (ID)** | 0.374 | 2 | 14.683 | < 0.001 |
| | **Isopods (I)** | 1.936 | 1 | 151.941 | < 0.001 |
| | **B x ID** | 0.369 | 2 | 14.492 | < 0.001 |
| | **ID x I** | 0.400 | 2 | 15.693 | < 0.001 |
| | **Residuals** | 1.975 | 155 | | |

Table 3S. Water holding capacity (WHC) changes pre and post UV radiation. WHC of the dead leaves (n =30 per species) was assessed by gravimetric differences between dry and soak litter (Pérez-Harguindeguy and Díaz, 2013).

| **Species** | **WHC (%)** | | |
|---|---|---|---|
| | **Pre UV** | **Post UV** | **Change** |
| ***C. humilis*** | 115.41 ± 2.35 | 144.72 ± 1.48 | > 25.39 % |
| ***R. sphaerocarpa*** | 85.14 ± 2.48 | 102.74 ± 4.17 | > 20.67 % |
| ***S. tenacissima*** | 64.61 ± 1.02 | 73.22 ± 1 | > 13.32 % |

# Chapter 3. Engineering effects of a terrestrial predator on litter decomposition

## 3.1 Abstract

1. Decomposition of plant organic matter is a key ecosystem process where the complex decomposers' food web and the diversity of plant substrates are the two main biotic drivers.
2. Empirical evidence on the interaction of these two biotic components is scarce, and we know little on how higher trophic levels (e.g. soil predators) may indirectly affect decomposition through their effects on prey (decomposers).
3. Predators may influence decomposition in two ways. First, by initiating trophic cascades (top-down control) which negatively affect decomposers numbers by direct predation (Density-mediated indirect interactions, DMII) or by affecting decomposer foraging behavior (Trait-mediated indirect interactions, TMII). Another, far less explored mechanism by which predators can affect decomposition is from ecological engineering effects (EEE).
4. In EEE, traces of predator activity (e.g. excreta) may provide nutrients that can boost microbial activity and ultimately benefit secondary decomposers that accelerate decomposition.
5. Here, we present the results of an experiment in which detritivores (isopods) were free to choose patches differing in predation risk (i.e., the presence of wolf spiders) when foraging for litter (either monospecific or 3-species mixtures). Despite the high impact of predators on detritivores (both on mortality and behavior), isopods selected litter from patches with predator signs, the identity and diversity of the litter, prevail over predator top-down control, making predators to enhance rather than inhibit decomposition.

**Key words:** Biodiversity Ecosystem Functioning, Ecological Engineering Ecosystem, Fear of predation, Top-down control

## 3.2 Introduction

Decomposition is a key ecosystem process related to nutrient availability, primary productivity, and carbon sequestration (Brussaard, 1997; De Deyn, *et al.*, 2008). Climate and biotic factors are among the main drivers of this process (Aerts, 1997; Coûteaux, *et al.*, 1995), and the soil food web and the complex interactions occurring within, are the main components of the biotic component of decomposition (Moore *et al.*, 2004), bringing this ecosystem process at the forefront of biodiversity and ecosystem functioning (BEF) research (Hattenschwiler & Gasser, 2005).

Leaf quality is a main factor of decomposition (Heal, *et al.*, 1997; Viketoft *et al.*, 2009), as species identity and litter diversity control bottom up decomposition processes(Gartner & Cardon, 2004; Hättenschwiler, *et al.*, 2005b; Schuster & Dukes, 2014). Opposite, food web traits control top-down decomposition processes. How top-down control may cascade down the food to affect decomposition has recently gained wide attention (Buchkowski, 2016; Lensing & Wise, 2006; Melguizo-Ruiz *et al.*, 2019).

In soils, top-down control driven by predators may occur in two ways: 1) consumptive (density-mediated indirect interactions; DMII), through the regulation of decomposers abundance, and 2) non-consumptive effects, which in turn can be divided in two main kinds, i) Trait-mediated indirect interactions (TMII), in which cascading effects resulting from predators induce changes on prey traits (usually foraging behavior and activity), and sometimes force prey to forage elsewhere (fear of predation; Schmitz & Barton, 2014; Schmitz *et al.*, 2004; Sitvarin *et al.*, 2016); and the far less explored, ii) ecological engineering effects (EEE), by which predator activity induces changes in the habitat that can indirectly benefit their prey and microorganisms, thereby enhancing decomposition rates, as shown recently in aquatic ecosystems (Majdi, *et al.*, 2016).

A growing body of evidence suggests that non-consumptive effects may have a stronger impact on ecosystems than DMII (Stephan, *et al.*, 2017). The few studies addressing TMII on decomposition resulted in negative impacts of predators (Buchkowski, 2016; Hawlena, *et al.*, 2012). However, in decomposition studies, positive effects have also been documented (see Ngai & Srivastava, 2006, Lawrence

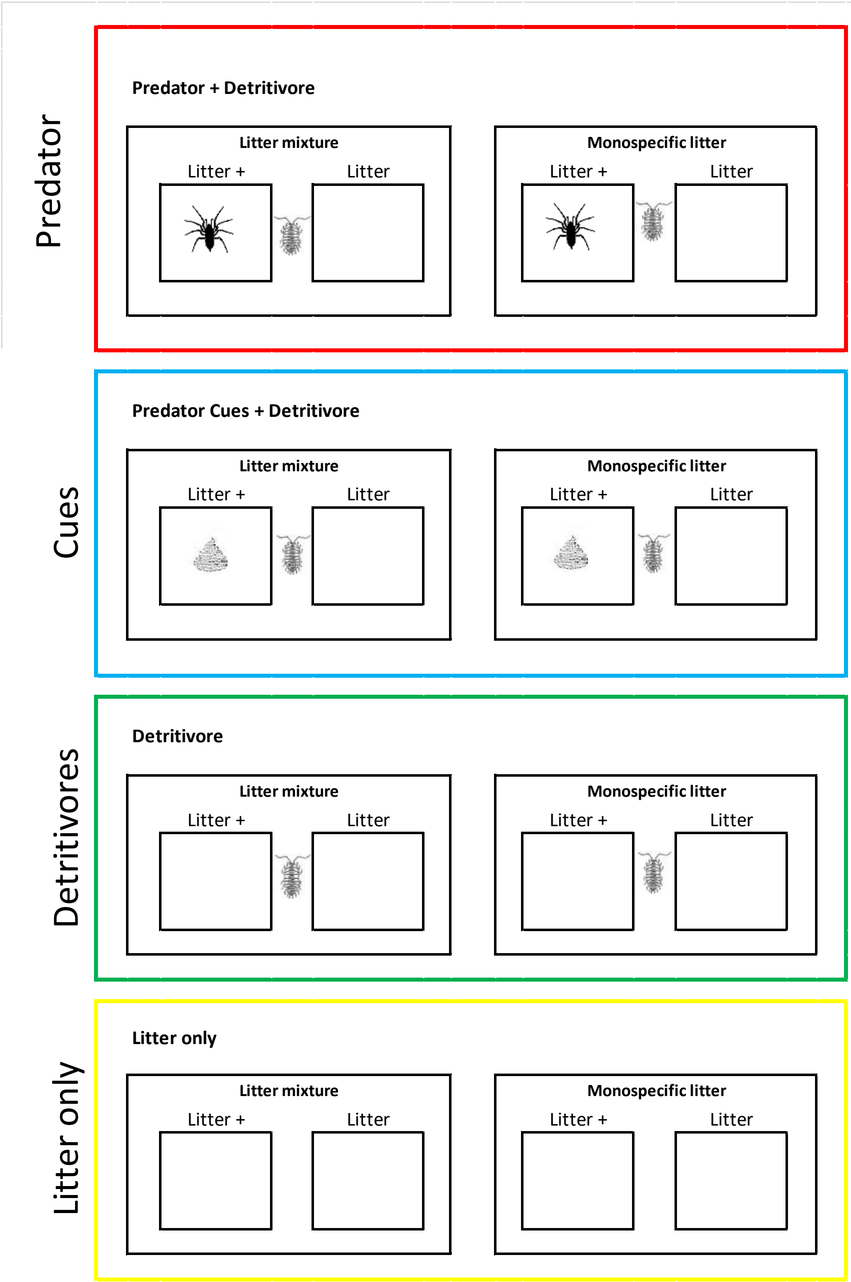
& Wise, 2004; Lensing and Wise 2006; Melguizo-Ruiz *et al*. 2019). The results of some of the latter studies could be explained by the density-reduction of micro- and macro-decomposers by predators, resulting in the rise of microbial activity, finally leading to an increase in decomposition rates (Crowther, *et al*., 2012; but see Melguizo-Ruiz *et al*. 2019). Alternatively, EEE could be behind the positive results of predators on decomposition (Lawton & Jones, 1993; Majdi *et al*., 2013) occurring through the input of high quality resources by traces of predator activity rich in protein-N such as egestion, excretions, carcasses and exuviae, enhancing nutrient content on basal resources. Thus far, there is only one single example that demonstrates how predators enhance decomposition through engineering effects, the effect of flatworm mucus in an aquatic ecosystem (Majdi, *et al*., 2016). Similar effects could also be common in soil food webs; however, to date this hypothesis remains untested. Indeed, in the soil, these high-quality resources may alter the flow of energy on food webs (Hawlena & Schmitz, 2010) stimulating microbial (Guenet, *et al*., 2010; Schmitz, *et al*., 2010) and detritivore activity, particularly of those detritivores that depend on microorganisms. A good example are isopods, which besides feeding mainly on plant detritus, they may also consume fungi covering decaying leaf litter, and faeces and carcasses of other invertebrates (Crowther, *et al*., 2012; Hornung, *et al*., 1998; Zimmer, *et al*., 2005).

In summary, biodiversity can affect decomposition from EEE, and from top-down and bottom-up forces, and it is not clear how all these forces act together to determine litter decomposition. Litter identity and diversity can control decomposition from the bottom up by the diversity of nutrients that they contain and also, when more than one plant species of litter is present in a mixture, by litter interactions that can lead to synergistic or antagonistic effects (Gartner & Cardon, 2004; Hunter, *et al*., 2003; Santonja, *et al*., 2015). Actually, interactions between bottom-up and top-down control have been previously found, as the synergistic effects of litter mixtures may depend on the presence or absence of detritivores (De Oliveira, *et al*., 2010; Hattenschwiler & Gasser, 2005), from which we can conclude that there are top-down bottom-up synergies on litter decomposition. However, when top-down control is initiated from higher trophic levels (e.g., predators) and the predators that impose it may also induce relevant EEEs, the interaction with the bottom-up effects of litter identity and diversity are largely unknown. One possible prediction to understand the potential outcomes of such complex interactions is that because litter mixtures increase habitat complexity, they can potentially contribute to decrease predation rate upon detritivores (Kalinkat, Brose & Rall, 2013), thereby enhancing decomposition. However, many other mechanisms could be at play.

Here, we designed a food chain, patch-choice experiment designed to test simultaneously for DMII, TMII and EEE on litter decomposition and their interaction with bottom-up effects from litter identity and diversity (litter mixtures). The assembled food chain consisted of leaf litter (Fig. 1), isopods (detritivores) and a large wolf spider (predator). The basic mesocosm included two identical patches regarding to litter content, with both patches containing either monospecific litter belonging to one of three species, or the mixture of the three species. These patches were enclosed within a plastic container. The differences in the two patches among treatments related to whether they contained just litter, or additionally included either a spider or just spider cues (traces of spider activity). Isopods were released within the mesocosm outside these patches and could freely choose what patch to enter to consume litter. The patch containers had holes that allowed isopods to enter and exit but the holes were small enough to prevent the spiders from exiting. By estimating litter mass loss, and isopod mortality among mesocosms we were able to test for DMII, TMII and EEE and their interaction with the litter identity and diversity bottom-up effects. The spider presence served to test for DMII, and the patch with spider traces of activity served to test for TMII and EEE, for which we predicted opposite outcomes; i.e., lower or higher decomposition respectively for TMII or EEE when compared to treatments without either spider or spider cues.

The above design is novel because for the first time allows testing for trophic cascades on decomposition due to numerical and/or behavioral responses on behalf of the detritivores, at the same time that permitted testing whether predator activity brought engineering effects that would enhance decomposition. Finally, because we manipulated litter identity and diversity the design allowed testing whether there were synergies on decomposition between predators (whether from DMII, TMII or EEE) and bottom-up effects.

Figure 1. Food chain patch choice experiment to test simultaneously for top-down: Density-mediated Indirect Interactions (DMII), Trait-mediated Indirect Interactions (TMII) and Ecological Engineering Effects (EEE) on litter decomposition and its interaction with bottom-up effects from litter identity and diversity (litter mixtures). The assembled food chain consisted of leaf litter (basal resources), isopods (detritivores) and a large wolf spider (predator). Each mesocosm contained two identical litter patches with either monospecific or 3-sp mixture litter, depending on the Litter Treatment. The "Litter+" patches had just litter, spider cues (traces of spider activity) or a spider. Released isopods within the mesocosm could freely choose between patches to enter and consume litter. Holes in the patch boxes were small enough to allow the isopods to enter but prevented spiders from exiting the patch



## 3.3 Materials and Methods

### 3.3.1 Collection of litter and arthropods

Litter and animals were collected in and around the Cabo de Gata Nature Park (Almería, Spain), a semi-arid area which is the driest terrestrial ecosystem in Europe (mean annual rainfall ca. 200 mm – Peinado *et al*., 1992). We selected three frequent plant species in the study area, *Chamaerops humilis* L. (*Chamaerops*), a dwarf palm tree species, *Retama sphaerocarpa* L. (Boiss) (*Retama*), a legume shrub, for which we used the cladodes as leaves are extremely small and short-lived, and *Stipa tenacissima* L., a tussock-grass species (*Stipa*). *Retama* and *Stipa* litter were collected north-west of Cabo de Gata, in the Tabernas basin (37°02' N, 2°24' W) and *Chamaerops* litter in Cabo de Gata-Nijar Nature Park (36°43' N, 2°11' W. Plant material was hand collected as litter from standing plants and oven-dried at 60°C for 72 h.

As detritivore, we used the isopod *Porcellio ornatus* (L.), a highly abundant species in the study site. Juvenile individuals (ca. 1 cm; average fresh mass 0.69 ± 0.18 mg, n=50) were hand-collected one week before the starting of the experiment, and from the same localities as the litter species. The isopods were kept in groups of 60-80 individuals in 25x25x5cm plastic containers and fed with original plants of wild *Avena sp*, which was collected from the field site. Water was provided with a test tube filled with water and sealed with cotton, from which the isopods could directly drink. As predator we used the Iberian tarantula, *Lycosa hispanica,* a territorial and burrowing wolf spider (Moya-Laraño, *et al*., 2002). Large juvenile individuals within their last instars (mean fresh mass 892.68 ± 96.13 mg, n=50) were collected around the same area where we collected the isopods and litter. The spiders were kept separately in 12 cm ø x 18 cm height containers filled up to 2cm with soil from the field sites, and fed once a week with crickets of the species *Acheta domestica* coming from commercial suppliers until the experiment started. All animals were kept at room temperature and a humidifier allowed maintaining RH around 70%.

### 3.3.2 Experimental design

We designed a trophic chain patch choice experiment. The basic mesocosm consisted of a 50 x 33 x 7 cm tray (Fig. 1) which included two leaf-litter patches at 20 cm from each other, and each enclosed in a 20x15x5cm plastic container with four 0.5 cm-ø holes on the longer side and 3 on the shorter, which allowed isopods to freely enter to feed on the leaf litter, and exit at their will. However, the holes prevented the much larger spiders enclosed within some of the patches from exiting. Across treatments, one of the patches of the mesocosm (“Litter+” patch) included a conventional food chain experiment (Moya-Laraño, *et al.*, 2002) incorporating either only litter, litter plus detritivores (isopods) in the mesocosm (freely moving around among patches) or an enclosed predator (spider), in addition to the litter and the isopods. We added another treatment in which the “Litter+” patch included only cues or traces of spider activity, but no spider. In all treatments, the other patch in the mesocosm (“Litter”) contained litter only. The litter within each mesocosm was homogeneous between patches and was either monospecific and belonging to each of three species; or a mixture of the three species (mixture). If DMII were at play we predicted that the “Litter+” patches with spider would have lower decomposition rates than the “Litter+” patches from mesocosms containing only isopods and litter, and that the isopod mortality in the latter mesocosms would be higher than in those mesocosms containing a spider. A total of 80 mesocosms were randomly assigned to each of 4 Patch Treatments (Predator + Detritivores, Predator cues + Detritivores, Detritivores, Litter only), which differed in what was included in the “Litter+” patch. Then, 5 mesocosms of each Patch Treatment were randomly assigned to each of 4 Litter Treatments, in which both patches included an equal amount of a single species of litter (making 3 Monospecific treatments one for each species) or a mixture of the three species (Mixture). Because the species in the mixtures were carefully separated and independently weighed at the end of the experiment, this design allowed distinguishing species identity from mixture effects. If TMII were at play we predicted that the “Litter+” patches with traces of spider activity (cues) but without spider would have lower decomposition rates than the “Litter+” patches from mesocosms containing only isopods, as well as relatively more isopod activity in the “Litter” patches, were no spiders cues are present. However, if on the other hand EEE were at play and would override TMII effects, we predicted the opposite, that decomposition in “Litter+” patches with traces of spider activity would be higher than in “Litter+” from mesocosms with only isopods and litter. In order to test if predators could interfere with bottom-up effects, we also tested for interactions between all of the above and the identity and diversity of the litter. This design also allowed to test whether predators induced shifts in space used by isopods, if the three-dimensional structure of litter mixtures increased survival from predation and if isopods affected mixture effects (Hattenschwiler & Gasser, 2005).

### 3.3.3 Details on experimental procedures

Mesocosms containing monospecific litter, included 3 g (dry mass) of *Stipa*, *Retama* or *Chamaerops*, and those containing 3-species mixtures included 1 g of each species. All patches had a drinker to supply water to the animals and filter paper on the bottom. To collect spider cues we settled a single wolf spider in a plastic box with filter paper on the bottom. We kept the spiders for 15 days fed with juvenile stages of *Gryllus bimaculatus* crickets collected in the same site where the spiders were collected. After 15 days the spider was removed and the filter paper impregnated with excreta, prey remains, silk and exuviae was used in the "Litter+" patches of the "Predator cues + Detritivores" patch treatment. Additionally we used the drinker used by the spider. For all the rest of the patches we use clean filter paper.

At the beginning of the experiment, we released 15 immature isopods in the middle of the mesocosm, which were free to enter either patch. Every 15 days we recorded the isopods surviving and replaced them and all the carcasses with 15 fresh isopods from the laboratory stock. At the end of the experiment we reported the accumulated number of isopods disappearing or found dead in the mesocosms. Every 15 days we also randomly switched the spiders among mesocosms in the "Predator + Detritivore" treatment in order to minimize the effects of spider identity. At this same moment we also replaced the filter paper in all treatments, and for the "Litter+" patch in the "Predator cues + Detritivore" treatment, we used a filter paper recently used by a spider during the previous 15 days. Systematically, the spiders that were releasing the cues were also randomly shuffled among mesocosms.  The experiment was conducted in at room temperature with artificial light (12:12h dark:light) and maintained are about 70% humidity with the help of a humidifier. The experiment ran for 92 days between January 30th and May 2nd 2018. At the end of the experiment we oven-dried the remaining litter (60ºC for 72h) and weighed it in a scale to the nearest 0.001g. The litter belonging to different species in the mixtures was carefully separated before weighing, which allowed testing for species identity effects in the overall design, in addition to testing for mixture effects.

## 3.4 Statistical analyses

All analyses were performed in R 3.5.3 (R Core Team, 2019). Since mesocosm was not significant and rather let to singular models when included as a random effects in Generalized Linear Mixed Models, all analyses were Generalized Linear Models including only fixed effects. Decomposition was analyzed as the percentage of the difference in mass loss (i.e., [initial_mass - final_mass]/initial_mass), which was included as the dependent variable in a series of GLMs with normally distributed errors (function “glm” in the “stats” R package). When the normality assumption of the model residuals was not met we used the Box-Cox transformation (function “boxcox” under the “MASS” R package). Isopod mortality (number death) was analyzed by means of a GLM with a “quasipoisson” distribution to control for overdispersion (i.e. mean<variance). Since some GLMs included up to 4-way interactions, we applied backward elimination. To this end we started with a full saturated model with the 4-way, and all 3-way and 2-way interactions and the main effects. We then systematically removed the higher order interactions if these were not significant (or the AIC value was higher) until a final model with significant interactions and the lower level interactions and main effects are included. Post-hoc tests were Tukey tests performed under the library “emmeans” (Lenth, 2019). This same library was used to backtransform the predicted means and standard errors from the models to the original scale for graphical purposes. A first GLM model on decomposition served to test for a trophic cascade (either via DMII or TMII) or EEE and their synergistic effects with litter identity and diversity, for which we included for analysis only the decomposition data within the “Litter+” patches. The factors included were “Litter species”, “Litter treatment” and “Patch treatment”. A model including all the data on decomposition, with “Litter+” and “Litter” patches, served to compare the “Litter+” patches against the “Litter” patches to test whether predator presence or traces of predator activity led to EEE (i.e., if within “Predator + Detritivores” and “Predator cues + Detritivores” treatment decomposition was higher in “Litter+” relatively to “Litter” patches). In addition to the three factors above this model included “Patch” as a factor. The detritivore mortality model was run at the mesocosm level (only in those three treatments containing detritivores) and included the factors “Litter species”, “Litter treatment” and “Patch treatment”. We ran planned comparisons (orthogonal contrasts) by first comparing if there were differences

between “Predator cues + Detritivores” relatively to “Detritivores” treatment (e.g. by the stress induced from TMII), and if this was not significant pooling these two treatments and compare it to the “Predator + Detritivores” treatment. A switch in space use from anti-predator behavior was inferred by running a model including only the “Litter” patches and the three patch treatments including isopods. If, beyond DMII, TMII or EEE in the “Litter+” patches, the presence of the spider on the “Litter+” patch let to isopods switching or biasing their foraging activity towards the “Litter” patch, we predicted that decomposition should be higher in the “Litter” patches in the “Predator + Detritivores” treatment relatively to the “Detritivores” treatment. If the presence of predator cues had a similar effect, we predicted that decomposition should be higher in the “Litter” patches of the “Predator cues + Detritivores” treatment relatively to the “Detritivores” treatment. We tested these two hypotheses also using planned comparisons. First testing for the last hypothesis and if it were not significant pooling both treatments and comparing them to the treatment with spiders.

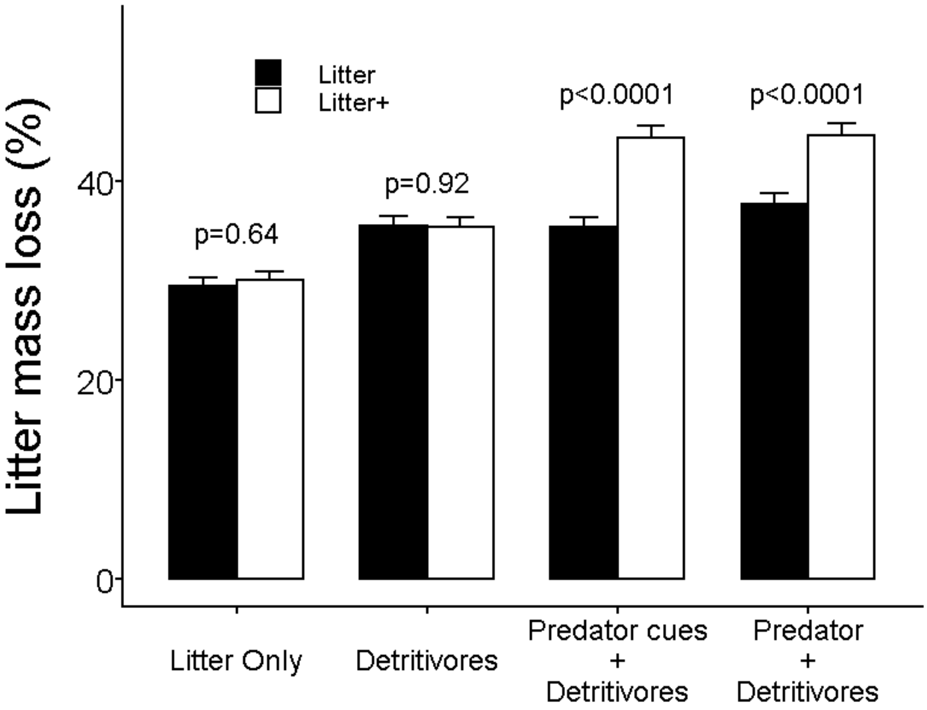
## 3.5 Results

We found no evidence of trophic cascades on decomposition. In fact, within the “Litter+” patches, decomposition was substantially higher when either a spider or spider cues were present as compared to the patches in which only detritivores were present (Fig. 2), just the opposite of what it would be expected from a trophic cascade. The backward elimination procedure of a GLM using the data including only the “Litter+” patches produced a final model with two second order significant interactions: “Litter Species X Patch Treatment” and “Litter Treatment X Patch Treatment” (Table 1; Fig. 3 and 4).

Table 1. General Linear Model results testing for DMII, TMII and EEE including only the decomposition data from the “Litter+” patches.

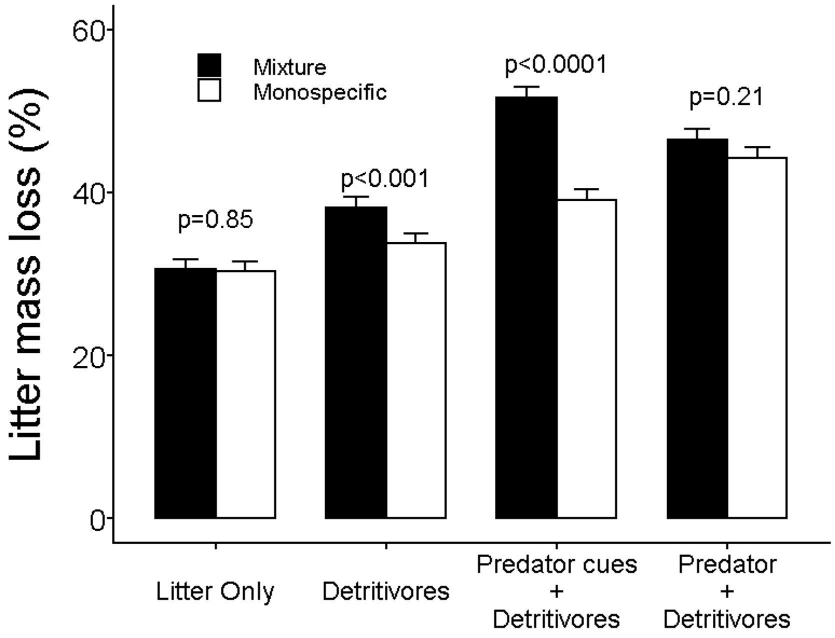
| | LR Chisq | Df | Pr(>Chisq) |
|---|---|---|---|
| **Litter Species** | 222.045 | 2 | < 0.0001 |
| **Litter Treatment** | 1.426 | 1 | 0.2324 |
| **Patch Treatment** | 137.345 | 3 | < 0.0001 |
| **Litter Species x Litter Treatment** | 3.373 | 2 | 0.1851 |
| **Litter Species x Patch Treatment** | 21.44 | 6 | 0.0015 |
| **Litter Treatment x Patch Treatment** | 24.31 | 3 | < 0.0001 |

Figure 3. Litter mass loss (%) comparing “Litter+” vs “Litter” patches across patch treatments. Bars indicate GLM model predicted means and SE after back transformation (from boxcox)



Overall *C. humilis* and *R. sphaerocarpa* decomposed about twice as fast as did *S. tenacissima*. Detritivores tended to accelerate decomposition relatively to the “Litter only” treatment; although, this was not the case for *S. tenacissima* (Fig.3) or litter monocultures (Fig. 4). However, the additional presence of either spiders or spider cues on the “Litter+” patches compared to the patches with only detritivores, substantially increased decomposition both in *S. tenacissima* and litter monocultures (Fig. 3 and 4). Additionally, synergistic mixture effects were only meaningful when either detritivores (Z = 2.6, P = 0.01) or detritivores plus spider cues but no spiders (Z = 6.7, P < 0.0001) were present. Treatments without detritivores (Z = 0.18, P = 0.857) or with predators (Z = 1.24, P = 0.215) failed to show synergistic mixture effects (Table 1, Fig. 2).

Figure 4. Litter mass loss (%) comparing mixture effects across patch treatments. Bars indicate GLM model predicted means plus SEs after back transformation (from boxcox)

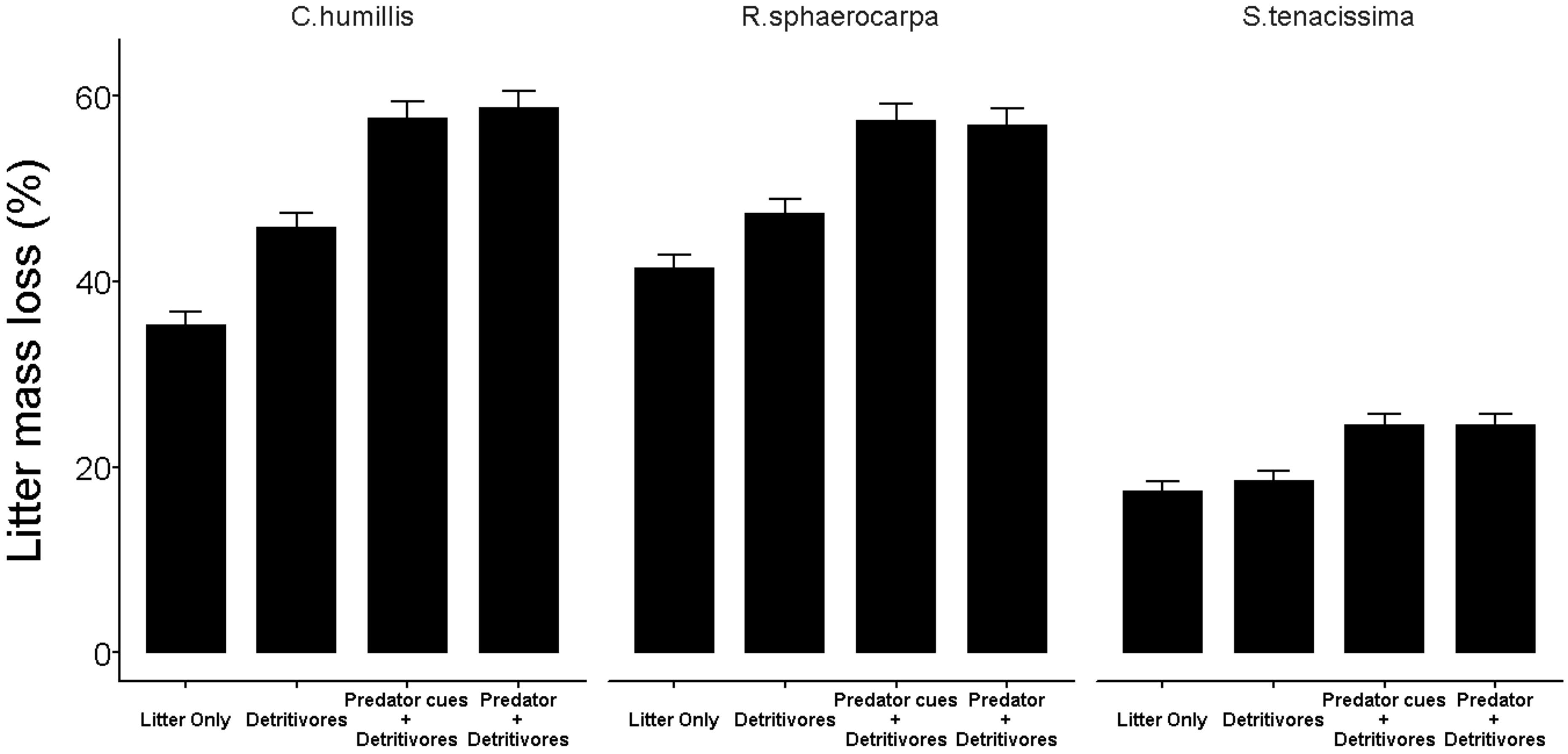


The above results suggest that the effect of predators on decomposition are facilitating rather than a form of conventional top-down control. Indeed, in a new model including the data from both patches in the mesocosms we found a highly significant “Patch Treatment X Patch” interaction ($\chi^2$ = 28.5, d.f. = 3, P < 0.0001; Table 2, Fig. 2), and when we compared the “Litter+” against the “Litter” patches in those treatments in which either predators (Z = -4.6, P < 0.0001) or predator cues (Z = -6.2, P < 0.0001) were present, we found that decomposition was ca. 1.22X higher in “Litter+” patches, further supporting the engineering facilitation hypothesis.

Table 2. General Linear Model results testing for EEE including data from both patches (Litter + and Litter).

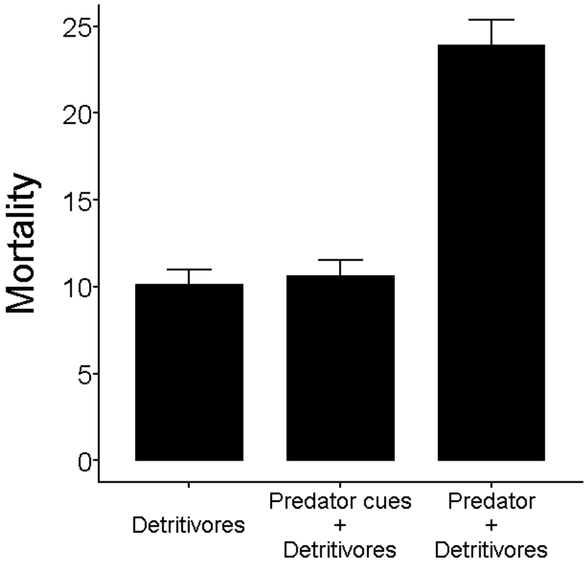
| | **LR Chisq** | **Df** | **Pr(>Chisq)** |
|---|---|---|---|
| **Litter Species** | 227.309 | 2 | < 0.0001 |
| **Litter Treatment** | 0.568 | 1 | 0.4511 |
| **Patch Treatment** | 72.787 | 3 | < 0.0001 |
| **Patch** | 3.181 | 1 | 0.0744 |
| **Litter Species x Litter Treatment** | 4.684 | 2 | 0.0961 |
| **Litter Species x Patch Treatment** | 35.982 | 6 | < 0.0001 |
| **Litter Species x Patch** | 5.831 | 2 | 0.0541 |
| **Litter Treatment x Patch Treatment** | 17.201 | 3 | < 0.0001 |
| **Litter Treatment x Patch** | 2.454 | 1 | 0.1172 |
| **Patch Treatment x Patch** | 28.487 | 3 | < 0.0001 |

Figure 2. Litter mass loss (%) of Litter Species across patch treatments. Bars indicate GLM model predicted means plus SEs after back transformation (from boxcox).



Despite the lack of either a density-mediated or a behavioral trophic cascade, we found evidence for both predation effects on the detritivores as well as for anti-predatory behavior. At the mesocosm level we found a strong significant effect of the Patch Treatment on isopod mortality ($\chi^2 = 106.6$, d.f.=2, $P < 0.0001$; Table 3, Fig. 5).

Figure 5. Dead isopods across patch treatments. Bars indicate GLM predicted means plus SEs after backtransformation from a quasipoisson GLM model.



However, there were no differences in mortality between the spider cues treatment and the detritivore treatment, indicating no nutritional effects of spider cues on detritivore survival (Planned comparison contrast, $Z = 0.42$, $P = 0.668$). We thus pooled these two treatments and compared the result to the treatment with spiders to test for predation effects. The results suggested strong predation effects as the mortality in the treatments with spiders was 2.3X that of the treatments without spiders (Planned comparison contrast, $Z = 10.36$, $P < 0.0001$). We failed to find engineering structural effects of litter mixtures as there was no significant interaction between Patch Treatment and Litter Treatment on detritivore mortality (i.e., the final model had no interactions, Table 3). A significant interaction would be expected if litter complexity (Litter Treatment) increased the survival of isopods within the predator treatment only.

Table 3. Generalized Linear Model ("quasipoisson" distribution) results testing for predator and structural effects of litter mixtures on isopod mortality.

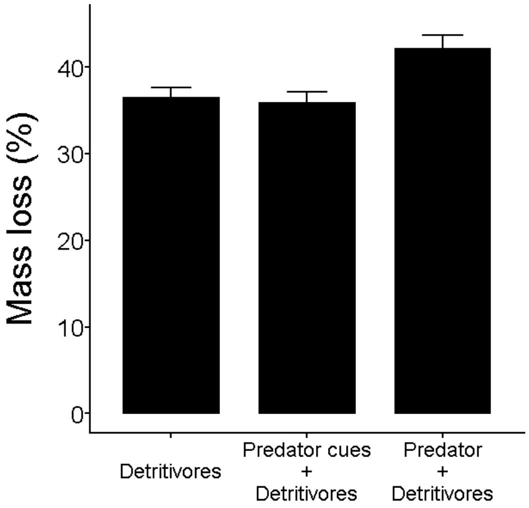
| | LR Chisq | Df | Pr(>Chisq) |
|---|---|---|---|
| **Patch Treatment** | 106.552 | 2 | < 0.0001 |
| **Litter Treatment** | 3.098 | 1 | 0.0783 |

Table 4. General Linear Model results, testing for anti-predatory behavior measured as differences in biomass loss (dry mass) among neighbor "Litter" patches. A patch treatment significant effect may indicate that prey were biasing their behavior towards patches free of predators (see also Fig. 6)

| | Chisq | Df | Pr(>Chisq) |
|---|---|---|---|
| **Litter Species** | 448.74 | 2 | < 0.0001 |
| **Litter Treatment** | 5.05 | 1 | < 0.01 |
| **Patch Treatment** | 6.71 | 2 | < 0.01 |
| **Dead Isopods** | 2.21 | 1 | 0.1368 |

We also found evidence of anti-predatory behavior when comparing the decomposition data on the "Litter" patches (i.e., those patches that contained litter only, disregarding the data on the "Litter+" patch within the mesocosm). There were significant differences among Patch Treatments on decomposition rate ($\chi^2$ = 6.71, d.f.=2, P = 0.035; Table 4, Fig. 6), indicating that the detritivores were affecting the decomposition rate differently in the "Litter" patch depending on what was present on the other ("Litter+") patch within the mesocosm. There were no differences in decomposition of the "Litter" patch between the spider cues treatment and the detritivore treatment, indicating no anti-predatory behavior in response to spider cues alone (Planned comparison contrast, Z = -0.41, P = 0.679). We thus pooled these two treatments and compared the result to the treatment with spiders to test for anti-predatory behavior in response to the presence of spiders. We found evidence for anti-predatory behavior as in the treatments with spiders the decomposition rate in the "Litter" patch was ca. 1.2X higher than in the same patch within the other two treatments (Planned comparison contrast, Z = 2.58, P = 0.01). This result demonstrates that despite the facilitation effects of predators on decomposition, when predators were present, the detritivores tended to bias their foraging activity on litter towards the patch free of enemies.

Figure 6. Anti-predatory behavior identified as litter mass loss in the “Litter” patch (i.e., the neighbor to the “Litter+” patch in the mesocosm; free of either spider or spider cues depending on the patch treatment). Bars indicate GLM model predicted means plus SEs.



## 3.6 Discussion

Our results support the hypothesis that the traces of spider activity contribute to accelerate litter decomposition by stimulating the foraging rate of their own prey. This acceleration occurred despite the fact that prey mortality rate from predation was twice as large when spiders were present, and despite the fact that prey showed anti-predatory behavior, biasing their foraging activity towards the enemy free patch in the treatments were the predator were present. Thus, we found the opposite of what would be expected in a trophic cascade, in which top-down control from predators, either on detritivore numbers or on detritivore behavior, would lead to lower consumption of basal resources (leaf litter).

Additionally, we found relevant and novel synergies between the predators and the litter bottom-up effects. First, the synergistic effects of litter mixtures only appeared when detritivores were present; as found in previous studies (De Oliveira, *et al*., 2010; Hattenschwiler & Gasser, 2005), or when spider cues were present in the absence of the spider. The presence of the spider, however, compensated the synergistic effect of the plant mixtures, as litter monocultures and mixtures had identical decomposition rates in the patches with spiders, probably because the spiders imposed top-down control on detritivore numbers and behavior. However, overall, the presence of spiders or spider cues had a stronger effect on accelerating decomposition than that of mixtures, and rather intuitively, the strongest effect was that which included the synergistic effects between the mixture and the spider cues, this later being the only treatment combination reaching above 50% decomposition (Fig. 4). Further synergistic effects were found in monocultures and in the more recalcitrant litter *S. tenacissima*, where the addition of isopods did not increase decomposition rates relatively to the treatments that had litter only. Instead, the stimulating effect of the spider traces of activity, in combination with the detritivores, increased decomposition in monocultures and *S. tenacissima* relatively to patch treatments in which only litter was provided, an effect that isopods alone could not induce.

We did not find support to the hypothesis that litter mixtures, by increasing habitat complexity, decrease predation rate on isopods. There was no support for the hypothesis of a nutritional advantage of either mixtures or spider cues, as isopod survival was unaffected by neither mixture treatments nor spider cues.

Usually, predators exert top-down non-consumptive effects on food webs by changing the behavior of their prey, either suppressing their activity or inducing a shift in the prey use of space (Schmitz & Barton, 2014; Schmitz *et al*., 2010; Sitvarin *et al*., 2016). We found evidence for a shift in space use, as decomposition (litter consumption) was higher in the "Litter" patches that had a spider on the neighbor patch, but not in those that had only spider traces of activity on the neighbor patch. The lack of anti-predatory response towards spider cues may not be surprising as isopods have been found to show anti-predatory behavior only when conspecific prey remains were present (Yao *et al*., 2009). Since prey remains in the "Predator cues + Detritivores" treatment came from crickets while actual isopods were being killed in the patch with spider, this alone could explain the differences between these two treatments. However, recently another type of non-consumptive effects, by which the predators modify the physical conditions of their surroundings, enhancing the habitat of the prey and promoting microbial growth and litter decomposition, has been proposed in aquatic habitats (Majdi, *et al*., 2016). These ecological engineering effects of predators could be more important than previously thought, but to our knowledge, focusing on decomposition in terrestrial habitats no formal test of this type of effects had been performed prior to the present work. Here, we tested this idea for the first time in a terrestrial system by using a food chain patch choice experiment, which in addition to testing for predator engineering effects, simultaneously allowed testing for density-mediated and trait-mediated indirect interactions, and the potential synergies of the different predator effects with the bottom-up effects of plant litter diversity. The fact that predator cues function synergistically with litter diversity to boost decomposition open new avenues of biodiversity ecosystem functioning research.

We can only speculate about what mechanisms led to the observed synergy between the three actors: predator cues, detritivores and litter. Predator cues likely increased nutrient availability enhancing fungi and bacteria growth both on the litter and in the gut of the detritivores, but these traces of predator activity also likely brought new bacteria and fungi that could not be present otherwise. The increase in nutrients could also be directly affecting the feeding performance of detritivores, and this enhanced performance in turn could feedback on the cue-litter mixture, further enhancing the growth of microbiota. Future studies should address all these questions and disentangle the effects of the different actors. One intriguing finding is the fact that despite isopods having suffered twice as much mortality in the “Litter+” patches with predators relatively to the “Litter+” patch with spider cues, the decomposition rates were nearly as high in both types of patches. The above suggests some kind of compensatory mechanism, such as the carcasses of the dead isopods further enhancing the growth of fungi and bacteria, or increasing the nutrient availability of the alive isopods thereby boosting their performance.

Our findings have consequences to explain why large predators may enhance the populations of their prey in field experiments, leading to an increase in decomposition rates, as found in dry beech forests (Melguizo-Ruiz *et al.,* 2019). The conventional explanation of behavioral or density-mediated trophic cascades occurring through the dynamics of the system, eventually leading to enhancing decomposition, is now complemented with the non-mutually exclusive hypothesis of predator facilitation of the decomposer fauna via the traces of predator activity. Given the large diversity of soil food webs (Bardgett & Van Der Putten, 2014; Brussaard, 1998; Moretti *et al*., 2017; Wall & Lynch, 2000), there is plenty of room for both mechanisms to be operating together. Future field experiments should be conducted to distinguish among all these possibilities.

In conclusion, in this study we devised a top-down control patch-choice experiment that allowed testing for behavioral and density-mediated trophic cascades on decomposition at the same time that testing the potential effect of predator cues facilitating decomposition, as well as the potential synergism of all of the above with the bottom-up effect of litter diversity. We found that despite feeding heavily on the detritivores, the net effect of predators is that of facilitating decomposition through their traces of activity, and that this effect is highly synergistic with litter identiy and diversity. Since plant decomposition is a central process in terrestrial ecosystems, our findings open a new horizon for BEF research.

## 3.7 References

Aerts, R. (1997). Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. *Oikos*, *79*(3), 439. doi:10.2307/3546886

Bardgett, R. D., & Van Der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature 515*, *505*(7528), 505–511. doi:10.1038/nature13855

Brussaard, L. (1997). Biodiversity and ecosystem functioning in soil. *Ambio*, *26*(8), 563–570. Retrieved from http://www.jstor.org/stable/4314670

Brussaard, Lijbert. (1998). Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology*, *9*(September 1997), 123–135. doi:10.1016/S0929-1393(98)00066-3

Buchkowski, R. W. (2016). Top-down consumptive and trait-mediated control do affect soil food webs: It's time for a new model. *Soil Biology and Biochemistry*, *102*, 29–32. doi:10.1016/j.soilbio.2016.06.033

Couteaux, M.-M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and liter quality. *Trends in Ecology & Evolution*, *10*(2), 63–66. doi:10.1016/S0169-5347(00)88978-

Crowther, T. W., Boddy, L., & Hefin Jones, T. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. *The ISME Journal*, *6*(11), 1992–2001. doi:10.1038/ismej.2012.53

De Deyn, G. B., Cornelissen, J. H. C., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, *11*(5), 516–531. doi:10.1111/j.1461-0248.2008.01164.x

De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, *24*(4), 937–946. doi:10.1111/j.1365-2435.2010.01694.x

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, *104*(2), 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, *25*(6), 372–80. doi:10.1016/j.tree.2010.01.010

Guenet, B., Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, *91*(10), 2850–61. doi:10.1890/09-1968.1

Hattenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, *102*(5), 1519–1524. doi:10.1073/pnas.0404977102

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Hawlena, D., Strickland, M. S., Bradford, M. A., & Schmitz, O. J. (2012). Fear of predation slows plant-litter decomposition. *Science, 336*(June), 1434–1438.

Hawlena, Dror, & Schmitz, O. J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences*, *107*(35), 15503–15507. doi:10.1073/pnas.1009300107

Heal, O. W., Anderson, J. M., & Swift, M. J. (1997). Plant litter quality and decomposition: an historical overview. In C. G. & K. E. Giller (Eds.), *Driven By nature: Plant litter quality and decomposition* (pp. 3–32). Wallingford, Inglaterra: CAB International.

Hornung, E., Farkas, S., & Fischer, E. (1998). Tests on the Isopod Porcellio scaber. In *Handbook of soil invertebrate toxicity tests* (pp. 208–226).

Hunter, M. D., Adl, S., Pringle, C. M., & Coleman, D. C. (2003). Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition.

*Pedobiologia*, *47*(2), 101–115. doi:10.1078/0031-4056-00174

Kalinkat, G., Brose, U., & Rall, B. C. (2013). Habitat structure alters top-down control in litter communities. *Oecologia*, *172*(3), 877–887. doi:10.1007/s00442-012-2530-6

Lawrence, K. L., & Wise, D. H. (2004). Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, *48*(2), 149–157. doi:10.1016/j.pedobi.2003.11.001

Lawton, J. H., & Jones, C. G. (1993). Linking species and ecosystem perspectives. *Trends in Ecology & Evolution*, *8*(9), 311–313. doi:10.1016/0169-5347(93)90236-I

Lensing, J. R., & Wise, D. H. (2006). Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences*, *103*(42), 15502–15505. doi:10.1073/pnas.0607064103

Lenth, R. (2019). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.5.1.

Majdi, N., Boiché, A., Traunspurger, W., & Lecerf, A. (2014). Predator effects on a detritus-based food web are primarily mediated by non-trophic interactions. *The Journal of Animal Ecology*, *83*(4), 953–62. doi:10.1111/1365-2656.12189

Majdi, N., Kreuzinger-Janik, B., & Traunspurger, W. (2016). Effects of flatworm predators on sediment communities and ecosystem functions: a microcosm approach. *Hydrobiologia*, *776*(1), 193–207. doi:10.1007/s10750-016-2751-5

Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., … Moya-Laraño, J. (2019). Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. *Journal of Animal Ecology*, (January), 1365-2656.13101. doi:10.1111/1365-2656.13101

Moore, J. C., Berlow, E. L., Coleman, D. C., De Suiter, P. C., Dong, Q., Hastings, A., … Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*(7), 584–600. doi:10.1111/j.1461-0248.2004.00606.x

Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., … Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567. doi:10.1111/1365-2435.12776

Moya-Laraño, J., Orta-Ocaña, J. M., Barrientos, J. A., Bach, C., & Wise, D. H. (2002). Territoriality in a cannibalistic burrowing wolf spider. *Ecology*, *83*(2), 356–361. doi:10.1890/0012-9658(2002)083[0356:TIACBW]2.0.CO;2

Ngai, J. T., & Srivastava, D. S. (2006). Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. *Science*, *314*(5801), 963–963. doi:10.1126/science.1132598

Peinado, M., Alcaraz, F., & Martínez-Parras, J. M. (1992). *Vegetation of Southeastern Spain*. (Cramer, Ed.).

Santonja, M., Fernandez, C., Gauquelin, T., & Baldy, V. (2015). Climate change effects on litter decomposition: intensive drought leads to a strong decrease of litter mixture interactions. *Plant and Soil*, *393*(1–2), 69–82. doi:10.1007/s11104-015-2471-z

Schmitz, O. J., & Barton, B. T. (2014). Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control. *Biological Control*, *75*, 87–96. doi:10.1016/j.biocontrol.2013.10.001

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. doi:10.1111/j.1461-0248.2010.01511.x

Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163. doi:10.1111/j.1461-0248.2003.00560.x

Schuster, M. J., & Dukes, J. S. (2014). Non-additive effects of invasive tree litter shift seasonal N release: a potential invasion feedback. *Oikos*, *123*(9), 1101–1111. doi:10.1111/oik.01078

Sitvarin, M. I., Rypstra, A. L., & Harwood, J. D. (2016). Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*, *125*(8), 1057–1068. doi:10.1111/oik.03190

Stephan, J. G., Stenberg, J. A., & Björkman, C. (2017). Consumptive and nonconsumptive effect ratios depend on interaction between plant quality and hunting behavior of omnivorous predators. *Ecology and Evolution*, *7*(7), 2327–2339. doi:10.1002/ece3.2828

Team, R. C. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M. P., Petchey, O., Palmborg, C., & Huss-Danell, K. (2009). Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology*, *90*(1), 90–9. doi:10.1890/08-0382.1

Wall, D. H., & Lynch, J. (2000). Soil Biodiversity and Ecosystem Functioning. *Biological Resource Management Connecting Science and Policy*, 283–290. doi:10.1007/978-3-662-04033-1

Yao, M., Rosenfeld, J., Attridge, S., Sidhu, S., Aksenov, V., & Rollo, C. D. (2009). The Ancient Chemistry of Avoiding Risks of Predation and Disease. *Evolutionary Biology*, *36*(3), 267–281. doi:10.1007/s11692-009-9069-4

Zimmer, M., Kautz, G., & Topp, W. (2005). Do woodlice and earthworms interact synergistically in leaf litter decomposition? *Functional Ecology*, *19*(1), 7–16. doi:10.1111/j.0269-8463.2005.00926.x

# Chapter 4.

## Contrasting decomposition patterns in fertility islands and the surrounding bare soil

Prado López, M., Moya-Laraño, J., Pugnaire, F.I. Contrasting decomposition patterns in
fertility islands and the surrounding bare soil.
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## 4.1 Abstract

1. Fertility islands in drylands may strongly influence nutrient cycling and carbon sequestration by the accumulation of litter of different species, creating mixtures of leaf litter. Decomposition of these mixtures may depend on biotic and abiotic factors in rather unknown ways.
2. We addressed how shrub understory conditions contrast with gaps between shrubs to influence decomposition of leaf litter mixtures. We hypothesized that under shrub canopies, mainly biotic-driven decomposition would result in synergies, whereas away from shrubs, mainly abiotic-driven decomposition would lead to additive effects.
3. We conducted a field experiment in a Ziziphus lotus community on sand dunes. Under certain conditions, Ziziphus lotus typically forms fertility islands, which are threatened by anthropogenic disturbances in the Mediterranean coasts of SE Spain. We manipulated litter richness in litterbags (mesocosms) that allowed most invertebrate fauna to move freely in and out, while samples were exposed to UV radiation and other abiotic components. These mesocosm were located in the understory of Z. lotus shrubs and in gaps between shrubs. After 184, 367 and 597 days in the field, we assessed the rate of mass loss of three common species, Chamaerops humilis, Retama sphaerocarpa and Stipa tenacissima in monospecific as well as in mixtures of two and three species.
4. Decomposition under shrubs depended on the identity of plant species litter, with no effect of litter diversity. Under canopies, decomposition showed antagonistic effects regardless of plant species richness, but again its intensity depended on the species making up the mix. The strength of these antagonistic effects increased with time and dependent on the litter species. Decomposition in gaps resulted in negligible effects among species, with only a mild synergy effect for one of them.
5. We suggest that biotic decomposition operates under shrubs and abiotic decomposition acts in gaps. These results have implications for nutrient cycling and particularly on carbon sequestration and soil organic matter stabilization in drylands. They provide insights into decomposition in a context of global environmental change. We conclude that the high spatial heterogeneity in drylands

should be considered in decomposition models to enhance their accuracy and predictive power concerning decomposition rates, nutrient cycles and carbon sequestration.

**Key words**: Biodiversity-ecosystem functioning, Fertility islands, Leaf litter mixtures, Non-additive effects, Priming effects

## 4.2 Introduction

Fertility islands play a fundamental role particularly in dryland plant communities, where the scarcity of soil nutrients and extreme conditions constrain plant primary productivity (Moorhead & Reynolds, 1991; Throop & Archer, 2009). The study of fertility islands in drylands has been considered in the light of facilitation which is a positive interaction among organisms contributing to the recruitment, survival and reproductive success of other species (Michalet & Pugnaire, 2016). The microenvironment modifications under shrub canopy include the decrease of solar radiation (Moro *et al*. 1997) , soil and nutrient accretion (Pugnaire *et al*. 2004; Throop & Archer, 2009; Zhang & Zak, 2010), the decrease of soil evaporation (Safriel, *et al*., 2005) and soil temperature (Hobbie, 1992; Pugnaire *et al*. 1996; Moro *et al*. 1997; Throop & Archer, 2009) and consequent increment of moisture, as well as nutrient availability (Brooker *et al*., 2008¸ Pugnaire *et al*. 2001).

Decomposition under shrub canopies in drylands is usually slow (Diedhiou, Dossa, Badiane, & Diedhiou, 2009; Predick *et al*., 2018; Throop & Archer, 2009), consistent with the fact that carbon sequestration is higher under shrubs (Brooker *et al*., 2008). However, models of decomposition and nutrient cycling in fertility islands has largely neglected the interactions between abiotic and biotic factors, such as thermal- and photo degradation, soil abrasion and the mix of litter form different species (Diedhiou, Dossa, Badiane, & Diedhiou, 2009; Predick *et al*., 2018; Throop & Archer, 2009).

In contrast to the slow decomposition rate observed under shrub canopies, decomposition in gaps is usually high due to the prevalence of abiotic factors (Predick *et al*., 2018; Throop. & Archer, 2007; Throop & Archer, 20 09), such as higher photo- degradation, diel temperature oscillations, and soil abrasion (Throop & Archer, 2009), which contribute to litter fragmentation (Hewins, *et al*, 2013; Throop. & Archer, 2007) and microbial inoculation (Moorhead & Reynolds, 1991) increasing decomposition rates (Levi *et al*., 2009; Throop & Archer, 2009; Uselman, *et al*., 2011). These contrasting patterns in decomposition have main implications concerning nutrient cycling and carbon sequestration. Thus, in a context of global environmental change it is important to understand how these two components of the ecosystem affect biogeochemical cycles.

One of the decomposition mechanisms less explored in drylands is the effect of leaf litter mixtures, despite the fact that fertility islands gather a relatively high diversity of shrubs, grasses and forbs that lead to litter mixtures of different species (Barnes *et al*., 2015; Schlesinger *et al*., 1990). In these patches, litter mixes may decompose differentially (Gartner & Cardon, 2004; Hunter, *et al*., 2003; Santonja, *et al*., 2015). Decomposition in litter mixtures can result in either additive or non-additive effects, which in turn can result in synergies and antagonisms (Gartner & Cardon, 2004). Non-additive effects appear when a particular species decomposes at the same rate in monospecific and in mixtures, whereas non-additive effects imply that decomposition of a particular species decompose faster (synergies) or slower (antagonisms) in combination with other litter species than when decomposing with same-species litter (Hunter, *et al*., 2003; Santonja, *et al*., 2015).

Litter mixture effects have been usually ascribed to the diversity of functional plant traits (Viketoft *et al*., 2009) rather than to species richness (Gessner *et al*., 2010). The diversity of physical-chemical litter traits has been linked to processes such as nutrient transfer by leaching from high- to poor-quality leaves (Heal, Anderson, & Swift, 1997), which provide with a large array of nutrients to soil organisms enhancing decomposition (Gartner & Cardon, 2004; Hättenschwiler, *et al*., 2005b; Schuster & Dukes, 2014). Additionally, litter mixtures provide a complex physical structure with favorable micro-environmental conditions for micro- and macro-decomposers (Gartner & Cardon, 2004; Hättenschwiler, *et al*., 2005; Schuster & Dukes, 2014).

The study of litter mixture effects has been conducted almost exclusively in mesic ecosystems, and as a consequence the assessment of abiotic factors such as photodegradation and soil abrasion in drylands has mostly been investigated in monocultures (Almagro, *et al*., 2015; Almagro, *et al*., 2016; Martínez-Yrízar, *et al*., 2007; Verhoef *et al*., 2000). Thus, we do not know to what extent abiotic factors such as photodegradation, high temperatures, lack of water and soil abrasion may affect decomposition in leaf litter mixtures (Birkhofer *et al*., 2011; García-Palacios *et al*., 2016; Hooper & Vitousek, 1997; Wardle *et al*., 1997).

In a 600-day field experiment in SE Spain (the driest place in Europe) we assessed litter decomposition in a gradient of species richness from monospecific to 2 and 3 species mixtures, under shrub canopies and in gaps. As the favorable microenvironment under the shrub canopy may enhance biotic activity, which may in turn trigger synergies in litter decomposition (De Oliveira, Hättenschwiler, & Tanya Handa, 2010; Hattenschwiler & Gasser, 2005), we predicted stronger synergies in mixtures under shrub canopies. As in mesic habitats, we also predicted higher decomposition rates away from shrubs, which could be due to the predominance of abiotic factors such as photodegradation and abrasion (Austin & Vivanco, 2006). As evidence of more biotic activity under shrub canopies, we predicted that leaf litter under shrubs would host higher abundances of soil fauna.

The assessment of decomposition of leaf litter mixtures under and away from shrubs will help us to understand the role of fertility islands on nutrient cycling in drylands and elucidate the role of biotic (litter mixtures) factors. In addition, it will provide a very rough and preliminary idea of how the several abiotic factors that differ in and out shrubs in drylands (UV, moisture and soil movement) could affect decomposition (Barnes *et al*., 2015). Measuring the role of fertility islands during decomposition will also improve our understanding about the fate of nutrients, and particularly carbon, in drylands and ultimately aid to enhancing the predictive ability of current decomposition models based on climate and litter quality (Whitford *et al*., 2016).

## 4.3 Methods

We selected Ziziphus lotus, a deciduous shrub restricted to priority conservation lands in the Mediterranean area of SE Spain (Habitat 5220*, Directive 92/43/EEC). Although, this species is not restricted to dune systems, a population in Cabo de Gata-Níjar Natural Park (an UNESCO Biosphere preserve), is threatened by agricultural, urban sprawl and exotic plant invasions (Guirado, Segura, & Castillo, 2018; Tirado, 2009). Ziziphus lotus is a typical ecosystem engineer that creates fertility islands where temperature is lower and air humidity higher. It creates massive accumulations of sand, richer in organic matter, nitrogen and phosphorous than the surrounding matrix, mostly consisting on bare soil and scattered small shrubs, grass and forbs (Tirado, 2009; Tirado & Pugnaire, 2003). This shrub species is a winter deciduous (Guirado, Segura, & Castillo, 2018; Zouaoui, Ksontini, & Ferchichi, 2014). This means that under Z. lotus, the maximum UV radiation occurs in winter, when it is at its minimum.

The experiment took place between January 2017 and August 2018. We used three plant species with contrasting physical and chemical characteristics (Table 1); Chamaerops humilis L., Retama sphaerocarpa L. and Stipa tenacissima L. Plant litter was hand collected as standing-death material, choosing only recently senesced leaves which had been exposed to UV for short time (as assessed by color). Stipa tenacissima litter and R. sphaerocarpa cladodes were collected from a community in the Tabernas desert (37°03′00″N, 2°23′29″W) whereas litter from the palm C. humilis was collected from Cabo de Gata-Nijar Nature Park (36°46'56.42"N, 2°14'31.13"W), both sites in Almeria, Spain. Before to onset of the experiment, all litter was oven-dried at 60°C for 72 h, and we then prepared litter bags each containing 3 g (dry weight) of 10 cm approx litter pieces of. We also determined leaf functional traits including carbon (C) and nitrogen (N) content using a C-N analyzer (LECO Truspec, St. Joseph, MI, USA). Water holding capacity (WHC) and specific leaf area (SLA) were calculated according to Pérez-Harguindeguy et al. (2013). The selected species show substantial differences in the measured traits (Table 1).

Table 1. Chemical and physical characteristics of *Chamaerops humilis*, *Retama sphaerocarpa* and *Stipa tenacissima* litter collected in Almeria province, SE Spain. Values are Mean ± 1 SE (n = 3). Values in a column with the same superscript letter are not significantly different from each other (Tukey-test).

| | **C (mg / g$^{-1}$)** | **N (mg / g$^{-1}$)** | **WHC (%)** | **C/N (mg / g$^{-1}$)** | **SLA (cm$^2$/g$^{-1}$)** |
|---|---|---|---|---|---|
| ***C. humilis*** | 47.6 ± 0.03$^b$ | 1.65 ± 0.01$^c$ | 115.41 ± 2.35$^c$ | 37.13 ± 0.95$^b$ | 51.67 ± 2.87$^c$ |
| ***R. sphaerocarpa*** | 48.19 ± 0.02$^c$ | 1.89 ± 0.01$^b$ | 85.14 ± 2.48$^b$ | 27.24 ± 0.07$^a$ | 26.59 ± 0.43$^a$ |
| ***S. tenacissima*** | 46.5 ± 0.01$^a$ | 0.57 ± 0.001$^a$ | 64.61 ± 1.02$^a$ | 90.58 ± 0.33$^c$ | 38.43 ± 1.62$^b$ |

The litterbags were built using a novel three-dimensional design (20x20x5cm, hereafter mesocosms); the mesh size on the top and sides was 0.5cm which allowed the access of most micro, meso- and macrofauna as well as soil a plant material dragged by wind (Fig.1S). The bottom of the mesocosms, however, was covered with finer 1.2mm mesh to prevent the loss of plant material from leaching (e.g., Melguizo-Ruiz et al. 2919). These mesocosms were designed to prevent litter compaction and microclimate alteration, while allowing most light to go through the mesocosm. Indeed, a luximeter test estimated that only 16% of the natural light failed to reach the litter within the mesocosm.

To test the effect of leaf litter mixtures on decomposition under and away from the shrubs (position treatment), we prepared mesocosms in mixtures using all possible combinations of two and three-species, as well as a monospecific treatment of each litter species. A total of 280 mesocosms were settled under and away of 20 individuals of Z. lotus. Each of these shrubs measured 119 m2 on average. The litter boxes thus contained one single species of litter (20 litter boxes for each species and position treatment), 2-sp mixtures (20 litter boxes for each 2-species combination and position treatment) or 3-sp mixtures (20 litter boxes with the 3-species mixture and position treatment). Because in order to measure decomposition, each species was carefully separated from each other in the mixtures before obtaining final weights (e.g. Prado et al. submitted), this design allowed distinguishing the effect of identity from that of diversity (species richness 1, 2, 3) on decomposition. All mesocosms contained 3 g of litter (dry weight) regardless of the treatment. Mesocosms in treatments with 2 species mixtures had 1.5 g of each species, and the treatment with the 3 species mixture contained 1 g of each species. Finally monospecific treatments contained 3g of a single litter species. Five of the 20 replicates for each treatment were collected 6 months after settlement (07/13/2017, collecting date 1), and another five after 12 months (01/13/2018, collecting date 2).The remaining 10 litter boxes were collected 20 months (08/30/2018, collecting date 3) after settlement. Before oven-drying the litter (60ºC 72h) to estimate mass loss, we also extracted the soil mesofauna for 5 mesocosms of each species (in the monospecific treatment only) and for collecting day 1 and 2 only, for which we used Berlese funnels (incandescent 55W bulbs) during 72 hrs. Spiders, pseudoscorpions, Diplura, and Prostigmata and Mesostigmata mites were assigned to predators, and all Astigmata, Oribatida mites and Collembola, Psocoptera, Julidae, Protura to decomposers.

Overall we had 7 treatments x 2 position levels (under and away from shrubs) x 3 collection dates x 5 or 10 replicates.

All analyses were performed using R 3.6.1 (R Core Team, 2019). Litter mass loss was calculated as the percentage of the difference in mass loss per year as: [(M0-Mf)/ M0]*100*t-1, where M0 is the initial dry mass of the litter, Mf is the mass of the litter in the collection date and t is the time elapsed (in years) from settlement to collection. Further, we also documented decomposition constants (k), distinguishing those cases in which decomposition showed substantial differences (e.g., based on the identity of the species or under and away from shrubs). To estimate k we included collection date as Julian date in years and fitted the linear model: log(Mf/M0) ~ kt to estimate k from least-squares linear regression (e.g., Melguizo-Ruiz et al. 2019), fixing the intercept at 0 (i.e., at day 0 log(Mf/M0) is exactly 0).

To assess leaf litter mixture effects, we calculated an improved net diversity effect index based on the RII index to study biotic interactions (Armas, et al., 2004), as this difference/sum ratio index is very well behaved statistically. To that end, we used the recorded mass loss of a species in the mixture (M) and in monospecific treatments (S).

NDE= (M-S)/(M+S)

NDE is positive when a species decomposes more in the mixture than in monospecific, and vice versa. We determined the effects of decomposition set (under canopy vs away from canopy), species richness (Monospecific vs 2-sp mixtures vs 3-sp mixtures), on litter mass loss using Generalized Linear Mixed Models with normally distributed errors (library "lme4"). Plant was included as a random factor, and date, species identity, position and species richness as fixed factors. In all these models we used backward elimination starting with models with third order interactions and eliminating non-significant terms, finally keeping only the final model with all significant terms for the interactions. When necessary (e.g. differences among plant species), we ran Tukey post-hoc tests of significance to know which groups differed from each other. The abundance of decomposers and predators under and away from shrubs were analyzed by means of a GLM with a negative binomial distribucton to control for overdispersion (function "glm.nb" in MASS). Biomass loss data were boxcox-transformed to account for normality deviations of residuals among treatments. Data was back-transformed using the “make.tran” function in “emmeans”. The function “eff_size” was also used to compare Cohen’s effect sizes when necessary.

## 4.4. Results

We found higher mass loss in gaps only after 12 and 20 months of decomposition but no differences after 6 months (Table 2; Fig 1). Decomposition rate clearly decreased over time (Fig. 1,2). Decomposition under shrubs and in gaps also depended on the species identity in the mixtures (Table 2; Fig. 3). While Retama (Z=0.80; p = 0.992) decomposed equally under shrubs (k = 0.71 year-1, %95 CI: [0.49, 0.92]) and in bar soil (k = 0.88 year-1 [0.56, 1.17]), and Stipa showed a non-significant trend towards decomposing faster in bare soil (k = 0.73 year-1 [0.53, 0.75]) than under shrubs (k = 0.44 year-1 [0.31, 0.56]; Z=0.91; p = 0.056), Chamaerops decomposed remarkably faster in bare soil (k = 0.83 year-1 [0.58, 1.08]) than under shrub canopies (k = 0.37 year-1 [0.17, 0.57]; Z = 4.32; p <.0001). Contrary to what we expected, there were no differences in mass loss over the gradient of richness in mixtures nor any significant interaction with position (Fig. 4), date of collection (Fig. 2S) or species identity (Fig. 3S).

Figure 1. Mass loss rate (% year-1) depending on position and collecting date. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).

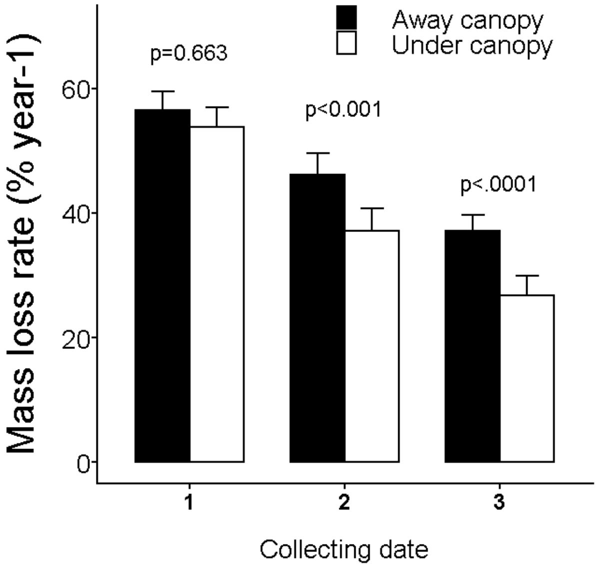
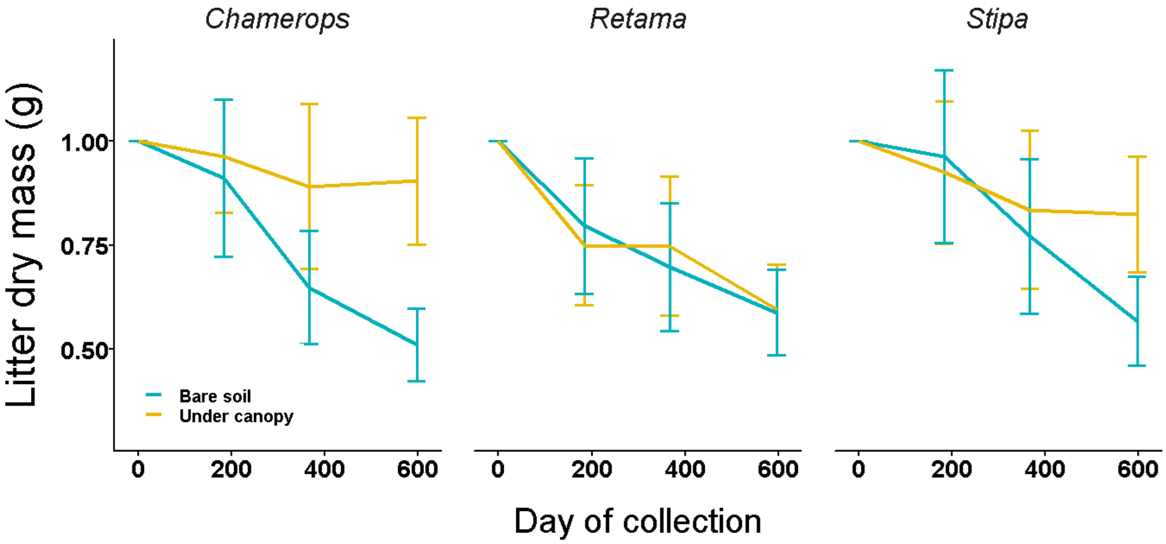


Figure 2. Decomposition rate along the time (dry mass (g)) by species under and away from shrubs. Bars indicate SE.



### 4.4.1 Mixture effects

The model testing litter mixture effects had a significant Position x Date of collection interaction (Table 3; Fig. 5) and Position x Species Identity interaction (Table 3; Fig. 6). Decomposition of litter mixtures under shrub canopies were mostly antagonic through the 600 days of the experiment, which were far more severe under canopies and tended to increase in magnitude over time. The significant Position x Species Identity interaction revealed that *Chamaerops* had the strongest antagonism under shrub canopies and mild synergistic effects away from shrubs.

Figure 3. Effects of position and species identity on decomposition. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).

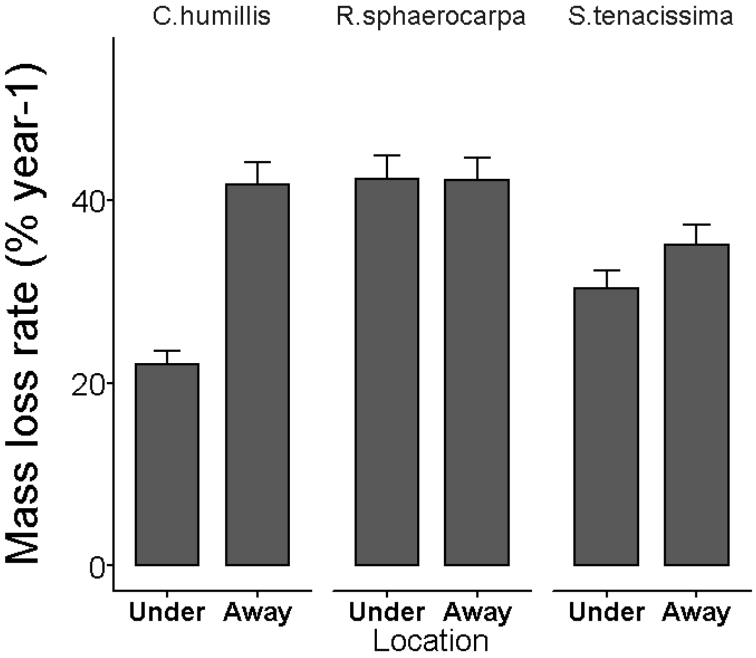


Figure 4. Mass loss rate (% year-1) decomposition depending on position and litter species richness. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).

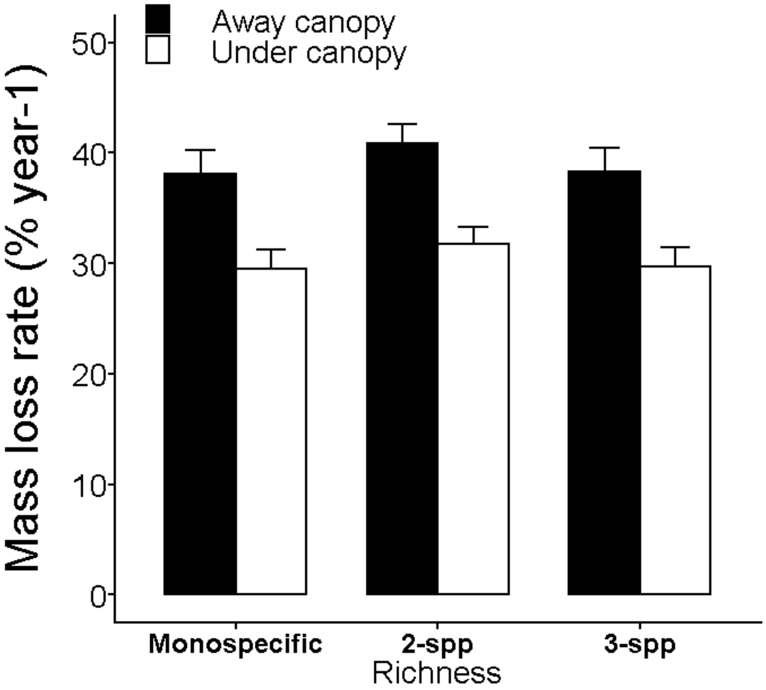


Table 2. Generalized linear model results (F-values) of litter decomposition after 600 days of decomposition.

| | **F** | **Df** | **Df.res** | **Pr(>F)** |
|---|---|---|---|---|
| (Intercept) | 265.246 | 1 | 85.35 | <0.001 |
| **Date of Collection (DC)** | 32.991 | 2 | 36.21 | <0.001 |
| **Position (P)** | 11.504 | 1 | 436.18 | <0.001 |
| **Species identity (ID)** | 2.461 | 2 | 436.08 | 0.086 |
| **Mixtures** | 1.193 | 2 | 437.02 | 0.304 |
| **P x ID** | 14.850 | 2 | 436.45 | <0.001 |
| **P x DC** | 5.918 | 2 | 436.5 | <0.001 |

Table 3. Generalized linear models (F-values) on leaf litter mixtures mass loss.

| | **F** | **Df** | **Df.res** | **Pr(>F)** |
|---|---|---|---|---|
| (Intercept) | 14.040 | 1 | 73.88 | <0.001 |
| **Date of Collection (DC)** | 31.227 | 2 | 41.12 | <0.001 |
| **Position (P)** | 8.851 | 1 | 322.14 | <0.01 |
| **Species identity (ID)** | 3.162 | 2 | 322.02 | **0.043** |
| **P x DC** | 3.290 | 2 | 322.54 | **0.038** |
| **P x ID** | 9.277 | 2 | 322.31 | <0.001 |

Figure 5. Net diversity effect (NDE index) after 600 days of experiment depending on the litter mesocosm position and date of collection. Positive values mean synergies and negative values antagonisms. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).

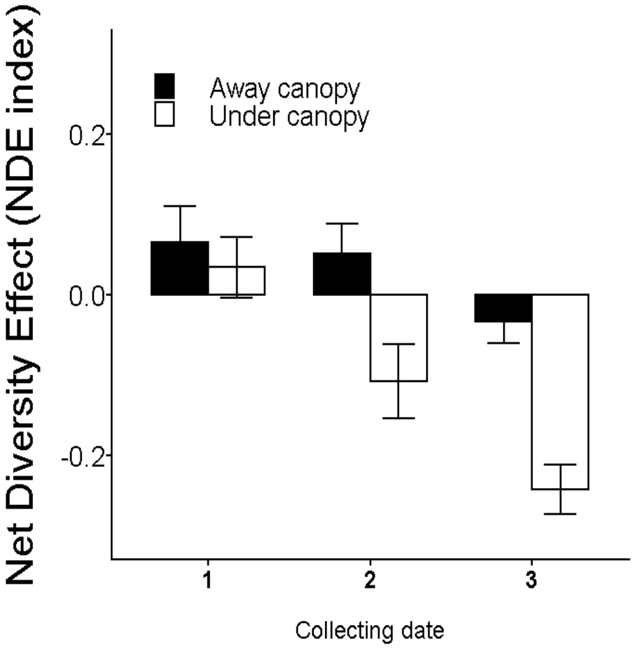
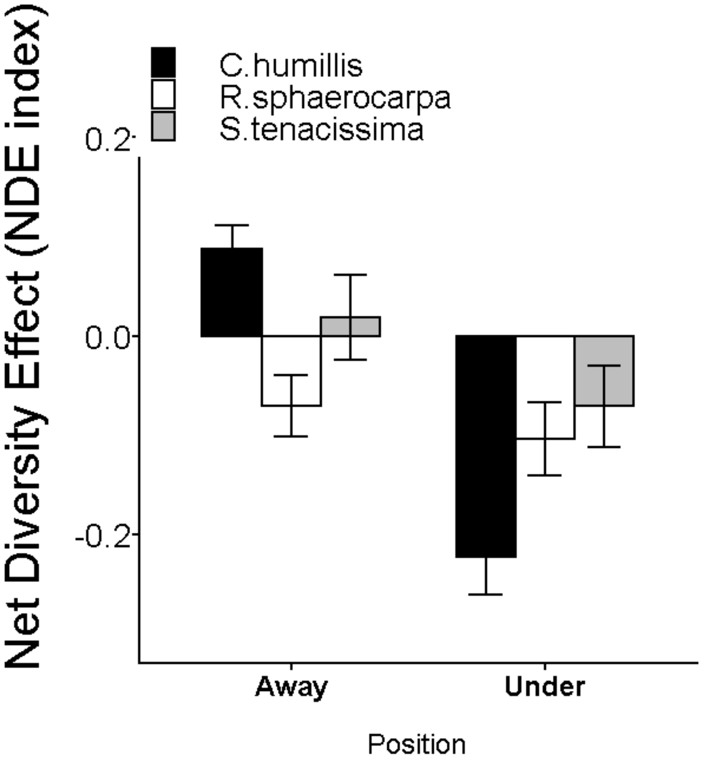


Figure 6. Net diversity effect (NDE index) after 600 days of experiment depending on position and species identity. Positive values mean synergies and negative values antagonisms. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).



## Fauna abundance in mesocosms away and under shrub canopies

Both decomposers ($\chi_1^2$ = 19.45; p < 0.0001) and predators ($\chi_1^2$ = 9.73; p = 0.002) were more abundant in mesocosms below *Z. lotus* canopies than in gaps (Fig. 4S). There were no differences in the abundances of either decomposers ($\chi_1^2$ = 3.9; p < 0.142) or predators ($\chi_1^2$ = 3.1; p = 0.216) among litter of the different plant species.

## 4.5 Discussion

Our data show that decomposition under shrubs and in gaps may have implications for the overall nutrient cycling and specifically in carbon fluxes in drylands. Decomposition under shrub canopies, mainly driven by biotic components enhanced by higher moisture conditions, may result in greater accumulation and longer stabilization of organic matter, consequence of antagonisms in litter mixtures and a generalized low decomposition rate (Cotrufo *et al*., 2015). In contrast, decomposition in gaps, mainly abiotic-induced, may lead to a massive loss of carbon, released as $CO_2$ directly to the atmosphere, without passing through soil pools (Austin & Vivanco, 2006). Supporting the hypothesis that biotic interactions are more important under the shrub canopies, we found that both decomposers and predators were more abundant in the litter mesocosms below *Z. lotus* than in gaps.

Decomposition rate under shrub canopies was substantially lower than in gaps, as reported by previous studies (Gliksman *et al*., 2018; Predick *et al*., 2018; Throop. & Archer, 2007; Throop & Archer, 2009). In addition, decomposition of litter mixtures under shrub canopies resulted in significantly more intense antagonisms than in gaps. This lower decomposition and higher antagonisms may be consequence of several factors such as the high quantity of antioxidants in the litter of *Z. lotus* which retard decomposition and decreases microbial activity (Li *et al*., 2018; Naili, *et al*., 2010). As our mesocosms were designed to allow the entrance of meso- and macrofauna (mesh size of 0.5 cm), this could also have facilitated the entrance of *Z. lotus* litter fragments that could have negatively affected decomposition by interacting with our litter samples and producing unwanted effects. Future studies should test this hypothesis including different combinations of litter of *Z. lotus* with litter of the most common plants that integrate the cluster of fertility islands.

Beyond biotic activity under the shrub, the phenology patterns of *Z. lotus* can explain also the lower decomposition rates under shrub canopy. In the summer season, *Z. lotus* shrubs keep their leaves which help reducing temperature underneath, reduce evaporation and also the incidence of UV radiation when rainfall is at its minimum and UV radiation at its maximum (Almagro, Martínez-López, Maestre, & Rey, 2017). On the contrary, in winter time *Z. lotus* shrubs lose their leaves (Guirado, Segura, & Castillo, 2018; Zouaoui, Ksontini, & Ferchichi, 2014), when UV radiation is at its minimum. This timing of litter fall can delay decomposition under shrubs compared to gaps, as the latter have been exposed to the abiotic factors more intensely all year around.

The very low abundance of macrodetritivores in the study site (none was observed within the mesocosms) may also explain the lower decomposition rates and the absence of synergistic effects in *Retama* and *Stipa* when decomposed under shrub canopies. The greater soil meso-fauna abundance under shrub canopy may be promoted by the lower intensity of UV radiation and temperature and higher moisture (Predick *et al*., 2018). However, and despite this fact (Fig. 1S), decomposition was significantly lower, which implied that the impact of meso-fauna is not as big as the abiotic factors in gaps that affect decomposition stronger than biotic factors (Austin, 2011). However, the role of soil fauna during decomposition under shrub canopies may have a transcendental role in the fate of nutrients and soil organic carbon since it has been observed that biotic decomposition contributes considerably to soil organic matter accumulation (Cotrufo *et al*., 2015; Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013; Soong, Parton, Calderon, Campbell, & Cotrufo, 2015). In addition, the higher abundance of predators underneath shrubs may not necessarily be detrimental to decomposers, but may rather facilitate detritivore abundances, as recently demonstrated in a field experiment (Melguizo-Ruiz et al. 2919).

This prevailing impact of biotic drivers (microorganisms and meso fauna) under shrub canopies may explain the differences in decomposition between species, as decomposers degrade more efficiently high quality species i.e. *Retama*, and produce unbalances on the proportion of litter with high/low quality in mixtures, and these unbalances can result in critical modification of decomposition rates and nutrient cycling (Hattenschwiler & Gasser, 2005). Under shrub canopies, the quick decomposition of *Retama* (the species with the highest content of nitrogen) may lead to slower decomposition of *Chamaerops* and *Stipa* (species with higher content of carbon), partially explaining the observed antagonisms. However, *Retama* was also clearly affected by the other plants under shrubs as its decomposition was also antagonistic. Whereas in gaps, the greater impact of photodegradation on carbon compounds could have intensified the negative influence of other species on *Retama* which still showed antagonistic decomposition. This difference in decomposition rates between species may be due to the relevance of particular functional traits such as WHC and SLA as predictors of non-additive effects during decomposition in drylands, i.e. *Chamaerops* in mixtures away from shrubs, showed significant synergies, whereas markedly antagonistic effects under shrub canopy. This contrasting behavior may be related to the higher WHC and SLA relatively to *Retama* and *Stipa*. WHC and SLA have been observed to provide high composition capacity in burial rather than in light exposed litter (Liu *et al*., 2017). These results suggest that leaf functional traits such as WHC and SLA may be a key component for the improvement of the prediction of non-additive effects in leaf litter mixture and the overall decomposition models in drylands. Hence, we suggest that decomposition experiments in drylands should include combinations of litter with different functional traits to test this hypothesis.

The substantially higher mass loss away from shrubs in our experiment, exemplifies the dominance of abiotic drivers during decomposition in drylands (Gaxiola & Armesto, 2015; Predick *et al*., 2018; Rey *et al*., 2012). The higher photo and thermal degradation and higher soil infiltration into mesocosms away from shrubs, may produce greater physical break down of litter, in contrast to what occurs under shrub canopies, where the reduction of soil movement associated with higher under-canopy herbaceous and other smaller shrubs biomass (Tirado & Pugnaire, 2005), may reduce the impact of soil abrasion and UV incidence (Throop & Archer, 2009). Additionally, decomposition away from shrubs may be influenced by the coupling between the abiotic impact and the activity of microorganisms adapted to climatic adverse conditions as it happens in the very well documented photopriming effects (Baker, Allison, & Frey, 2015). Hence, we suggest more intense simultaneous abiotic-biotic multiplicative effects during decomposition away from shrubs than under shrub canopy. While soil abrasion operates continually along the decomposition process, photo- and thermal degradation operate at a daily scale through the dark-light cycles. This coupling of abiotic-biotic factors may enhance microbial activity and microbial colonization (Day, Bliss, Tomes, Ruhland, & Guénon, 2018; Lin, Karlen, Ralph, & King, 2018) resulting ultimately in priming effects. However, a recent experiment using the same litter species failed to document priming effects when the litter was exposed to UV light for several months in the laboratory (Prado et al. submitted).

A different mechanism to explain higher decomposition away from shrubs in our study is the burial of the mesocosms which may conduct to minimize the impact of photo- and thermal degradation as well as soil abrasion and increment the humidity which may enhance the microbial activity. This type of soil-litter mixtures has been reported as a factor to increase decomposition away from shrubs in burial litter rather than in light exposed litter (Liu *et al*., 2017; Throop. & Archer, 2007).

Conventionally, the expression of synergies have been related to biotic drivers (De Oliveira, Hättenschwiler, & Tanya Handa, 2010; Hattenschwiler & Gasser, 2005). However, we reported that decomposition away from shrubs conducted to some slightly noticeable synergies than under shrub canopy (where all effects were antagonic). Under the assumption that decomposition away from shrubs was mainly driven by abiotic factors, we suggest that abiotic factors are the main driver for the expression of leaf litter mixture effects in drylands, where abiotic factors (e.g. sand abrasion) may play the "shredding" function that soil fauna plays in mesic ecosystems as is occurring in photopriming effects.

The results of this experiment suggested that different drivers operate in litter mixture effects in dry ecosystems than in mesic environments, where biotic decomposition usually trigger synergistic effects in mixtures (De Oliveira *et al*., 2010; Hattenschwiler & Gasser, 2005). In drylands, biotic effects seem to be of a different nature, producing mostly antagonistic effects. In a context of global environmental change which include climate and land use change, our results suggest that the loss of plant cover and the increment of the intensity of UV radiation may have relevant implications on overall decomposition and nutrient cycling and specially in carbon fluxes. This is especially important for some species such as *Chamaerops* which seems to be more sensible to soil abrasion, perhaps related to its relatively high SLA. Moreover, it seems relevant to take into account the differences in mass loss related to species identity, since the uneven decomposition rates may drive nutrient availability in fertility islands in ways that are largely unknown. We suggest that the combination of abiotic and biotic factors during decomposition under and away from shrubs, are a major factor to consider in decomposition models in drylands as well as the general impact of leaf litter mixture effects.

## 4.6 Acknowledgements

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## 4.7 References

Almagro, M., Maestre, F. T., Martínez-López, J., Valencia, E., & Rey, A. (2015). Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. *Soil Biology and Biochemistry*, *90*, 214–223. doi:10.1016/j.soilbio.2015.08.006

Almagro, M., Martínez-López, J., Maestre, F. T., & Rey, A. (2017). The contribution of photodegradation to litter decomposition in semiarid mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. *Ecosystems*, *20*(3), 527–542. doi:10.1007/s10021-016-0036-5

Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*(10), 2682–2686. doi:10.1890/03-0650

Austin, A. T. (2011). Has water limited our imagination for aridland biogeochemistry? *Trends in Ecology & Evolution*, *26*(5), 229–235. doi:10.1016/j.tree.2011.02.003

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, *442*(7102), 555–558. doi:10.1038/nature05038

Baker, N. R., & Allison, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology*, *96*(7), 1994–2003. doi:10.1890/14-1482.1

Barnes, P. W., Throop, H. L., Archer, S. R., Breshears, D. D., Mcculley, R. L., & Tobler, M. A. (2015). Sunlight and soil–litter mixing: drivers of litter decomposition in drylands. In U. Lüttge & W. Beyschlag (Eds.), *Progress in Botany* (Vol. 76, pp. 273–302). Cham: Springer International Publishing. doi:10.1007/978-3-319-08807-5

Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., & Wolters, V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biology and Biochemistry*, *43*(10), 2200–2207. doi:10.1016/j.soilbio.2011.07.008

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., … Michalet, R. (2008). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, *96*(1), 18–34. doi:10.1111/j.1365-2745.2007.01295.x

Cheung, J. Y., Tillotson, D. L., Yelamarty, R. V, & Scaduto, R. C. (1989). Cytosolic free calcium concentration in individual cardiac myocytes in primary culture. *The American Journal of Physiology*, *256*(6 Pt 1), C1120-30. doi:10.1152/ajpcell.1989.256.6.C1120

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. doi:10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995. doi:10.1111/gcb.12113

Day, T. A., Bliss, M. S., Tomes, A. R., Ruhland, C. T., & Guénon, R. (2018). Desert leaf litter decay: Coupling of microbial respiration, water-soluble fractions and photodegradation. *Global Change Biology*, *24*(11), 5454–5470. doi:10.1111/gcb.14438

De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, *24*(4), 937–946. doi:10.1111/j.1365-2435.2010.01694.x

Diedhiou, S., Dossa, E. L., Badiane, A. N., & Diedhiou, I. (2009). Decomposition and spatial microbial heterogeneity associated with native shrubs in soils of agroecosystems in semi-arid Senegal, *Pedobiologia*. doi:10.1016/j.pedobi.2008.11.002

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, *19*(5), 554–563. doi:10.1111/ele.12590

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, *104*(2), 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gaxiola, A., & Armesto, J. J. (2015). Understanding litter decomposition in semiarid ecosystems: linking leaf traits, UV exposure and rainfall variability. *Frontiers in Plant Science*, *6*(March), 140. doi:10.3389/fpls.2015.00140

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, *25*(6), 372–80. doi:10.1016/j.tree.2010.01.010

Gliksman, D., Haenel, S., Osem, Y., Yakir, D., Zangy, E., Preisler, Y., & Grünzweig, J. M. (2018). Litter decomposition in Mediterranean pine forests is enhanced by reduced canopy cover. *Plant and Soil*, *422*(1–2), 317–329. doi:10.1007/s11104-017-3366-y

Gorai, M., Maraghni, M., & Neffati, M. (2011). Plant Ecology & Diversity Relationship between phenological traits and water potential patterns of the wild jujube Ziziphus lotus ( L .) Lam . in southern Tunisia, *Plant Ecology and Diversity*. doi:10.1080/17550874.2010.500337

Guirado, E., Segura, D. A., & Castillo, G. (2018). Remote - sensing - derived fractures and shrub patterns to identify groundwater dependence. *Ecohydrology*, (December 2017), 1–11. doi:10.1002/eco.1933

Hattenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, *102*(5), 1519–1524. doi:10.1073/pnas.0404977102

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Heal, O. W., Anderson, J. M., & Swift, M. J. (1997). Plant litter quality and decomposition: an historical overview. In C. G. & K. E. Giller (Eds.), *Driven By nature: Plant litter quality and decomposition* (pp. 3–32). Wallingford, Inglaterra: CAB International.

Hewins, D. B., Archer, S. R., Okin, G. S., McCulley, R. L., & Throop, H. L. (2013). Soil–Litter Mixing Accelerates Decomposition in a Chihuahuan Desert Grassland. *Ecosystems, 16*(2), 183–195. doi:10.1007/s10021-012-9604-5

Hobbie, S. E. (1992). Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution*, *7*(10), 336–9. doi:10.1016/0169-5347(92)90126-V

Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*. doi:10.1126/science.277.5330.1302

Hunter, M. D., Adl, S., Pringle, C. M., & Coleman, D. C. (2003). Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia*, *47*(2), 101–115. doi:10.1078/0031-4056-00174

Levi, E., Archer, S., Rasmussen, C., Throop, H., Hewins, D., & Cover, L. (2009). *Soil-litter mixing accelerates decomposition and facilitates soil aggregation in a shrub-invaded Sonoran Desert grassland*.

Li, Y., Chen, X., Veen, G. F. C., Eisenhauer, N., Liang, Y., Zhou, X., Ma, K. (2018). Negative effects of litter richness on root decomposition in the presence of detritivores. *Functional Ecology*, *32*(4), 1079–1090. doi:10.1111/1365-2435.13057

Lin, Y., Karlen, S. D., Ralph, J., & King, J. Y. (2018). Short-term facilitation of microbial litter decomposition by ultraviolet radiation. *Science of The Total Environment*, *615*, 838–848. doi:10.1016/j.scitotenv.2017.09.239

Liu, G., Wang, L., Jiang, L., Pan, X., Huang, Z., Dong, M., & Cornelissen, J. H. C. (2017).

Specific leaf area predicts dryland litter decomposition via two mechanisms. *Journal of Ecology*, (May), n/a-n/a. doi:10.1111/1365-2745.12868

Martínez-Yrízar, A., Núñez, S., & Búrquez, A. (2007). Leaf litter decomposition in a southern Sonoran Desert ecosystem, northwestern Mexico: Effects of habitat and litter quality. *Acta Oecologica*, *32*(3), 291–300. doi:10.1016/j.actao.2007.05.010

Michalet, R., & Pugnaire, F. I. (2016). Facilitation in communities: Underlying mechanisms, community and ecosystem implications. *Functional Ecology*, *30*(1), 3–9. doi:10.1111/1365-2435.12602

Naili, M. B., Alghazeer, R. O., Saleh, N. A., & Al-Najjar, A. Y. (2010). Evaluation of antibacterial and antioxidant activities of Artemisia campestris (Astraceae) and Ziziphus lotus (Rhamnacea). *Arabian Journal of Chemistry*, *3*(2), 79–84. doi:10.1016/j.arabjc.2010.02.002

Pérez-Harguindeguy, N., & Díaz, S. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. doi:http://dx.doi.org/10.1071/BT12225

Predick, K. I., Archer, S. R., Aguillon, S. M., Keller, D. A., Throop, H. L., & Barnes, P. W. (2018). UV-B radiation and shrub canopy effects on surface litter decomposition in a shrub-invaded dry grassland. *Journal of Arid Environments*, *157*(July), 13–21. doi:10.1016/j.jaridenv.2018.06.007

Price, C. M., & Pettijohn, D. E. (1986). Biodiversity and litter decomposition in terrestrial ecosystems. *Experimental Cell Research*, *166*(2), 295–311. doi:10.1016/0014-4827(86)90478-7

Rey, A., Belelli-Marchesini, L., Were, A., Serrano-ortiz, P., Etiope, G., Papale, D., … Pegoraro, E. (2012). Wind as a main driver of the net ecosystem carbon balance of a semiarid Mediterranean steppe in the South East of Spain. *Global Change Biology*, *18*(2), 539–554. doi:10.1111/j.1365-2486.2011.02534.x

Santonja, M., Fernandez, C., Gauquelin, T., & Baldy, V. (2015). Climate change effects on litter decomposition: intensive drought leads to a strong decrease of litter mixture interactions. *Plant and Soil*, *393*(1–2), 69–82. doi:10.1007/s11104-015-2471-z

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science (New York, N.Y.)*, *247*(4946), 1043–8. doi:10.1126/science.247.4946.1043

Schuster, M. J., & Dukes, J. S. (2014). Non-additive effects of invasive tree litter shift seasonal N release: a potential invasion feedback. *Oikos*, *123*(9), 1101–1111. doi:10.1111/oik.01078

Soong, J. L., Parton, W. J., Calderon, F., Campbell, E. E., & Cotrufo, M. F. (2015). A new conceptual model on the fate and controls of fresh and pyrolized plant litter decomposition. *Biogeochemistry*, *124*, 27–44. doi:10.1007/s10533-015-0079-2

Tan, A. W., & Nuttall, F. Q. (1975). Characteristics of the dephosphorylated form of phosphorylase purified from rat liver and measurement of its activity in crude liver preparations. *Biochimica et Biophysica Acta*, *410*(1), 45–60. doi:10.1016/0005-2744(75)90206-5

Team, R. C. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Throop., & Archer, S. R. (2007). Interrelationships Among Shrub Encroachment, Land Management, and Litter Decomposition in a Semidesert Grassland. *Ecological Applications*, *17*(6), 1809–1823.

Throop, H. L., & Archer, S. R. (2009). Resolving the Dryland Decomposition Conundrum: Some New Perspectives on Potential Drivers. (U. Lüttge, W. Beyschlag, B. Büdel, & D. Francis, Eds.), *Progress in Botany* (Vol. 70). Berlin, Heidelberg: Springer Berlin Heidelberg. doi:10.1007/978-3-540-68421-3

Tirado, R. (2009). Matorrales arborescentes con Ziziphus. In y M. R. y M. Ministerio de Medio Ambiente (Ed.), *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España.*

Tirado, R., & Pugnaire, F. I. (2003). Shrub spatial aggregation and consequences for reproductive success, 296–301. doi:10.1007/s00442-003-1264-x

Tirado, R., & Pugnaire, F. I. (2005). Community structure and positive interactions in constraining environments. *Oikos*, *111*(3), 437–444. doi:10.1111/j.1600-0706.2005.14094.x

Uselman, S. M., Snyder, K. A., Blank, R. R., & Jones, T. J. (2011). UVB exposure does not accelerate rates of litter decomposition in a semi-arid riparian ecosystem. *Soil Biology and Biochemistry*, *43*(6), 1254–1265. doi:10.1016/j.soilbio.2011.02.016

Verhoef, H. A., Verspagen, J. M. H., & Zoomer, H. R. (2000). Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. *Biology and Fertility of Soils*, *31*(5), 366–371. doi:10.1007/s003749900181

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M. P., Petchey, O., Palmborg, C., & Huss-Danell, K. (2009). Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology*, *90*(1), 90–9. doi:10.1890/08-0382.1

Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and Plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, *79*(2), 247–258.

Whitford, A. W. G., Meentemeyer, V., Seastedt, T. R., Cromack, K., Crossley, D. A., Santos, P., … Waide, J. B. (2016). Exceptions to the AET Model : Deserts and Clear-Cut Forest. *Ecology*, *62*(1), 275–277.

Zhang, Q., & Zak, J. C. (2010). Effects of Gap Size on Litter Decomposition and Microbial Activity in a Subtropical Forest. *America*, *76*(7), 2196–2204.

Zouaoui, R., Ksontini, M., & Ferchichi, A. L. I. (2014). Comparative phenological study of Ziziphus lotus ( L .) Lam . in the arid area of Tunisia. *Pak. J. Bot*, *46*(5), 1611–1620.

[dataset] Prado-López, M.,Pugnaire, F.I., Moya-Laraño, J. 2019. Decomposition in fertility islands. http://dx.doi.org/10.20350/digitalCSIC/10523. CSIC digital repository:

http://hdl.handle.net/10261/197292

[dataset] Prado-López, M.,Pugnaire, F.I., Moya-Laraño, J. 2019. Soil fauna in fertility islands. http://dx.doi.org/10.20350/digitalCSIC/10524. CSIC digital repository: https://digital.csic.es/handle/10261/197293

## 4.8 Supplementary material

Figure 1S. Mesocosms were custom designed using plastic screen with a mesh size of 0.5cm, which allowed the entrance of meso and macrofauna, UV radiation and soil. Mesocosms were attached to the ground and placed under and away from canopies of *Zyzyphus lotus*.

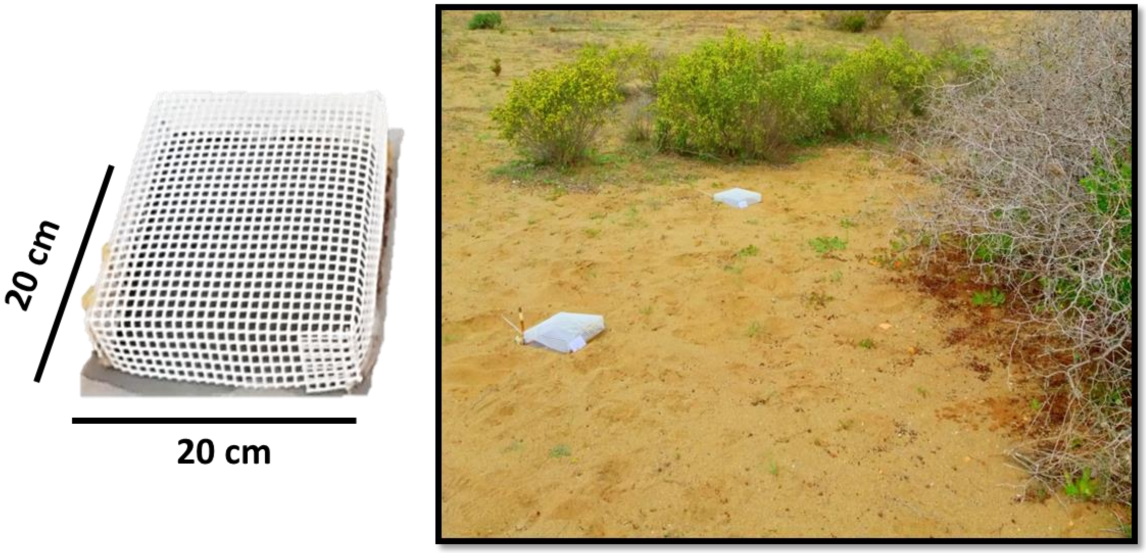


Figure 2S. Decomposition by species identity in leaf litter mixtures across gradient of richness. Bars indicate GLM model predicted means and SE after back transformation (from boxcox).

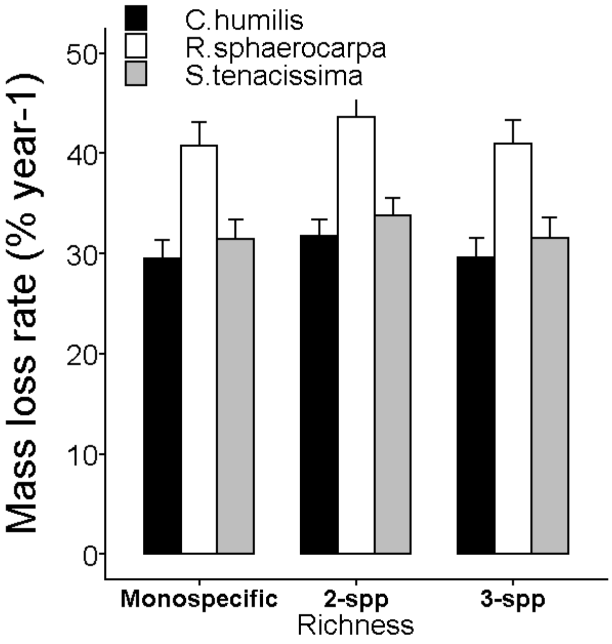
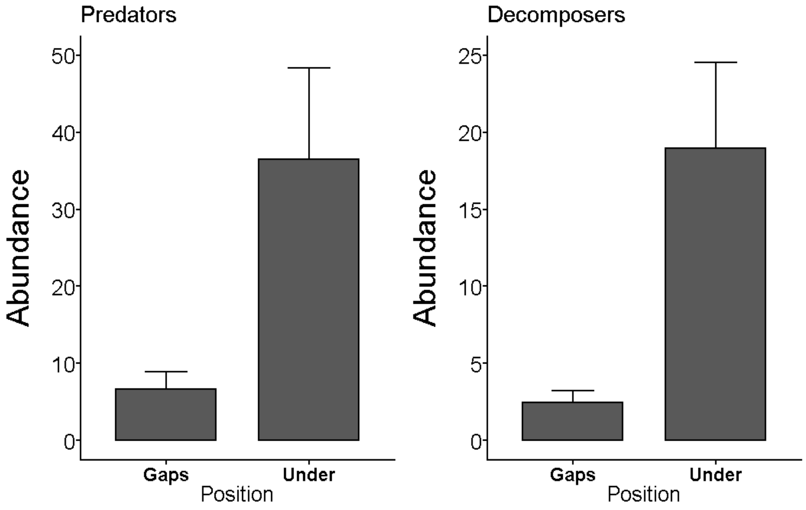


Figure 3S. Decomposition along dates of collection in leaf litter mixtures across gradient of richness. Bars indicate GLM model predicted means and SE after back transformation (from boxcox)

Figure 4S. Abundance of soil mesofauna, under and away from shrub canopy.



# Chapter 5. Discussion

Desertification and drier and hotter conditions are often identified as the most likely effects of global environmental change in Mediterranean ecosystems (Alessandri et al., 2014). The natural low fertility in drylands is expected to intensify and threaten ecosystem functions such as decomposition and primary productivity with consequences in the loss of ecosystem services including nutrient cycling and soil carbon storage (Carpenter et al., 2009; Maestre et al., 2012; Verstraete, 1986). Understanding soil ecosystem processes such as the interaction between abiotic and biotic factors in decomposition create the opportunity to acquire knowledge which could help design strategies to mitigate desertification effects, and the conservation and restoration of drylands in a context of environmental and land use changes.

The study of decomposition in drylands has usually neglected the role of soil predators and litter mixtures, focusing mainly on UV radiation. The scarcity of information on these soil processes in drylands demand an effort to address decomposition including the interaction between UV radiation and biotic components such as microorganisms, soil fauna and mixtures of leaf litter, which accumulate under fertility islands.

Here, I will discuss and summarize the main findings of my PhD research and place them in a broader scientific context, highlighting the relevance of the interactions between biotic and abiotic factors in the relationship between biodiversity and ecosystem functioning in drylands. At the end of this Discussion the main conclusions and suggestions for future research are provided.

## 5.1 Main findings

- UV radiation has a minor effect if compared to microbes in their legacy effects on detritivore-driven decomposition (chapter 2). UV radiation accounted for a small proportion (<3%) of the total litter mass loss, and was equivalent to that of microbes alone. I did not find photopriming effects as there were no cumulative decomposition produced by UV radiation and microbial activity. Instead, microbes had important legacy effects on detritivores as I found substantial cumulative effects of microbes and detritivores adding up to 42% of total decomposition. In addition, the removal of microbial activity reverted litter mixture synergies.

- The three plant species used in this experiment (*Chamaerops humilis*, *Retama sphaerocarpa,* and *Stipa tenacissima*) were equally affected by photodegradation and microorganisms, but detritivores promoted the mass loss of *Retama* and *Chamaerops* more strongly than that of *Stipa.*
- Through this study I was able to confirm that, in drylands, leaf litter mixtures stimulated decomposition more than monocultures. UV radiation induced mass loss in monocultures more strongly than in litter mixtures, although in both cases UV radiation had minor incidence (<3% of overall decomposition). Additionally, decomposition of leaf litter mixture effects was not triggered by UV radiation as expected. On the contrary, litter mixtures decomposition depended more on microbial and detritivore activity.
- Microorganisms are a key component for decomposition in drylands. The use of antibiotics showed the legacy effects priming, affecting the performance of isopods, which had strong consequences for litter mass loss. Actually, the legacy effects of biocides were stronger when isopods were involved in decomposition.
- Microorganisms also modulated decomposition of litter mixtures, since the elimination of microorganisms had a dramatic effect on the sign and magnitude of non-additive effects. Species identity was an important factor in the interaction with biocides. *Retama* and *Stipa* had synergies in litter decomposition in the presence of microorganisms, but no effects when microorganisms were absent. By contrast, *Chamaerops* showed strong antagonistic effects when microbes were removed and null effects when present.
- The presence of predator, predator traces of activity and isopods showed that the conjunction of all of these factors enhanced decomposition more than the single presence of isopods (Chapter 3).
- Isopods exhibited antipredator behavior only when the predator was present, but not with predator traces. However, this antipredator behavior did not result in trophic cascades but rather strong ecological engineering effects on decomposition.

- Leaf litter mixtures played a fundamental role in decomposition on the presence of soil fauna. Overall, mixtures had higher decomposition than monospecific litter regardless of spider or spider traces of activity. However, the presence of spider, spider traces of activity or isopods in mixtures, generated synergies which meant an improvement of the efficiency of decomposition over treatments without soil fauna. These results show how previously unexplored synergies among biodiversity components may largely contribute to decomposition in dryland ecosystems.
- Mass loss under *Z. lotus* canopies was significantly slower than in gaps. Decomposition of litter mixtures under the canopy resulted in antagonistic effects, while in gaps they were non-additive.
- Plant species identity is an important factor. *Stipa* and *Chamaerops* decomposed faster in gaps than under *Z. lotus* canopies, while *Retama* decomposed at the same rate regardless of location.
- Leaf litter mixtures decomposition in the lab can drastically differ from results in the field. Under controlled conditions, mixtures decomposition increased relative to monospecific litter, while in the field there were no differences between monospecific, two- and three-species mixtures. In addition, *S. tenacissima* decomposed much less in the lab than the other species in the field, suggesting that mechanisms other than the ones studied here are responsible for litter decomposing, making it less recalcitrant in natural conditions.

## 5.2 The impact of UV radiation on soil biotic decomposition drivers

It has been proposed that photodegradation is the stronger abiotic driver of decomposition in drylands (Austin & Vivanco, 2006), however its influence on biotic drivers is largely unknown (Gliksman et al., 2017). For example, so far there was no information on how UV radiation may interact with detritivores and how decomposition in standing death litter contributed to nutrient cycling in comparison with decomposition of ground litter at a secondary stage. These knowledge gap led to mismatches between predicted and observed decomposition in models simply based on climate and litter chemical variables (Austin, 2011; King, et al, 2012; Throop & Archer, 2009).

Litter decomposition under high UV and low water availability suggests that UV radiation was a minor driver of decomposition and that it only enhanced decomposition in monocultures very early in decomposition. This effect counters the reported by Wang *et al.* (2017), who found that UV radiation did not cause mass loss in the early stages of decomposition but rather after 12 – 29 months.

There is limited evidence that UV radiation causes photopriming effects. Moreover, the effects of UV radiation and microbial activity separately caused as much mass loss as in combination, showing that UV radiation had no effects during the early stages of decomposition, in contrast with previous studies that found positive effects of UV radiation in the form of photopriming (Foereid *et al*., 2010; Huang *et al*., 2017; Ma, *et al*., 2012; Predick *et al*., 2018). There are reports of negative UV effects on microbial activity, either because UV radiation causes damage on microorganisms' DNA (Baker *et al*., 2015; Hughes *et al*., 2003; Johnson, 2003; Rohwer *et al*., 2000), or because the liberation of complex molecules that interfere with decomposition, such as antioxidants (Brandt, *et al*., 2009; Duguay & Klironomos, 2000; Gehrke *et al*., 1995; Moody, *et al*., 1999; Pancotto *et al*., 2003; Rozema *et al*., 1997; Verhoef *et al*., 2000; Wang, *et al*., 2015).

I found no effects of UV radiation on isopod performance in latter stages of decomposition, suggesting UV legacy effects were negligible. However, the presence of isopods and microorganisms was determinant for litter mass loss. After 280 days of decomposition, UV radiation had no significant consequences on biotic activity, and decreased rather than increased decomposition. In addition, there was no evidence of UV legacy effects on microbial- or detritivore-induced decomposition. Earlier reports (Brandt, *et al*., 2009; Gliksman *et al*., 2017; Lin, *et al*., 2018; Yanni, *et al*., 2015) show that light/dark phases could enhance decomposition, since during daytime photodegradation will impact on carbon complex molecules such as lignin and cellulose that affect microbial activity, and in the dark phase, the higher moisture could facilitate microbial-driven decomposition.

The lack of photopriming effect after 200 days of UV radiation may be explained because the effects of photodegradation are not detectable before the first 12 months of decomposition. After that time litter chemistry changes and litter biodegradability increases. However, it is not after 12 – 29 months that the impact of photodegradation increases litter mass loss via biological decomposition  (Wang *et al*., 2017). Long-term studies are thus necessary to better understand the effects of UV radiation on biotic drivers of decomposition.

## 5.3 Leaf litter mixtures as keystone structures during decomposition in drylands

Evidence in the last two decades shows that decomposition of leaf litter mixtures is often substantially different than that of monospecific litter (García-Palacios, Maestre, Kattge, & Wall, 2013; Gartner & Cardon, 2004; Hattenschwiler & Gasser, 2005). However, decomposition in drylands has been often assessed in a simplistic way, using monospecific litter, even though plant patches in drylands host litter mixtures. Decomposition of leaf litter mixtures may thus be more frequent than previously thought. In this thesis I took a close look at decomposition of leaf litter mixtures in drylands and at how and array of biotic and abiotic factors affect additive and non-additive effects on mixture decomposition.

The importance of leaf litter mixtures as a key component to understand nutrient cycling and carbon sequestration in drylands needs to be highlighted. I showed that UV radiation had stronger impact on decomposition of litter in monospecific rather than in mixtures. However, during this first stage decomposition in monocultures was a very minor proportion (less than 2%) of the entire decomposition cycle. Since decomposition in drylands operate differentially in standing death litter and ground litter, I suggest that the impact of UV radiation in standing and ground litter would have entirely different consequences for nutrient cycling and carbon storage in drylands.

Since the main consequence of photodegradation on nutrient cycling is the release of C as $CO_2$ (Rutledge, *et al.*, 2010), in standing litter (monospecific), photodegradation and microbial activity lead to a loss of C to the atmosphere without passing the soil organic pools, as suggested by Austin, *et al.* (2016). However, this would be only a minor proportion of the observed mass loss (about 2%). In contrast, decomposition of litter in the ground (mostly in mixtures) contributes to the formation of soil organic matter and C stable compounds remaining longer in soil. Indeed, biotic decomposition contributes more importantly to the formation of these carbon complex compounds that are behind C stabilization (Cotrufo *et al.*, 2015, 2013; Soong, *et al.*, 2015).

Microorganisms and detritivores drive non-additive effects (mainly synergies), during decomposition in mixtures. Paradoxically, despite the greater abundance of soil fauna under shrub canopies, decomposition of leaf litter mixtures resulted in dominant antagonisms which were accompanied by lower decomposition rates as compared to litter in gaps. These contradictory results between the higher abundance of soil fauna and lower decomposition rates could be due the effects of the substances involved in the allelopathic effects of *Ziziphus* (Naili, *et al.*, 2010),which could also have antimicrobial effects and negatively affect the microbiota responsible of decomposition. The fact that antagonisms are stronger when biocides are applied support this hypothesis.

The interaction between biotic components on decomposition of leaf litter mixtures have been documented in detritivores (De Oliveira, *et al.*, 2010; Hattenschwiler & Gasser, 2005). However, this is the first time that the role of predators as an ecosystem engineer in litter mixtures is assessed. Predators dramatically improved the efficiency of decomposition in mixtures, in contrast with treatments without soil fauna.

## 5.4 The role of predators as ecological ecosystem engineers on decomposition

The role of top soil predators on leaf litter decomposition have been addressed as indirect, cascading effects. However, the link between soil predators and litter decomposition may be stronger than previously thought. We found that predators not only did control decomposition through the effects on detritivores but also by the addition of nutrients. nutriments, likely rich in N, in the form of metabolic waste, which may produce engineering ecosystem effects facilitating microbial growth which in turn may facilitate the effect of detritivores on decomposition. Moreover, the role of soil predators during decomposition may be more important in litter mixtures than in simplified substrates, since decomposition in litter mixtures was more efficient in the presence of predators. This goes beyond the well-documented effect of detritivores, which improve decomposition in mixtures (De Oliveira, *et al*., 2010; Hattenschwiler & Gasser, 2005).

In a context of diversity loss, the understanding of role of top soil predators and litter mixtures is critical, as large predators are the most vulnerable group or fauna facing land use change and other environmental disturbances (Duffy, 2002). In addition, the loss of vegetation cover in drylands could simplify the diversity of litter substrates, with consequences that are largely unknown for nutrient cycling and carbon sequestration.

# Chapter 6. Conclusions

In order to improve decomposition models in drylands it is critical to take into account the role of biotic components including detritivores, predators, plant species composition and microorganisms combined. Despite the overlooked role of soil fauna on the decomposition process in drylands (Estes *et al*., 2011; Goncharov & Tiunov, 2014; Kajak, 1995), I showed that the community of soil macroinvertebrates may have considerable implications in decomposition. It is also important to address decomposition of standing litter and ground litter separately, as well as to consider decomposition of leaf litter mixtures as a key ecosystem feature. Indeed, I showed that litter mixtures change the patterns of decomposition substantially with potential consequences to nutrient cycling that are largely unknown. Besides, more research is needed about how the loss of key ecosystem components, such as fertility islands (Valera & Salido, 2018) and the associated loss of diversity, may impact carbon fluxes in drylands.

1. In a laboratory experiment UV radiation had a minor effect on mass loss, and also did not interacted with microorganisms, hence no photopriming effects were observed. Lastly, the expression of non-additive effects was not triggered by UV radiation as it was predicted.
2. In contrast microorganisms are a key component for decomposition in drylands. The use of antibiotics during the first stage of decomposition, had legacy effects on the second stage, likely affecting the performance of isopods as it had strong consequences in the reduction of mass loss. Actually, the magnitude of the legacy effects of biocides was stronger when isopods were involved in decomposition.
3. The three plant species used in this experiment (*Retama sphaerocarpa, Chamaerops humilis* and *Stipa tenacissima*) were affected equally by photodegradation and microorganisms, but detritivores promoted the mass loss of *Retama* and *Chamaerops* more strongly than that of *Stipa.* The species identity is also an important factor during decomposition under shrub canopy, while *Stipa* and *Chamaerops* decomposed faster away than under shrub canopies, *Retama* decomposed at the same rate regardless of location.

4. Leaf litter mixtures stimulated decomposition relatively more than monocultures, although UV radiation induced more mass loss in monocultures than in litter mixtures, in both cases UV radiation had proportionally minor incidence.
5. Litter mixture effects depended more closely on microbial and detritivore activity, as well as on the level (stage) of decomposition of the litter. The elimination of microorganisms reverted litter mixture synergies into antagonisms.
6. Leaf litter mixtures were fundamental during decomposition on the presence of soil fauna. Mixtures had higher decomposition than monospecific regardless of spider or spider traces of activity. However, the presence of spider, spider traces of activity or isopods, generated synergies over treatments without soil fauna. These results show how previously unexplored synergies among biodiversity components may largely contribute to decomposition in dryland ecosystems.
7. Since microbes are also involved in synergistic effects in mixtures and we also found litter species-identity effects, we suggest that biodiversity is much more important driving decomposition in drylands than previously thought, providing new insights on how biotic factors affect dryland ecosystem processes.
8. The assessment of leaf litter mixture decomposition in the laboratory resulted in a drastic different pattern than in the field. Whereas in controlled conditions decomposition in mixtures clearly increased relative to monospecific litter, in the field there were no differences in mass loss between monospecific, two- and three-species mixtures. In addition, *S. tenacissima* decomposed much less in the laboratory experiment as compared to the other species than in the field, suggesting that mechanisms other than the ones studied in the laboratory are responsible for decomposing this litter, making it less recalcitrant in natural conditions.
9. Species identity was an important factor also interacting with biocides. *Retama* and *Stipa* presented synergies in litter with microorganisms but null effects when microorganisms were not present. In contrast, *Chamaerops* presented strong antagonistic effects when microbes were removed and null effects otherwise.
10. The combination of predator traces of activity and isopods increased decomposition in a higher degree than the single presence of isopods. In

ecological engineering effects, the traces of predator activity (e.g. excreta) provide with some extra nutrients that can boost microbial activity and ultimately benefit secondary decomposers and accelerate decomposition.

11. Despite the high impact of predators on the detritivores (both on mortality and on behavior), multiple synergistic predator ecological engineering effects with the identity and diversity of the litter, prevail over predator top-down control, making predators to enhance rather than inhibit decomposition.
12. Isopods exhibited antipredator behavior only in predator presence but not in the presence of predator traces of activity. This antipredator behavior did not result in behavioral trophic cascades but rather in strong ecological engineering effects on decomposition.
13. Litter mass loss under shrub canopy was significantly slower and decomposition of mixtures resulted in predominantly antagonistic effects, contrasting to decomposition away from shrubs where it was faster and non-additive effects null or very mild. Decomposition under shrubs is likely biotically driven, as suggested by the higher abundances of mesofauna under shrub canopies as compared to locations away from shrubs.

# References

Abelho, M. (2016). Litter traits and decomposer complexity set the stage for a global decomposition model. *Functional Ecology*, n/a-n/a. doi:10.1111/1365-2435.12640

Adair, E. C., Parton, W. J., King, J. Y., Brandt, L. A., & Lin, Y. (2017). Accounting for photodegradation dramatically improves prediction of carbon losses in dryland systems. *Ecosphere*, *8*(7), e01892. doi:10.1002/ecs2.1892

Aerts, R. (1997). Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. *Oikos*, *79*(3), 439. doi:10.2307/3546886

Alessandri, A., De Felice, M., Zeng, N., Mariotti, A., Pan, Y., Cherchi, A., … Artale, V. (2015). Robust assessment of the expansion and retreat of Mediterranean climate in the 21st century. *Scientific Reports*, *4*(1), 7211. doi:10.1038/srep07211

Allen, E. B. (1995). Wildland Shrub and Arid Land Restoration. In *Restoration Ecology: Limits and Possibilities in Arid and Semiarid Lands* (p. 7).

Almagro, M., Maestre, F. T., Martínez-López, J., Valencia, E., & Rey, A. (2015). Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands. *Soil Biology and Biochemistry*, *90*, 214–223. doi:10.1016/j.soilbio.2015.08.006

Almagro, M., Martínez-López, J., Maestre, F. T., & Rey, A. (2017). The contribution of photodegradation to litter decomposition in semiarid mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. *Ecosystems*, *20*(3), 527–542. doi:10.1007/s10021-016-0036-5

Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*(10), 2682–2686. doi:10.1890/03-0650

Austin, A. T. (2011). Has water limited our imagination for aridland biogeochemistry? *Trends in Ecology & Evolution*, *26*(5), 229–235. doi:10.1016/j.tree.2011.02.003

Austin, A. T., & Ballare, C. L. (2010). Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, *107*(10), 4618–4622. doi:10.1073/pnas.0909396107

Austin, A. T., Méndez, M. S., & Ballaré, C. L. (2016). Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(16), 4392–7. doi:10.1073/pnas.1516157113

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, *442*(7102), 555–558. doi:10.1038/nature05038

Badalucco, L., Pomaré, F., Grego, S., Landi, L., & Nannipieri, P. (1994). Activity and degradation of streptomycin and cycloheximide in soil. *Biology and Fertility of Soils*, *18*(4), 334–340. doi:10.1007/BF00570637

Baker, N. R., & Allison, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology*, *96*(7), 1994–2003. doi:10.1890/14-1482.1

Baker, N. R., Allison, S. D., & Frey, S. D. (2015). Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. *Ecology*, *96*(7), 1994–2003. doi:10.1890/14-1482.1

Ballaré, C. L. (2014). Light regulation of plant defense. *Annual Review of Plant Biology*, *65*(1), 335–63. doi:10.1146/annurev-arplant-050213-040145

Bardgett, R. D., & Van Der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature 515*, *505*(7528), 505–511. doi:10.1038/nature13855

Barnes, P. W., Throop, H. L., Archer, S. R., Breshears, D. D., Mcculley, R. L., & Tobler, M. A. (2015). Sunlight and soil–litter mixing: drivers of litter decomposition in drylands. In U. Lüttge & W. Beyschlag (Eds.), *Progress in Botany* (Vol. 76, pp. 273–302). Cham: Springer International Publishing. doi:10.1007/978-3-319-08807-5

Barnes, P. W., Throop, H. L., Hewins, D. B., Abbene, M. L., & Archer, S. R. (2012). Soil coverage reduces photodegradation and promotes the development of soil-microbial films on dryland leaf litter. *Ecosystems*, *15*(2), 311–321. doi:10.1007/s10021-011-9511-1

Barthel, W., & Markwardt, F. (1975). Aggregation of blood platelets by adrenaline and its uptake. *Biochemical Pharmacology*, *24*(20), 1903–1904. doi:10.1016/0006-2952(75)90415-3

Berg, B., McClaugherty, C., & Ekbohm, G. (2003). *Plant litter, decomposition, humus formation, carbon sequestration*. Berlin: Springer-Verlag.

Birkhofer, K., Diekötter, T., Boch, S., Fischer, M., Müller, J., Socher, S., & Wolters, V. (2011). Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biology and Biochemistry*, *43*(10), 2200–2207. doi:10.1016/j.soilbio.2011.07.008

Boelter, J., Quadros, A., & Araujo, P. (2009). The feeding rates and preferences of a neotropical terrestrial isopod (Oniscidea). *Nauplius*, *17*(2), 107–113. Retrieved from http://crustacea.org.br/artigos/900_20_05_boelter,_quadros,_araujo.pdf

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., & Wood, S. A. (2015). Understanding the dominant controls on litter decomposition. *Journal of Ecology*, *104*(1), 229–238. doi:10.1111/1365-2745.12507

Brandt, L. A., Bohnet, C., & King, J. Y. (2009a). Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research: Biogeosciences*, *114*(G02004), 1–13. doi:10.1029/2008JG000772

Brandt, L. A., Bohnet, C., & King, J. Y. (2009b). Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. *Journal of Geophysical Research: Biogeosciences*, *114*(G2), 1–13. doi:10.1029/2008JG000772

Brandt, L. A., King, J. Y., Hobbie, S. E., Milchunas, D. G., & Sinsabaugh, R. L. (2010). The Role of Photodegradation in Surface Litter Decomposition Across a Grassland Ecosystem Precipitation Gradient. *Ecosystems*, *13*(5), 765–781. doi:10.1007/s10021-010-

9353-2

Brandt, L. A., King, J. Y., & Milchunas, D. G. (2007). Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. *Global Change Biology*, *13*(10), 2193–2205. doi:10.1111/j.1365-2486.2007.01428.x

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., … Michalet, R. (2008). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*, *96*(1), 18–34. doi:10.1111/j.1365-2745.2007.01295.x

Brussaard, L. (1997). Biodiversity and ecosystem functioning in soil. *Ambio*, *26*(8), 563–570. Retrieved from http://www.jstor.org/stable/4314670

Brussaard, Lijbert. (1997). Biodiversity and Ecosystem Functioning in Soil. *Ambio*, *26*(8), 563–570.

Brussaard, Lijbert. (1998). Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology*, *9*(September 1997), 123–135. doi:10.1016/S0929-1393(98)00066-3

Brussaard, Lijbert, Pulleman, M. M., Ou??draogo, ??lis??e, Mando, A., & Six, J. (2007). Soil fauna and soil function in the fabric of the food web. *Pedobiologia*, *50*(6), 447–462. doi:10.1016/j.pedobi.2006.10.007

Buchkowski, R. W. (2016). Top-down consumptive and trait-mediated control do affect soil food webs: It's time for a new model. *Soil Biology and Biochemistry*, *102*, 29–32. doi:10.1016/j.soilbio.2016.06.033

Bünemann, E. K., Bongiorno, G., Bai, Z., Creamer, R. E., De Deyn, G., de Goede, R., … Brussaard, L. (2018). Soil quality – A critical review. *Soil Biology and Biochemistry*, *120*(January), 105–125. doi:10.1016/j.soilbio.2018.01.030

Carpenter, S. R., Mooney, H. a, Agard, J., Capistrano, D., DeFries, R. S., Diaz, S., … Whyte, A. (2009). Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences*, *106*(5), 1305–

1312. doi:10.1073/pnas.0808772106

Castro-Díez, P., Alonso, Á., & Romero-Blanco, A. (2019). Effects of litter mixing on litter decomposition and soil properties along simulated invasion gradients of non-native trees. *Plant and Soil*, *442*(1–2), 79–96. doi:10.1007/s11104-019-04160-4

Chen, M., Parton, W. J., Adair, E. C., Asao, S., Hartman, M. D., & Gao, W. (2016). Simulation of the effects of photodecay on long-term litter decay using DayCent. *Ecosphere*, *7*(12), e01631. doi:10.1002/ecs2.1631

Chen, S. K., Edwards, C. A., & Subler, S. (2001). A microcosm approach for evaluating the effects of the fungicides benomyl and captan on soil ecological processes and plant growth. *Applied Soil Ecology*, *18*(1), 69–82. doi:10.1016/S0929-1393(01)00135-4

Cheung, J. Y., Tillotson, D. L., Yelamarty, R. V, & Scaduto, R. C. (1989). Cytosolic free calcium concentration in individual cardiac myocytes in primary culture. *The American Journal of Physiology*, *256*(6 Pt 1), C1120-30. doi:10.1152/ajpcell.1989.256.6.C1120

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015a). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. doi:10.1038/ngeo2520

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015b). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. doi:10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995. doi:10.1111/gcb.12113

Couˆteaux, M.-M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and liter quality. *Trends in Ecology & Evolution*, *10*(2), 63–66. doi:10.1016/S0169-5347(00)88978-8

Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., … Callaham, M. A. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, *110*, 116–133. doi:10.1016/j.soilbio.2017.03.008

Crowther, T. W., Boddy, L., & Hefin Jones, T. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. *The ISME Journal*, *6*(11), 1992–2001. doi:10.1038/ismej.2012.53

Day, T. A., Bliss, M. S., Tomes, A. R., Ruhland, C. T., & Guénon, R. (2018). Desert leaf litter decay: Coupling of microbial respiration, water-soluble fractions and photodegradation. *Global Change Biology*, *24*(11), 5454–5470. doi:10.1111/gcb.14438

Day, T. A., Guénon, R., & Ruhland, C. T. (2015). Photodegradation of plant litter in the Sonoran Desert varies by litter type and age. *Soil Biology and Biochemistry*, *89*, 109–122. doi:10.1016/j.soilbio.2015.06.029

Day, T. A., Zhang, E. T., & Ruhland, C. T. (2007). Exposure to solar UV-B radiation accelerates mass and lignin loss of Larrea tridentata litter in the Sonoran Desert. *Plant Ecology*, *193*(2), 185–194. doi:10.1007/s11258-006-9257-6

De Deyn, G. B., Cornelissen, J. H. C., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, *11*(5), 516–531. doi:10.1111/j.1461-0248.2008.01164.x

De Oliveira, T., Hättenschwiler, S., & Tanya Handa, I. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, *24*(4), 937–946. doi:10.1111/j.1365-2435.2010.01694.x

Delgado-Baquerizo, M., Maestre, F. T., Gallardo, A., Bowker, M. a, Wallenstein, M. D., Quero, J. L., … Zaady, E. (2013). Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, *502*(7473), 672–6. doi:10.1038/nature12670

Diedhiou, S., Dossa, E. L., Badiane, A. N., & Diedhiou, I. (2009). Decomposition and spatial microbial heterogeneity associated with native shrubs in soils of agroecosystems in semi-arid Senegal, *52*. doi:10.1016/j.pedobi.2008.11.002

Đinh, S. T., Gális, I., & Baldwin, I. (2013). UVB radiation and 17-hydroxygeranyllinalool diterpene glycosides provide durable resistance against mirid ( Tupiocoris notatus ) attack in field-grown Nicotiana attenuata plants. *Plant, Cell & Environment*, *36*(3), 590–606. doi:10.1111/j.1365-3040.2012.02598.x

Doblas-Miranda, E., Sánchez-Piñero, F., & González-Megías, A. (2009). Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem. *Applied Soil Ecology*, *41*(3), 329–335. doi:10.1016/j.apsoil.2008.12.008

Dregne, H. E. (2002). Land Degradation in the Drylands. *Arid Land Research and Management*, *16*(2), 99–132. doi:10.1080/153249802317304422

Duffy, J. E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, *99*(2), 201–219. doi:10.1034/j.1600-0706.2002.990201.x

Duguay, K. J., & Klironomos, J. N. (2000). Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi. *Applied Soil Ecology*, *14*(2), 157–164. doi:10.1016/S0929-1393(00)00049-4

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, *333*(6040), 301–6. doi:10.1126/science.1205106

Feckler, A., Goedkoop, W., Zubrod, J. P., Schulz, R., & Bundschuh, M. (2016). Exposure pathway-dependent effects of the fungicide epoxiconazole on a decomposer-detritivore system. *Science of The Total Environment*. doi:10.1016/j.scitotenv.2016.07.088

Feng, S., & Fu, Q. (2013). Expansion of global drylands under a warming climate. *Atmospheric Chemistry and Physics*, *13*(19), 10081–10094. doi:10.5194/acp-13-10081-2013

Foereid, B., Bellarby, J., Meier-Augenstein, W., & Kemp, H. (2010a). Does light exposure make plant litter more degradable? *Plant and Soil*, *333*(1), 275–285. doi:10.1007/s11104-

010-0342-1

Foereid, B., Bellarby, J., Meier-Augenstein, W., & Kemp, H. (2010b). Does light exposure make plant litter more degradable? *Plant and Soil*, *333*(1–2), 275–285. doi:10.1007/s11104-010-0342-1

Foereid, B., Rivero, M. J., Primo, O., & Ortiz, I. (2011). Modelling photodegradation in the global carbon cycle. *Soil Biology and Biochemistry*, *43*(6), 1383–1386. doi:10.1016/j.soilbio.2011.03.004

Gallardo, A., & Merino, J. (1993). Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality. *Ecology*. doi:10.2307/1939510

Gallo, M. E., Sinsabaugh, R. L., & Cabaniss, S. E. (2006). The role of ultraviolet radiation in litter decomposition in arid ecosystems. *Applied Soil Ecology*, *34*(1), 82–91. doi:10.1016/j.apsoil.2005.12.006

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, *16*(8), 1045–1053. doi:10.1111/ele.12137

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hättenschwiler, S. (2015). The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, (November), 1–11. doi:10.1111/1365-2435.12589

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, *19*(5), 554–563. doi:10.1111/ele.12590

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, *104*(2), 230–246. doi:10.1111/j.0030-1299.2004.12738.x

Gaxiola, A., & Armesto, J. J. (2015). Understanding litter decomposition in semiarid ecosystems: linking leaf traits, UV exposure and rainfall variability. *Frontiers in Plant*

*Science*, *6*(March), 140. doi:10.3389/fpls.2015.00140

Gehrke, C., Johanson, U., Callaghan, T. V., Chadwick, D., & Robinson, C. H. (1995). The Impact of Enhanced Ultraviolet-B Radiation on Litter Quality and Decomposition Processes in Vaccinium Leaves from the Subarctic. *Oikos*, *72*(2), 213. doi:10.2307/3546223

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, *25*(6), 372–80. doi:10.1016/j.tree.2010.01.010

Gliksman, D., Haenel, S., Osem, Y., Yakir, D., Zangy, E., Preisler, Y., & Grünzweig, J. M. (2018). Litter decomposition in Mediterranean pine forests is enhanced by reduced canopy cover. *Plant and Soil*, *422*(1–2), 317–329. doi:10.1007/s11104-017-3366-y

Gliksman, D., Navon, Y., Dumbur, R., Haenel, S., & Grünzweig, J. M. (2018). Higher rates of decomposition in standing vs. surface litter in a Mediterranean ecosystem during the dry and the wet seasons. *Plant and Soil*, 1–13. doi:10.1007/s11104-018-3696-4

Gliksman, D., Rey, A., Seligmann, R., Dumbur, R., Sperling, O., Navon, Y., … Grünzweig, J. M. (2017). Biotic degradation at night, abiotic degradation at day: positive feedbacks on litter decomposition in drylands. *Global Change Biology*, *23*(4), 1564–1574. doi:10.1111/gcb.13465

Goncharov, A. A., & Tiunov, A. V. (2014). Trophic chains in the soil. *Biology Bulletin Reviews*, *4*(5), 393–403. doi:10.1134/S207908641405003X

Gorai, M., Maraghni, M., & Neffati, M. (2011). Plant Ecology & Diversity Relationship between phenological traits and water potential patterns of the wild jujube Ziziphus lotus ( L .) Lam . in southern Tunisia, *0874*. doi:10.1080/17550874.2010.500337

Guenet, B., Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology*, *91*(10), 2850–61. doi:10.1890/09-1968.1

Guirado, E., Segura, D. A., & Castillo, G. (2018). Remote - sensing - derived fractures and shrub patterns to identify groundwater dependence. *Ecohydrology*, (December 2017), 1–11. doi:10.1002/eco.1933

Hassall, M., Adl, S., Berg, M., Griffiths, B., & Scheu, S. (2006). Soil fauna–microbe interactions: towards a conceptual framework for research. *European Journal of Soil Biology*, *42,* S54–S60. doi:10.1016/j.ejsobi.2006.07.007

Hattenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences*, *102*(5), 1519–1524. doi:10.1073/pnas.0404977102

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Hawlena, D., Strickland, M. S., Bradford, M. A., & Schmitz, O. J. (2012). Fear of predation slows plant-litter decomposition. *Science, 336*(June), 1434–1438.

Hawlena, Dror, & Schmitz, O. J. (2010a). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences*, *107*(35), 15503–15507. doi:10.1073/pnas.1009300107

Hawlena, Dror, & Schmitz, O. J. (2010b). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist*, *176*(5), 537–56. doi:10.1086/656495

Hawlena, Dror, & Zaguri, M. (2016). Fear and below-ground food-webs. *Soil Biology and Biochemistry*, *102*, 26–28. doi:10.1016/j.soilbio.2016.06.019

Heal, O. W., Anderson, J. M., & Swift, M. J. (1997). Plant litter quality and decomposition: an historical overview. In C. G. & K. E. Giller (Eds.), *Driven By nature: Plant litter quality and decomposition* (pp. 3–32). Wallingford, Inglaterra: CAB International.

Henry, H. A. L., Brizgys, K., & Field, C. B. (2008). Litter Decomposition in a California

Annual Grassland: Interactions Between Photodegradation and Litter Layer Thickness. *Ecosystems*, *11*(4), 545–554. doi:10.1007/s10021-008-9141-4

Herman, J. R. (2010). Global increase in UV irradiance during the past 30 years (1979–2008) estimated from satellite data. *Journal of Geophysical Research*, *115*(D4), D04203. doi:10.1029/2009JD012219

Hewins, D. B., Archer, S. R., Okin, G. S., McCulley, R. L., & Throop, H. L. (2013). Soil–Litter Mixing Accelerates Decomposition in a Chihuahuan Desert Grassland. *Ecosystems*, *16*(2), 183–195. doi:10.1007/s10021-012-9604-5

Hobbie, S. E. (1992). Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution*, *7*(10), 336–9. doi:10.1016/0169-5347(92)90126-V

Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*. doi:10.1126/science.277.5330.1302

Hornung, E., Farkas, S., & Fischer, E. (1998). Tests on the Isopod Porcellio scaber. In *Handbook of soil invertebrate toxicity tests* (pp. 208–226).

Huang, G., & Li, Y. (2017). Photodegradation effects are related to precipitation amount, precipitation frequency and litter traits in a desert ecosystem. *Soil Biology and Biochemistry*, *115*(December), 383–392. doi:10.1016/j.soilbio.2017.08.034

Huang, G., Zhao, H., & Li, Y. (2017). Litter decomposition in hyper-arid deserts: Photodegradation is still important. *Science of The Total Environment*, *601–602*, 784–792. doi:10.1016/j.scitotenv.2017.05.213

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*(2), 166–171. doi:10.1038/nclimate2837

Huete, A. R., & Jackson, R. D. (1987). Suitability of spectral indices for evaluating vegetation characteristics on arid rangelands. *Remote Sensing of Environment*, *23*(2), 213–232. doi:10.1016/0034-4257(87)90038-1

Hughes, K. a, Lawley, B., & Newsham, K. K. (2003). Solar UV-B Radiation Inhibits the Growth of Antarctic Terrestrial Fungi. *Applied and Environmental Microbiology*, *69*(3), 1488–1491. doi:10.1128/AEM.69.3.1488

Hunter, M. D., Adl, S., Pringle, C. M., & Coleman, D. C. (2003). Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia*, *47*(2), 101–115. doi:10.1078/0031-4056-00174

Ihnen, K., & Zimmer, M. (2008). Selective consumption and digestion of litter microbes by Porcellio scaber (Isopoda: Oniscidea). *Pedobiologia*, *51*(5–6), 335–342. doi:10.1016/j.pedobi.2007.06.001

Janssen, A., Sabelis, M. W., Magalhaes, S., Montserrat, M., & van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology*, *88*(11), 2713–2719. doi:10.1890/06-1408.1

Jesenšek, M. (1996). Recent climatic change in the world's drylands. *Geophysical Research Letters*, *23*(1), 61–64. doi:10.5817/SL2016-2-9

Jia, Y., Lv, Y., Kong, X., Jia, X., Tian, K., & Du, J. (2014). Insight into the indirect function of isopods in litter decomposition in mixed subtropical forests in China Insight into the indirect function of isopods in litter decomposition in mixed subtropical forests in China. *Applied Soil Ecology*, *86*(November), 174–181. doi:10.1016/j.apsoil.2014.10.015

Johnson, D. (2003). Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. *Research in Microbiology*, *154*(5), 315–20. doi:10.1016/S0923-2508(03)00078-0

Johnson, D., Krsek, M., Wellington, E. M. H., Stott, A. W., Cole, L., Bardgett, R. D., … Leake, J. R. (2005). Soil invertebrates disrupt carbon flow through fungal networks. *Science (New York, N.Y.)*, *309*(5737), 1047. doi:10.1126/science.1114769

Kajak, A. (1995). The role of soil predators in decomposition processes. *European Journal of Entomology*.

Kalinkat, G., Brose, U., & Rall, B. C. (2013). Habitat structure alters top-down control in litter communities. *Oecologia*, *172*(3), 877–887. doi:10.1007/s00442-012-2530-6

Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & de Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, *449*(7159), 213–217. doi:10.1038/nature06111

Keller, A. A., & Goldstein, R. A. (1998). Impact of Carbon Storage Through Restoration of Drylands on the Global Carbon Cycle. *Environmental Management*, *22*(5), 757–766. doi:10.1007/s002679900145

Kemp, P. R., Reynolds, J. F., Virginia, R. a., & Whitford, W. G. (2003). Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. *Journal of Arid Environments*, *53*(1), 21–39. doi:10.1006/jare.2002.1025

Kennedy, J. (1994). The archaeological recovery of smallpox victims in Hawaii: scientific investigation or public health threat? *Perspectives in Biology and Medicine*, *37*(4), 499–509. doi:10.1353/pbm.1994.0004

King, J. Y., Brandt, L. A., & Adair, E. C. (2012). Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. *Biogeochemistry*, *111*(1–3), 57–81. doi:10.1007/s10533-012-9737-9

Lavelle, P., Blanchart, E., Martin, a., Spain, a. V., & Martin, S. (1992). Impact of Soil Fauna on the properties of Soils in the Humid Tropics. *Myths and Science of Soils of the Tropics. SSSA Spe- Cial Publication No. 29.*, (29), 29.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., … Rossi, J.-P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, *42*(SUPPL. 1), S3–S15. doi:10.1016/j.ejsobi.2006.10.002

Lavelle, Patrick, Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A Hierarchical Model for Decomposition in Terrestrial Ecosystems: Application to Soils of the Humid Tropics. *Biotropica*, *25*(2), 130. doi:10.2307/2389178

Lawrence, K. L., & Wise, D. H. (2000). Spider predation on forest-floor Collembola and evidence for indirect effect on decomposition. *Pedobiologia*, *44*, 33–39.

Lawrence, K. L., & Wise, D. H. (2004). Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, *48*(2), 149–157. doi:10.1016/j.pedobi.2003.11.001

Lawton, J. H., & Jones, C. G. (1993). Linking species and ecosystem perspectives. *Trends in Ecology & Evolution*, *8*(9), 311–313. doi:10.1016/0169-5347(93)90236-I

Lee, H., Fitzgerald, J., Hewins, D. B., McCulley, R. L., Archer, S. R., Rahn, T., & Throop, H. L. (2014). Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment. *Soil Biology and Biochemistry*, *72*, 123–132. doi:10.1016/j.soilbio.2014.01.027

Lee, H., Rahn, T., & Throop, H. (2012). An accounting of C-based trace gas release during abiotic plant litter degradation. *Global Change Biology*, *18*(3), 1185–1195. doi:10.1111/j.1365-2486.2011.02579.x

Lensing, J. R., & Wise, D. H. (2006). Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences*, *103*(42), 15502–15505. doi:10.1073/pnas.0607064103

Lenth, R. (2019). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.5.1.

Levi, E., Archer, S., Rasmussen, C., Throop, H., Hewins, D., & Cover, L. (2009). *Soil-litter mixing accelerates decomposition and facilitates soil aggregation in a shrub-invaded Sonoran Desert grassland*.

Li, Y., Chen, X., Veen, G. F. C., Eisenhauer, N., Liang, Y., Zhou, X., … Ma, K. (2018). Negative effects of litter richness on root decomposition in the presence of detritivores. *Functional Ecology*, *32*(4), 1079–1090. doi:10.1111/1365-2435.13057

Lin, Y., Karlen, S. D., Ralph, J., & King, J. Y. (2018). Short-term facilitation of microbial litter decomposition by ultraviolet radiation. *Science of The Total Environment*, *615*, 838–848. doi:10.1016/j.scitotenv.2017.09.239

Lin, Y., & King, J. Y. (2014). Effects of UV Exposure and Litter Position on Decomposition in a California Grassland. *Ecosystems*, *17*(1), 158–168. doi:10.1007/s10021-013-9712-x

Lin, Y., King, J. Y., Karlen, S. D., & Ralph, J. (2015). Using 2D NMR spectroscopy to assess effects of UV radiation on cell wall chemistry during litter decomposition. *Biogeochemistry*, *125*(3), 427–436. doi:10.1007/s10533-015-0132-1

Lin, Y., Scarlett, R. D., & King, J. Y. (2015). Effects of UV photodegradation on subsequent microbial decomposition of Bromus diandrus litter. *Plant and Soil*, *395*(1–2), 263–271. doi:10.1007/s11104-015-2551-0

Liu, G., Wang, L., Jiang, L., Pan, X., Huang, Z., Dong, M., & Cornelissen, J. H. C. (2017). Specific leaf area predicts dryland litter decomposition via two mechanisms. *Journal of Ecology*, (May), n/a-n/a. doi:10.1111/1365-2745.12868

Ma, S., Baldocchi, D. D., Hatala, J. A., Detto, M., & Curiel Yuste, J. (2012). Are rain-induced ecosystem respiration pulses enhanced by legacies of antecedent photodegradation in semi-arid environments? *Agricultural and Forest Meteorology*, *154–155*, 203–213. doi:10.1016/j.agrformet.2011.11.007

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., … Zaady, E. (2012). Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. *Science*, *335*(6065), 214–218. doi:10.1126/science.1215442

Majdi, N., Boiché, A., Traunspurger, W., & Lecerf, A. (2014). Predator effects on a detritus-based food web are primarily mediated by non-trophic interactions. *The Journal of Animal Ecology*, *83*(4), 953–62. doi:10.1111/1365-2656.12189

Majdi, N., Kreuzinger-Janik, B., & Traunspurger, W. (2016). Effects of flatworm predators on sediment communities and ecosystem functions: a microcosm approach. *Hydrobiologia*, *776*(1), 193–207. doi:10.1007/s10750-016-2751-5

Manzoni, S., Jackson, R. B., Trofymow, J. a, & Porporato, A. (2008). The global stoichiometry of litter nitrogen mineralization. *Science (New York, N.Y.), 321*(5889), 684–686. doi:10.1126/science.1159792

Mao, B., Zhao, L., Zhao, Q., & Zeng, D. (2018). Effects of ultraviolet (UV) radiation and litter layer thickness on litter decomposition of two tree species in a semi-arid site of Northeast China. *Journal of Arid Land*, *10*(3), 416–428. doi:10.1007/s40333-018-0054-6

Martínez-Yrízar, A., Núñez, S., & Búrquez, A. (2007). Leaf litter decomposition in a southern Sonoran Desert ecosystem, northwestern Mexico: Effects of habitat and litter quality. *Acta Oecologica*, *32*(3), 291–300. doi:10.1016/j.actao.2007.05.010

Melguizo-Ruiz, N. (2016). *Determinantes ecológicos de la red trófica del suelo de los hayedos: disponibilidad hídrica, regulación por grandes depredadores y estructuras clave en la hojarasca*.

Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., … Moya-Laraño, J. (2019). Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. *Journal of Animal Ecology*, (January), 1365-2656.13101. doi:10.1111/1365-2656.13101

Michalet, R., & Pugnaire, F. I. (2016). Facilitation in communities: Underlying mechanisms, community and ecosystem implications. *Functional Ecology*, *30*(1), 3–9. doi:10.1111/1365-2435.12602

Moody, S. A., Newsham, K. K., Ayres, P. G., & Paul, N. D. (1999). Variation in the responses of litter and phylloplane fungi to UV-B radiation (290–315 nm). *Mycological Research*, *103*(11), 1469–1477. doi:10.1017/S0953756299008783

Moore, J. C., Berlow, E. L., Coleman, D. C., De Suiter, P. C., Dong, Q., Hastings, A., … Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*(7), 584–600. doi:10.1111/j.1461-0248.2004.00606.x

Moreira, F. M., Huising, E. J., & Bignell, D. E. (2012). *A handbook of tropical soil biology: sampling and characterization of below-ground biodiversity*. Routledge.

Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567. doi:10.1111/1365-2435.12776

Moya-Laraño, J., Orta-Ocaña, J. M., Barrientos, J. A., Bach, C., & Wise, D. H. (2002). Territoriality in a cannibalistic burrowing wolf spider. *Ecology*, *83*(2), 356–361. doi:10.1890/0012-9658(2002)083[0356:TIACBW]2.0.CO;2

Naili, M. B., Alghazeer, R. O., Saleh, N. A., & Al-Najjar, A. Y. (2010). Evaluation of antibacterial and antioxidant activities of Artemisia campestris (Astraceae) and Ziziphus lotus (Rhamnacea). *Arabian Journal of Chemistry*, *3*(2), 79–84. doi:10.1016/j.arabjc.2010.02.002

Ngai, J. T., & Srivastava, D. S. (2006). Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. *Science*, *314*(5801), 963–963. doi:10.1126/science.1132598

Norby, R. J., & Cotrufo, M. F. (1998). A question of litter quality. *Nature*, *396*(November), 12–13. doi:10.1038/23812

Ocde, O. (2016). Test No. 232: Collembolan Reproduction Test in Soil, (July). doi:10.1787/9789264264601-en

Pan, X., Song, Y.-B., Liu, G.-F., Hu, Y.-K., Ye, X.-H., Cornwell, W. K., Cornelissen, J. H. C. (2015). Functional traits drive the contribution of solar radiation to leaf litter decomposition among multiple arid-zone species. *Scientific Reports*, *5*(1), 13217. doi:10.1038/srep13217

Pancotto, V.A., Sala, O. E., Robson, T. M., Caldwell, M. M., Scopel, A. L., & Aires, B. (2005). Direct and indirect effects of solar ultraviolet-B radiation on long-term decomposition. *Global Change Biology*, *11*(11), 1982–1989. doi:10.1111/j.1365-2486.2005.01027.x

Pancotto, Veronica A., Sala, O. E., Cabello, M., Lopez, N. I., Matthew Robson, T., Ballare, C. L., Scopel, A. L. (2003). Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community. *Global*

*Change Biology*, *9*(10), 1465–1474. doi:10.1046/j.1365-2486.2003.00667.x

Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., Fasth, B. (2007). Global-Scale Similarities in Nitrogen Release Patterns During Long-Term Decomposition. *Science*, *315*(5810), 361–364. doi:10.1126/science.1134853

Paul, N. D., & Gwynn-Jones, D. (2003). Ecological roles of solar UV radiation: towards an integrated approach. *Trends in Ecology & Evolution*, *18*(1), 48–55. doi:10.1016/S0169-5347(02)00014-9

Pauli, F. (1964). Soil Fertility Problem in Arid and Semi-Arid Lands. *Nature*, *204*(4965), 1286–1288. doi:10.1038/2041286a0

Peinado, M., Alcaraz, F., & Martínez-Parras, J. M. (1992). *Vegetation of Southeastern Spain*. (Cramer, Ed.).

Pérez-Harguindeguy, N., & Díaz, S. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. doi:http://dx.doi.org/10.1071/BT12225

Predick, K. I., Archer, S. R., Aguillon, S. M., Keller, D. A., Throop, H. L., & Barnes, P. W. (2018). UV-B radiation and shrub canopy effects on surface litter decomposition in a shrub-invaded dry grassland. *Journal of Arid Environments*, *157*(July), 13–21. doi:10.1016/j.jaridenv.2018.06.007

Preisser, E. L., & Bolnick, D. I. (2008). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PloS One*, *3*(6), e2465. doi:10.1371/journal.pone.0002465

Preisser, E. L., Bolnick, D. I., & Benard, M. E. (2016). Scared to Death ? The Effects of Intimidation and Consumption in Predator-Prey Interactions. *Ecology*, *86*(2), 501–509.

Price, C. M., & Pettijohn, D. E. (1986). Biodiversity and litter decomposition in terrestrial ecosystems. *Experimental Cell Research*, *166*(2), 295–311. doi:10.1016/0014-4827(86)90478-7

Pugnaire, F. I., Armas, C., & Maestre, F. T. (2011). Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function. *Journal of Arid Environments*, *75*(12), 1310–1320. doi:10.1016/j.jaridenv.2011.01.016

Ramón Vallejo, V., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., & Vilagrosa, A. (2012). Perspectives in dryland restoration: approaches for climate change adaptation. *New Forests*, *43*(5–6), 561–579. doi:10.1007/s11056-012-9325-9

Rechner, O., & Poehling, H.-M. (2014). UV exposure induces resistance against herbivorous insects in broccoli. *Journal of Plant Diseases and Protection*, *121*(3), 125–132. doi:10.1007/BF03356500

Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., & Raimundo, J. (2011). Impact of land degradation on soil respiration in a steppe (Stipa tenacissima L.) semi-arid ecosystem in the SE of Spain. *Soil Biology and Biochemistry*, *43*(2), 393–403. doi:10.1016/j.soilbio.2010.11.007

Rey, Ana, Belelli-Marchesini, L., Were, A., Serrano-ortiz, P., Etiope, G., Papale, D., … Pegoraro, E. (2012). Wind as a main driver of the net ecosystem carbon balance of a semiarid Mediterranean steppe in the South East of Spain. *Global Change Biology*, *18*(2), 539–554. doi:10.1111/j.1365-2486.2011.02534.x

Reyes Reyes, M. V., Iñíguez, M. A., Hevia, M., Hildebrand, J. A., & Melcón, M. L. (2015). Description and clustering of echolocation signals of Commerson's dolphins ( Cephalorhynchus commersonii ) in Bahía San Julián, Argentina. *The Journal of the Acoustical Society of America*, *138*(4), 2046–2053. doi:10.1121/1.4929899

Reynolds, J. F., Smith, D. M. S., Lambin, E. F., Turner, B. L., Mortimore, M., Batterbury, S. P. J., … Walker, B. (2007). Global desertification: building a science for dryland development. *Science (New York, N.Y.)*, *316*(5826), 847–51. doi:10.1126/science.1131634

Rohwer, F., Segall, A., Steward, G., Seguritan, V., Breitbart, M., Wolven, F., & Farooq Azam, F. (2000). The complete genomic sequence of the marine phage Roseophage SIO1 shares homology with nonmarine phages. *Limnology and Oceanography*, *45*(2), 408–418.

doi:10.4319/lo.2000.45.2.0408

Rozema, J., Tosserams, M., Nelissen, H. J. M., Heerwaarden, L. Van, Broekman, R. a, & Flierman, N. (1997). Stratospheric ozone reduction and ecosystem processes: enhanced UV-B radiation affects chemical quality and decomposition of leaves of the dune grassland species Calamagrostis epigeios. *Plant Ecology*, *128*, 285–294. doi:10.1023/A:1009723210062

Rutledge, S., Campbell, D. I., Baldocchi, D., & Schipper, L. A. (2010). Photodegradation leads to increased carbon dioxide losses from terrestrial organic matter. *Global Change Biology*, *16*(11), 3065–3074. doi:10.1111/j.1365-2486.2009.02149.x

Sanders, D., & van Veen, F. J. F. (2011). Ecosystem engineering and predation: the multi-trophic impact of two ant species. *Journal of Animal Ecology*, *80*(3), 569–576. doi:10.1111/j.1365-2656.2010.01796.x

Santonja, M., Fernandez, C., Gauquelin, T., & Baldy, V. (2015). Climate change effects on litter decomposition: intensive drought leads to a strong decrease of litter mixture interactions. *Plant and Soil*, *393*(1–2), 69–82. doi:10.1007/s11104-015-2471-z

Schade, G. W., & Crutzen, P. J. (1999). CO emissions from degrading plant matter. *Tellus, Series B: Chemical and Physical Meteorology*, *51*(5), 909–918. doi:10.1034/j.1600-0889.1999.t01-4-00004.x

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science (New York, N.Y.)*, *247*(4946), 1043–8. doi:10.1126/science.247.4946.1043

Schmitz, O. J., & Barton, B. T. (2014). Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control. *Biological Control*, *75*, 87–96. doi:10.1016/j.biocontrol.2013.10.001

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. doi:10.1111/j.1461-0248.2010.01511.x

Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163. doi:10.1111/j.1461-0248.2003.00560.x

Schneider, F. D., & Brose, U. (2013). Beyond diversity: how nested predator effects control ecosystem functions. *The Journal of Animal Ecology*, *82*(1), 64–71. doi:10.1111/1365-2656.12010

Schuster, M. J., & Dukes, J. S. (2014). Non-additive effects of invasive tree litter shift seasonal N release: a potential invasion feedback. *Oikos*, *123*(9), 1101–1111. doi:10.1111/oik.01078

Sitvarin, M. I., & Rypstra, A. L. (2014). Fear of predation alters soil carbon dioxide flux and nitrogen content. *Biology Letters*, *10*(6), 20140366. doi:10.1098/rsbl.2014.0366

Sitvarin, M. I., Rypstra, A. L., & Harwood, J. D. (2016). Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*, *125*(8), 1057–1068. doi:10.1111/oik.03190

Smith, W. K., Gao, W., Steltzer, H., Wallenstein, M. D., & Tree, R. (2010). Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Global Change Biology*, *16*(1), 484–495. doi:10.1111/j.1365-2486.2009.01973.x

Solé, R. (2007). Scaling laws in the drier. *Nature*, *449*(7159), 151–153. doi:10.1038/449151a

Song, X., Peng, C., Jiang, H., Zhu, Q., & Wang, W. (2013). Direct and indirect effects of UV-B exposure on litter decomposition: a meta-analysis. *PloS One*, *8*(6), e68858. doi:10.1371/journal.pone.0068858

Song, X., Zhang, H., Jiang, H., Donaldson, L. A., & Wang, H. (2013). Influence of elevated UV-B radiation on leaf litter chemistry and subsequent decomposition in humid subtropical China. *Journal of Soils and Sediments*, *13*(5), 846–853. doi:10.1007/s11368-013-0661-y

Soong, J. L., Parton, W. J., Calderon, F., Campbell, E. E., & Cotrufo, M. F. (2015). A new conceptual model on the fate and controls of fresh and pyrolized plant litter decomposition. *Biogeochemistry*, *124*, 27–44. doi:10.1007/s10533-015-0079-2

Stephan, J. G., Stenberg, J. A., & Björkman, C. (2017). Consumptive and nonconsumptive effect ratios depend on interaction between plant quality and hunting behavior of omnivorous predators. *Ecology and Evolution*, *7*(7), 2327–2339. doi:10.1002/ece3.2828

Stringer, L. C., Dougill, A. J., Thomas, A. D., Spracklen, D. V., Chesterman, S., Speranza, C. I., … Kopolo, G. (2012). Challenges and opportunities in linking carbon sequestration, livelihoods and ecosystem service provision in drylands. *Environmental Science & Policy*, *19–20*, 121–135. doi:10.1016/j.envsci.2012.02.004

Tan, A. W., & Nuttall, F. Q. (1975). Characteristics of the dephosphorylated form of phosphorylase purified from rat liver and measurement of its activity in crude liver preparations. *Biochimica et Biophysica Acta*, *410*(1), 45–60. doi:10.1016/0005-2744(75)90206-5

Team, R. C. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Throop., & Archer, S. R. (2007). Interrelationships Among Shrub Encroachment, Land Management, and Litter Decomposition in a Semidesert Grassland. *Ecological Applications*, *17*(6), 1809–1823.

Throop, H. L., & Archer, S. R. (2009). *Resolving the Dryland Decomposition Conundrum: Some New Perspectives on Potential Drivers*. (U. Lüttge, W. Beyschlag, B. Büdel, & D. Francis, Eds.), *Progress in Botany* (Vol. 70). Berlin, Heidelberg: Springer Berlin Heidelberg. doi:10.1007/978-3-540-68421-3

Tirado Fernández, R. (2003). *Interacciones Positivas entre plantas: Mecanismos y consecuencias.*

Tirado, R. (2009). Matorrales arborescentes con Ziziphus. In y M. R. y M. Ministerio de Medio Ambiente (Ed.), *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España.*

Tirado, R., & Pugnaire, F. I. (2003). Shrub spatial aggregation and consequences for reproductive success, 296–301. doi:10.1007/s00442-003-1264-x

Tirado, R., & Pugnaire, F. I. (2005). Community structure and positive interactions in constraining environments. *Oikos*, *111*(3), 437–444. doi:10.1111/j.1600-0706.2005.14094.x

Tiunov, A. V. (2009). Particle size alters litter diversity effects on decomposition. *Soil Biology and Biochemistry*, *41*(1), 176–178. doi:10.1016/j.soilbio.2008.09.017

Uselman, S. M., Snyder, K. A., Blank, R. R., & Jones, T. J. (2011). UVB exposure does not accelerate rates of litter decomposition in a semi-arid riparian ecosystem. *Soil Biology and Biochemistry*, *43*(6), 1254–1265. doi:10.1016/j.soilbio.2011.02.016

Valera, F., & Salido, T. (2018). Regeneration of a keystone semiarid shrub over its range in Spain : habitat degradation overrides the positive effects of plant – animal mutualisms. *Plant Biology*, *20*, 1083–1092. doi:10.1111/plb.12870

Verduzco, V. S., Vivoni, E. R., Yépez, E. A., Rodríguez, J. C., Watts, C. J., Tarin, T., … Ivanov, V. Y. (2018). Climate Change Impacts on Net Ecosystem Productivity in a Subtropical Shrubland of Northwestern México. *Journal of Geophysical Research: Biogeosciences*, *123*(2), 688–711. doi:10.1002/2017JG004361

Verhoef, H. A., Verspagen, J. M. H., & Zoomer, H. R. (2000). Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. *Biology and Fertility of Soils*, *31*(5), 366–371. doi:10.1007/s003749900181

Verstraete, M. M. (1986). Defining desertification: A review. *Climatic Change*, *9*(1–2), 5–18. doi:10.1007/BF00140520

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M. P., Petchey, O., Palmborg, C., & Huss-Danell, K. (2009). Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology*, *90*(1), 90–9. doi:10.1890/08-0382.1

Wagg, C., Bender, S. F., Widmer, F., & van der Heijden, M. G. A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(14), 5266–70. doi:10.1073/pnas.1320054111

Wall, D. H., & Lynch, J. (2000). Soil Biodiversity and Ecosystem Functioning. *Biological Resource Management Connecting Science and Policy*, 283–290. doi:10.1007/978-3-662-04033-1

Wang, J., Liu, L., Wang, X., & Chen, Y. (2015). The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. *Global Change Biology*, *21*(5), 2095–104. doi:10.1111/gcb.12812

Wang, J., Liu, L., Wang, X., Yang, S., Zhang, B., Li, P., … Liu, W. (2017). High night-time humidity and dissolved organic carbon content support rapid decomposition of standing litter in a semi-arid landscape. *Functional Ecology*, *31*(8), 1659–1668. doi:10.1111/1365-2435.12854

Wang, J., Yang, S., Zhang, B., Liu, W., Deng, M., Chen, S., & Liu, L. (2017). Temporal dynamics of ultraviolet radiation impacts on litter decomposition in a semi-arid ecosystem. *Plant and Soil*, *419*(1–2), 71–81. doi:10.1007/s11104-017-3290-1

Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and Plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, *79*(2), 247–258.

Wardle, D. a, Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science (New York, N.Y.)*, *304*(5677), 1629–33. doi:10.1126/science.1094875

Whitford, A. W. G., Meentemeyer, V., Seastedt, T. R., Cromack, K., Crossley, D. A., Santos, P., … Waide, J. B. (2016). Exceptions to the AET Model : Deserts and Clear-Cut Forest. *Ecology*, *62*(1), 275–277.

Wu, X., Duffy, J. E., Reich, P. B., & Sun, S. (2011). A brown-world cascade in the dung decomposer food web of an alpine meadow: effects of predator interactions and warming.

*Ecological Monographs*, *81*(2), 313–328. doi:10.1890/10-0808.1

Yanni, S. F., Suddick, E. C., & Six, J. (2015). Photodegradation effects on CO2 emissions from litter and SOM and photo-facilitation of microbial decomposition in a California grassland. *Soil Biology and Biochemistry*, *91*, 40–49. doi:10.1016/j.soilbio.2015.08.021

Yao, M., Rosenfeld, J., Attridge, S., Sidhu, S., Aksenov, V., & Rollo, C. D. (2009). The Ancient Chemistry of Avoiding Risks of Predation and Disease. *Evolutionary Biology*, *36*(3), 267–281. doi:10.1007/s11692-009-9069-4

Yasui, T., Sumita, T., & Tsunogae, S. (2004). Stability of myofibrillar EDTA-ATPase in rabbit psoas fiber bundles. *Journal of Agricultural and Food Chemistry*, *23*(6), 1163–8. doi:10.1021/jf60202a030

Zepp, R. G., Callaghan, T. V., & Erickson, D. J. (1998). Effects of enhanced solar ultraviolet radiation on biogeochemical cycles. *Journal of Photochemistry and Photobiology B: Biology*, *46*(1–3), 69–82. doi:10.1016/S1011-1344(98)00186-9

Zepp, R. G., Erickson, D. J., Paul, N. D., & Sulzberger, B. (2007). Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochemical & Photobiological Sciences : Official Journal of the European Photochemistry Association and the European Society for Photobiology*, *6*(3), 286–300. doi:10.1039/b700021a

Zhang, Q., & Zak, J. C. (2010). Effects of Gap Size on Litter Decomposition and Microbial Activity in a Subtropical Forest. *America*, *76*(7), 2196–2204.

Zhang, X., & Wang, W. (2015). Control of climate and litter quality on leaf litter decomposition in different climatic zones. *Journal of Plant Research*, *128*(5), 791–802. doi:10.1007/s10265-015-0743-6

Zimmer, M., Kautz, G., & Topp, W. (2005). Do woodlice and earthworms interact synergistically in leaf litter decomposition? *Functional Ecology*, *19*(1), 7–16. doi:10.1111/j.0269-8463.2005.00926.x

Zimmer, M., & Topp, W. (1997). Does leaf litter quality influence population parameters of the common woodlouse, *Porcellio scaber* (Crustacea: Isopoda)? *Biology and Fertility of Soils*, *24*(4), 435–441. doi:10.1007/s003740050269

Zouaoui, R., Ksontini, M., & Ferchichi, A. L. I. (2014). Comparative phenological study of Ziziphus lotus ( L .) Lam . in the arid area of Tunisia. *Pak. J. Bot*, *46*(5), 1611–1620.

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