Connecting the Green and the Grey World – an Experimental Approach to Separate Climate, Vegetation and Geochemical Effects on Nutrient Cycling along a Climate Gradient

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For nature,

“May the force be with you”

- Obi-Wan Kenobi (1977, Star wars)

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List of abbreviations

ANOVA = analysis of variance
ADD = away decomposition difference
ADH = additional decomposition at home
AR = arid
C = carbon
CONAF = Corporación Nacional Forestal
DF = degrees of freedom
DFG = deutsche Forschungsgemeinschaft
E = evenness
F-ratio = mean square between/mean square within
H (chapter 2) = Shannon Wiener Index
H (chapter 3) = total home-field advantage for all species combined
HDD = home decomposition difference
HFA = home-field advantage
K = potassium
MAP = mean annual precipitation
ME = mediterranean
N = nitrogen
P = phosphorus
p value = statistical measurement used to validate a hypothesis against observed data
relative N/K loss = N loss (%)/K loss (%)
relative P/K loss = P loss (%)/K loss (%)
S = species richness
SA = semi-arid
SS = sum of squares
TE = temperate

Preface

This study falls in the EarthShape project, a Chilean-German initiative, that aims to understand how microorganisms, animals and plants shape the Earth's surface over time scales from the present-day to the distant geologic past. Over thirty projects use the same large climatic gradient, ranging from the hyper arid Atacama Desert to humid temperate forest, along the Chilean coastal range. The gradient is variable in climate and vegetation, while controlling for differences in bedrock type, and glacial and volcanic influences.

This study focusses on climate change impact on the link between vegetation and nutrient cycles. In particular, I evaluated climate influences on plant communities and litter decomposition, by using not only the differences along the mentioned climatic gradient, but also by performing reciprocal translocation and by using rainout shelters, which allowed me to experimentally disentangle the direct and indirect effects of climate change.

My project worked in very close collaboration with the Ecological Plant Geography group of the University of Marburg. With this collaboration several manuscripts (one published*, one accepted° and others in preparation) will complement this study on litter decomposition along the Chilean coastal cordillera.

This thesis aims to contribute to a deeper understanding of litter decomposition, its influences on carbon and nutrient cycles, and its relevance for Earth surface shaping processes.

April 2022 Liesbeth van den Brink

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* Canessa, Rafaella, **Brink, L. v. d.**, Saldana, A., Rios, R., Hatttenschwiler, S., Mueller, C., Prater, I., Tielbörger, K. and Bader, M.Y. (2021). Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. Journal of Ecology 109 (1), 447-458. 10.1111/1365-2745.13516

° Canessa, Rafaella, **Brink, L. v. d.**, Berdugo, M., Hatttenschwiler, S., Rios, R., Saldana, A., Tielbörger, K. and Bader, M.Y. Trait functional diversity explains mixture effects on litter decomposition at the arid end of a climate gradient. In review in Journal of Ecology

Summary

Climate change is likely to alter plant composition, productivity and litter decomposition. As ecosystems are shaped by specific small-scale climatic environments, the responses of plants to climate changes are likely system specific. Inter-annual precipitation is expected to become more variable with longer dry spells and sporadic but intense precipitation events. It is therefore important to understand the responses of plant communities to climate change in both directions (drought and sporadic but intense precipitation). Litter decomposition, a key component of the global carbon cycle, is greatly affected by the interplay of climate, decomposers and litter quality. Unfortunately, our current understanding of climate-change effects on plant composition and litter decomposition stems mainly from space-for-time studies along climate gradients, where biotic and climatic effects on litter decomposition are confounded. Experimental studies separating indirect from direct climate effects are needed that test the validity of the space-for-time approach.

In order to assess the influence of the magnitude of climate change on biomass production and community composition (richness, diversity and evenness) I translocated soil from two climates at a micro-climatic (opposite slopes) and a macro-climatic scale (among climates) in chapter 2. I found that plant communities do not respond to micro-climatic changes, except for biomass production, which was unexpectedly consistently higher on the drier slopes than on the wetter slopes. Macro-climatic changes triggered several responses: species richness had a consistent response to climate change and was higher in the semi-arid climate in both translocations, but diversity and evenness had contradicting, non-opposite responses. The non-generality of responses might be an indication that changes that occur during drier years are not easily recuperated during wetter years.

In the third chapter, I test the hypothesis that the decomposer community may be locally adapted to litter quality, providing a home-field advantage (HFA) resulting in accelerated decomposition of local compared to non-local litter, after accounting for decomposition differences due to litter quality. Although widely tested in temperate forests, this hypothesis remains controversial and lacks a deep understanding of its generality across climates. I therefore tested the HFA hypothesis for litter decomposition in four ecosystems along an extensive climatic gradient in Chile, using a translocation experiment involving litter from 20 species. In addition to comparing mass loss, I adopted a novel way to disentangle decomposer effects from climate effects, based on loss rates of decomposable *vs*. leachable nutrient fractions. I used the ratios of N and K losses and P and K losses to unravel the relative role of biotic mineralization (N and P loss) *vs*. physical leaching (K loss, driven by precipitation) along the climate gradient. My findings unequivocally contradicted the HFA hypothesis across a wide range of environments and 20 different litter types. A HFA effect was not found, and litter quality influenced litter decomposition much more strongly than origin or location of the litter. Our study questions the applicability of the HFA for litter decomposition and calls for more studies that include a large range of climatic conditions to understand the context-dependency of the HFA.

In the fourth chapter I combined large- and small scale reciprocal litter translocations, *in situ* precipitation manipulation, and a prominent climate gradient to study climate effects on litter decomposition. Interestingly, all experiments indicated clear positive effects of precipitation on

decomposition, but the decomposition of local litter at their home site indicated the opposite, due to indirect climate effects on litter quality. This indicates that space cannot substitute for time and highlights the need for experimental evidence in litter decomposition studies. Such evidence would improve predictions of models of the global carbon cycle that include interactions between climate and vegetation.

Even though plant communities and soil properties seem relatively robust to cope with inter-annual precipitation variability, the predicted precipitation variability for the next decades will most likely alter decomposition rates, which will affect carbon and nutrient cycling. To better predict the influence of climate change on the nutrient cycle, future studies should quantify litter production and plant community changes. A combination of a detailed quantification of plant community litter production with observations, translocations and manipulations of litter decomposition, will make it possible to correctly estimate the effect of future climate change on the nutrient cycle.

Zusammenfassung

Der Klimawandel wird vermutlich die Pflanzenzusammensetzung, die Produktivität und die Streuzersetzung verändern. Da Ökosysteme von spezifischen kleinräumigen klimatischen Umgebungen geprägt sind, sind die Reaktionen der Pflanzen auf Klimaveränderungen wahrscheinlich systemspezifisch. Es wird erwartet, dass Niederschläge stärker zwischen einzelnen Jahren variieren mit längeren Trockenperioden und sporadischen, aber intensiven, Regenfällen. Es ist daher wichtig, die Reaktionen von Pflanzengemeinschaften auf den Klimawandel in beide Richtungen zu verstehen (Trockenheit und sporadische intensive Regenfälle). Die Streuzersetzung, eine Schlüsselkomponente des globalen Kohlenstoffkreislaufs, wird durch das Zusammenspiel von Klima, Destruenten und Streuqualität stark beeinflusst. Leider basiert unser derzeitiges Verständnis der Auswirkungen des Klimawandels auf die Pflanzenzusammensetzung und den Streuabbau hauptsächlich auf space-for-time-Studien entlang von Klimagradienten. Entlang dieser Gradienten ändern sich jedoch sowohl biotische und klimatische Bedingungen, sodass deren Auswirkungen auf den Streuabbau miteinander vermischt werden. Es werden experimentelle Studien benötigt, in biotische und klimatische Bedingungen getrennt werden, um die Gültigkeit des Raum-für-Zeit-Ansatzes zu testen.

Um den Einfluss des Ausmaßes des Klimawandels auf die Biomasseproduktion und die Zusammensetzung der Planzengesellschaft (Artenanzahl, Diversität und Ausgewogenheit der Arten) zu bewerten, habe ich in Kapitel 2 Boden aus zwei Klimazonen auf einer mikroklimatischen (entgegen gerichtete Hänge) und einer makroklimatischen Skala (zwischen den Klimazonen) verlagert. Ich fand heraus, dass Pflanzengemeinschaften zum Großteil nicht auf mikroklimatische Veränderungen reagieren. Die einzige Ausnahme war die Biomasseproduktion, die unerwarteterweise an den trockeneren Hängen durchgängig höher war als an den feuchteren Hängen. Makroklimatische Veränderungen führten zu mehreren Reaktionen: Die Artenanzahl reagierte bei beiden Umsiedlungen einheitlich auf den Klimawandel, und war höher im Semi-Aride Klima, aber die Diversität und die Ausgewogenheit zeigten alle widersprüchliche, nicht gegensätzliche Reaktionen. Die Ungleichmäßigkeit der Reaktionen könnte ein Hinweis darauf sein, dass Veränderungen, die in trockeneren Jahren auftreten, in feuchteren Jahren nicht leicht wieder aufgeholt werden.

Im dritten Kapitel prüfte ich die sogenannte home-field-advantage (HFA) Hypothese, dass die Destruenten lokal an die Streuqualität angepasst sein könnten, was zu einem Heimvorteil führt. Sprich, die Zersetzung lokaler Streu im Vergleich zu nicht-lokaler Streu sollte beschleunigt sein auch wenn Zersetzungsunterschiede aufgrund der Streuqualität berücksichtigt wurden. Diese Hypothese ist nach wie vor umstritten, und es fehlt insbesondere ein Verständnis ihrer Gültigkeit in anderen Klimazonen als temporate Wäldern. Ich habe die HFA-Hypothese für die Zersetzung von Streu in vier Ökosystemen entlang eines ausgedehnten Klimagradienten in Chile getestet, indem ich Streu von 20 Arten verlagert habe. Zusätzlich zum Vergleich der Massenverluste wählte ich eine neue Methode, um die Auswirkungen der Destruenten von den Klimaeffekten zu trennen, und zwar auf der Grundlage der Verlustraten der zersetzbaren gegenüber den auswaschbaren Nährstoffanteilen. Ich nutzte das Verhältnis der N- und K-Verluste sowie der P- und K-Verluste, um die relative Rolle der biotischen Mineralisierung (N- und P-Verluste) gegenüber der physikalischen Auswaschung (K-Verluste durch Niederschläge) entlang des Klimagradienten zu entschlüsseln. Meine Ergebnisse widersprachen eindeutig der HFA-

Hypothese über das gesamte von mir untersuchte Spektrum an Umgebungen und 20 verschiedenen Streuarten. Stattdessen beeinflusste die Streuqualität die Zersetzung der Streu viel stärker als die Herkunft oder der Standort der Streu. Unsere Studie stellt die Anwendbarkeit der HFA für die Streuzersetzung in Frage und es erfordert weitere Studien über eine große Bandbreite an klimatischen Bedingungen, um die Kontextabhängigkeit der HFA zu verstehen.

Im vierten Kapitel kombinierte ich groß- und kleinräumige wechselseitige Streuverlagerungen, In-situ-Niederschlagsmanipulationen und einen Klimagradienten, um die Auswirkungen des Klimas auf die Streuzersetzung zu untersuchen. Interessanterweise zeigten alle Experimente deutlich positive Auswirkungen des Niederschlags auf die Zersetzung, aber die Zersetzung der lokalen Streu am Heimatstandort zeigte das Gegenteil aufgrund von indirekten Klimaeffekten auf die Streuqualität. Dies deutet darauf hin, dass der „space“ nicht der „time“ ersetzen kann, und unterstreicht die Notwendigkeit experimenteller Nachweise bei Studien zur Streuzersetzung. Ein solcher Nachweis würde die Vorhersagen von Modellen des globalen Kohlenstoffkreislaufs verbessern, die Wechselwirkungen zwischen Klima und Vegetation berücksichtigen.

Auch wenn Pflanzengemeinschaften und Bodeneigenschaften relativ robust zu sein scheinen, um mit den zwischenjährlichen Niederschlagsschwankungen fertig zu werden, wird der für die nächsten Jahrzehnte vorhergesagte Niederschlagsvariabilität höchstwahrscheinlich die Zersetzungsraten verändern, was sich auf den Kohlenstoff- und Nährstoffkreislauf auswirken wird. Um den Einfluss des Klimawandels auf den Nährstoffkreislauf besser vorhersagen zu können, sollten künftige Studien die Streuproduktion und die Veränderungen der Pflanzengemeinschaften quantifizieren. Eine Kombination aus einer detaillierten Quantifizierung der Streuproduktion von Pflanzengemeinschaften mit Beobachtungen, Umsiedlungen und Manipulationen der Streuzersetzung wird es ermöglichen, die Auswirkungen des künftigen Klimawandels auf den Nährstoffkreislauf korrekt abzuschätzen.

Chapter 1 – Introduction

1.1. State of the art

Climate change

'In recent decades, changes in climate have caused impacts on natural and human systems on all continents and across the oceans. Evidence of climate-change impacts is strongest and most comprehensive for natural systems' . . . . 'Many terrestrial, freshwater, and marine species have shifted their geographic ranges, seasonal activities, migration patterns, abundances, and species interactions in response to ongoing climate change (high confidence).'

Summary for Policy Makers (IPCC, 2014)

Climate is changing at an alarmingly quick pace and studies predict that extreme climatic events (e.g. extreme droughts, but also extreme rainfall) will likely happen more often (IPCC, 2014; Naumann *et al.*, 2018). They anticipate that drylands will expand and become even drier as a consequence (Huang *et al.*, 2016). For example, since 1960, el Niño southern oscillations (ENSO) have already intensified approximately 25%, and climatic models predict the occurrence of extreme el Niño/la Niña events to double, but also to enhance their intensity (Cai *et al.*, 2021), i.e. longer droughts and heavier rainfall events. These changes will likely have dramatic consequences on natural ecosystems, affecting single species to plant communities to biogeochemical cycles (Tilman and Downing, 1994; Gilman *et al.*, 2010; IPCC, 2014; Ripple *et al.*, 2020).

Impact of climate change on plant communities

The global carbon cycle is strongly affected by climate change. Direct effects of climate change, i.e. through changes in temperature or precipitation, are relatively known, and can trigger changes in reproduction, changes in phenology and changes in geographic range (McCarty, 2001; Pörtner and Farrell, 2008). However, indirect effects of climate on the vegetation, e.g. via growth rates, litter quality, or plant species composition (Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008; Suseela and Tharayil, 2018), are often more complicated to predict, because the relationships between, for example, biomass, plant composition and soil nutrients stocks are not linear (Grime, 1973; Tilman, Kilham and Kilham, 1982), and all are influenced by climate.

Different processes likely respond at different timescales, and might even vary over time, as the pools and processes are all linked through biogeochemical cycles (Shaver *et al.*, 2000; Walther *et al.*, 2002). For example, biomass production is influenced by many processes that all operate on different timescales, i.e. from quick responses to climate change in photosynthesis to slow responses in litter quality (Shaver *et al.*, 2000). However, climate change can trigger different responses in different ecosystems (Liancourt *et al.*, 2013; Tomiolo, Bilton and Tielbörger, 2020). Drought might have little effect on some plant communities, while it can have a large effect on other plant communities independent of the aridity of the sites (reviewed in Miranda *et al.*, 2011). Increasing precipitation, on the other hand, does not always release drought stress, but can also increase competition stress (Liancourt *et al.*, 2013).

Controlled (greenhouse) experiments often fail to match long-term observations in magnitude, and the responses sometimes even show opposite directions than observed in nature (Parmesan and Hanley, 2015). These contradicting responses across time scales, processes and trophic levels, together with the difficulties to re-create real-world responses in controlled environments, shows the need to conduct field experiments which account for the true complexities and interactions of species responses in climate change research (Parmesan and Hanley, 2015).

Impact of climate change on plant traits and litter quality

Plant traits and litter quality are determined by factors such as biogeographic history, biotic interactions, nutrient availability, or disturbance (Woodward and Diament, 1991; Chapman *et al.*, 2003; Wiens and Donoghue, 2004; Chapman, 2006; Bhalawe *et al.*, 2012; Zhu *et al.*, 2016) but also strongly depend on climate. Namely, climate has a direct effect on chemical and physiognomic leaf traits, like holocellulose:lignin ratio, carbon (C), nitrogen (N), and phosphorus (P) concentrations (Cornwell *et al.*, 2008; Graça and Poquet, 2014), leaf dry matter content, specific leaf area (SLA), and leaf toughness (Meentemeyer, 1978; Couteaux, Bottner and Berg, 1995; Hobbie, 1996; Aerts, 1997; Cornwell *et al.*, 2008; Andresen *et al.*, 2010; Melillo, Aber and Muratore, 2014). Therefore, in deserts leafs are usually of low litter quality, i.e. small, spiny and tough, with low SLA, high lignin and carbon content and low phosphorus content. On the contrary, in wetter ecosystems leaves are usually soft and exhibit opposite traits (Wright, Reich and Westoby, 2001; Wright *et al.*, 2004; Díaz *et al.*, 2016). These system specific adaptations to e.g. drought or competition, are costly (Orians and Solbrig, 1977), strongly vary among different climates (Graça and Poquet, 2014), and determine the decomposability of leaf litter. Due to the tight connection between climate and leaf traits, it is expected that climate change will also alter leaf quality and, by consequence, influence nutrient cycling via litter decomposition (Suseela and Tharayil, 2018; Prieto *et al.*, 2019).

Impact of climate change on nutrient cycling

Litter decomposition, i.e. the breakdown of organic matter and the release of its elements, accounts for about half of the global soil respiration (Raich and Schlesinger, 1992; Xu and Shang, 2016) and decomposition rates are therefore an important factor when considering climate change (Berg and McClaugherty, 2003). Decomposition rates depend on climate, the microorganisms in the soil (Cornwell *et al.*, 2008; Zhang *et al.*, 2008; García-Palacios *et al.*, 2013) and the quality of the litter (Cornwell *et al.*, 2008; Makkonen, Berg, *et al.*, 2012). Climate, soil biota and litter quality are highly interconnected, posing a methodological challenge to disentangle their effects on litter decomposition.

A popular hypothesis related to the biotic interactions among plants and microbial decomposers is the home-field advantage (HFA; Gholz *et al.*, 2000; Ayres, Steltzer, Simmons, *et al.*, 2009). This hypothesis states that, because of the close relationship between decomposers and plant litter, decomposer communities are locally adapted to the plant communities of which they break down litter (Scheu *et al.*, 2003; Ayres, Dromph and Bardgett, 2006). This “adaptation” should be manifested in accelerated decomposition when litter and decomposer communities come from the same site, compared to the decomposition of non-local litter (Gholz *et al.*, 2000; Ayres, Steltzer, Berg, *et al.*, 2009).

However, local "adaptation" in litter decomposition is related to an interaction between two communities of organisms (namely plants and microbes), which are both directly and indirectly affected by climate as well as by each other. For example, litter decomposition depends on the inherent ability of the microbial community of a specific site (*sensu* Keiser *et al.*, 2014), with higher ability (and thus, faster decomposition) in ecosystems where the functional breadth of the microbial community is large (Keiser *et al.*, 2014). Vice versa, the functional breadth of the microbial community depends on the litter quality of the site, and is wider when litter is of poorer quality, because the breakdown of litter of poorer quality requires more differently specialized decomposers, than the breakdown of litter of high quality (Keiser *et al.*, 2014). But, litter decomposition is also driven by climatic or general site conditions, which complicates detecting a home-field advantage. Precipitation, amongst others, has a large influence on decomposition, i.e. decomposition increases when precipitation increases (Aerts, 1997; Yahdjian, Sala and Austin, 2006; Suseela and Tharayil, 2018). To really understand if a home field advantage is present in litter decomposition, it is therefore important to distinguish between the different pathways of decomposition, i.e. microbial decomposition and leaching due to precipitation.

Reciprocal translocations and climate manipulations to understand climate change effects

Reciprocal translocations can give insights into the effect of climate change on ecosystem processes. Reciprocal translocations are commonly used to evaluate the effects of climate on litter decomposition, where litter from one or more areas are set to decompose in the original and other climates (e.g. Portillo-Estrada *et al.*, 2016; Keiser and Bradford, 2017; Lu *et al.*, 2017; Glassman *et al.*, 2018). In addition, they can be used to evaluate the home-field advantage hypothesis for decomposition, in order to evaluate the level of adaptation between the microbial decomposers and the litter from specific sites (Bocock *et al.*, 1960). Reciprocal translocation experiments have shown that climate and litter quality are major drivers of decomposition (Aerts, 1997; Makkonen, Berg, *et al.*, 2012; Araujo and Austin, 2015; Portillo-Estrada *et al.*, 2016), although their relative importance varies over time (Canessa *et al.*, 2021).

However, reciprocal translocations do not control for the specific microbial community which can mediate litter quality and climate effects (García-Palacios *et al.*, 2013), or interacting climatic variables. In order to separate the effect of one climatic variable (e.g. precipitation, temperature, radiation) from the indirect climatic effects through litter quality and microbial community, the reciprocal translocation can be combined with specific climate manipulations *in situ* along the climate gradient, e.g. rainout shelters (Yahdjian and Sala, 2002). These climate manipulations allow to manipulate a single factor of interest (e.g. precipitation). Most of the studies using precipitation manipulations found that decomposition decreased when precipitation was reduced (Yahdjian, Sala and Austin, 2006; Brandt, King and Milchunas, 2007; Andresen *et al.*, 2010; Santonja *et al.*, 2017; Zheng *et al.*, 2017; Zhou *et al.*, 2018). Another way of manipulating only climate is to translocate "small ecosystems" (i.e. soil with seeds and microbes) to another climate, which can give insight to the responses of plant communities without introducing the plants to a different soil (Tomiolo, Bilton and Tielbörger, 2020). Dryland ecosystems are ideal to perform reciprocal transplants of whole plant communities, as they often have a permanent seed bank. Additionally, to date litter decomposition studies in drylands remain particularly underrepresented, even though their documentation is key to predict ecosystem responses to global warming correctly (Shaver *et al.*, 2000), especially because drylands are expanding and becoming drier (Huang *et al.*, 2016).

To understand climate change effects on plant communities, soils and litter decomposition, in this thesis, I used a prominent climate gradient in combination with translocation experiments of soil and litter. The drought treatment, that was included in the two central sites, allowed us to disentangle the specific precipitation influence from the overall climate influence. The chosen climate gradient included three precipitation limited sites, and ranged from extremely arid, via semi-arid and mediterranean to wet temperate conditions in the Chilean coastal cordillera (Figure 1.1).

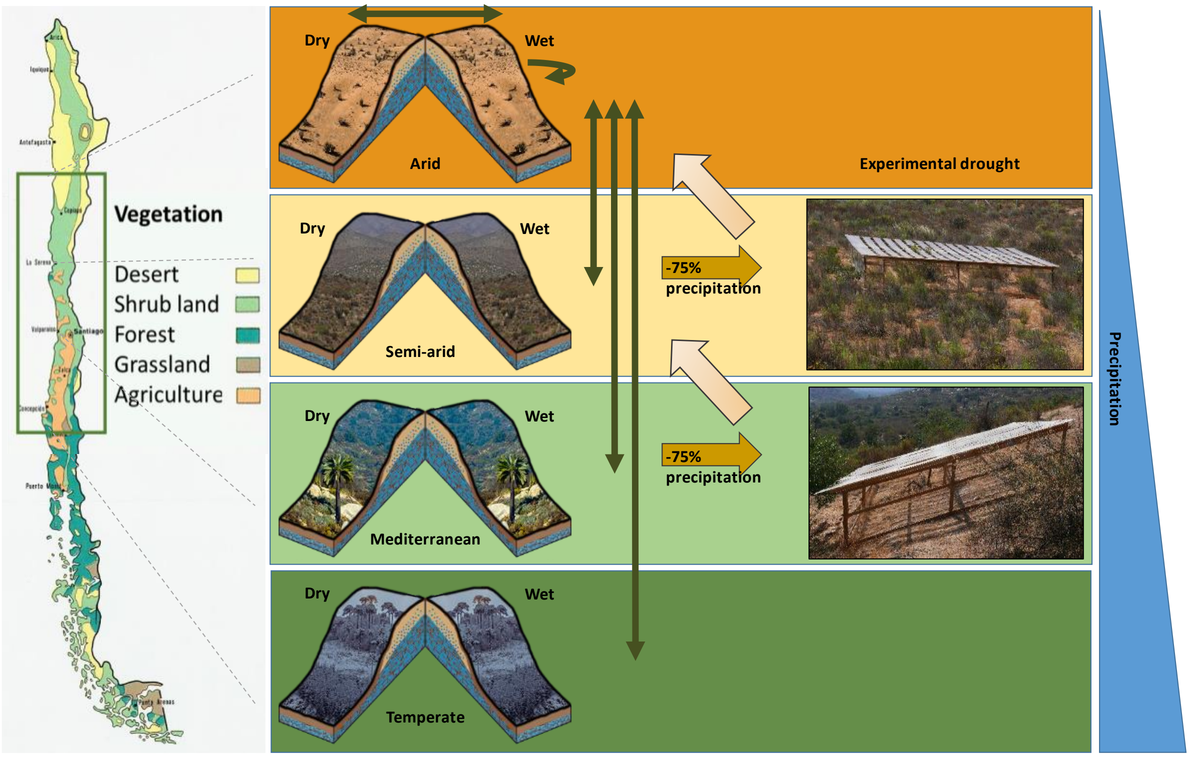

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Figure 1.1. *Climate gradient and experimental drought setup. Shown is a land-cover map showing the study site locations on the left (U.S. Central Intelligence Agency, 1972), and the experimental setup of the experiments on the right. At 4 sites along the gradient dry (north facing) and wet (south facing) slopes were chosen for the reciprocal transplant experiments (middle). In the two central sites, experimental drought was induced by rainout shelters (on the right). The rainout shelters reduce the percentage of rain which reaches the plot under the rainout shelter (dark arrow) by 75%, which mimics the average annual precipitation that falls in the adjacent drier site (light arrows). The drought treatment therefore has two controls: one at the same site, where climate is the same, and one at the drier adjacent site, where precipitation is similar as under the rainout shelter, but other aspects of the climate and environment are different.*

1.2. Objectives and hypothesis

To unravel the complex interactions between climate, soil fertility, plant communities and nutrient cycling, I present the results from three different reciprocal transplant experiments along a steep precipitation gradient along the Chilean coastal range (Figure 1.1). I addressed three main questions with these experiments.

1) Chapter 2: Does the magnitude and direction of climate change matter when assessing the responses of ecosystems?

2) Chapter 3: Do local decomposers have a higher affinity for local litter (home-field advantage, HFA), and is the occurrence of a HFA climate dependent?

3) Chapter 4: Can space substitute for time, and is decomposition mainly precipitation driven?

In chapter 2, I evaluated the influence of climate change on plant communities (i.e. biomass and species diversity) with a reciprocal transplant experiment of soil with seed bank in the two central climates, between slopes and between sites. I expected that the response to the climate changes would correlate with the magnitude of the change. I also expected that increasing humidity would trigger opposite responses than decreasing humidity. Furthermore, I expected that in the dry climate plant productivity would be less, while plant communities would be more diverse.

In chapter 3, I evaluated the adaptation of decomposers for their local litter (HFA) along a steep precipitation gradient. Due to this steep gradient, it was important to separate the confounding factors that occur in such gradients, i.e. the effect from decomposers and leaching. In order to distinguish between biotic decomposition and abiotic leaching, I used the relative loss of nitrogen (N) and phosphorus (P), which are structural elements that are mainly broken down by decomposers and divided them by the relative loss of potassium (K), which is leached by precipitation. With a full reciprocal transplant experiment, including all four sites (Figure 1.1, middle part), I tested if mass loss, N loss (%)/K loss (%) and P loss (%)/K loss (%) had additional decomposition “at home”, and if this additional decomposition was the result of a HFA, or if it was the product of the litter quality of the local species, or the ability of the decomposer community. Additionally, I tested if this effect was stronger on the arid end of the gradient, where water stress selects for a specialized plant and bacterial community.

In chapter 4, I evaluated the effect of precipitation on litter decomposition. In order to disentangle the effect of precipitation from climate, I used a full reciprocal transplant experiment along the gradient, dry and wet exposition within the sites as well as additional drought treatments. The addition of the rainout shelters makes it possible to test if decomposition is mainly affected by precipitation, as they disentangle the effect of precipitation from general climatic effects, i.e. the precipitation is manipulated, while the rest of the climate stays the same. Rainout shelters facilitate the comparison of litter decomposition within the same climate for “control” vs “drought treatment”, as well as the comparison of similar precipitation across the gradient (i.e. “mediterranean drought” = “semi-arid control” and “semi-arid drought” = “arid control”). I tested the overarching hypothesis that space can substitute for time by testing if decomposition along this gradient is mainly precipitation driven. I hypothesized that decomposition would be higher in the control plots, on the wetter slopes and towards the wetter end of the gradient, due to favorable climatic conditions for decomposition (i.e. more humidity) and higher litter quality at wetter sites.

Contribution statement

Author	Author position	Scientific ideas %	Data generation %	Analysis / interpretation %	Paper writing %
Liesbeth van den Brink	1	20%	90%	100% / 20%	65%
Rafaella Canessa	2	0%	0%	0% / 10%	5%
Harald Neidhardt	3	0%	10%	0% /10%	5%
Pierre Liancourt	4	0%	0%	0% / 10%	8%
Lohengrin A. Cavieres	5	0%	0%	0% /10%	2%
Yvonne Oelmann	6	20%	0%	0% /10%	5%
Maaike Y. Bader	7	0%	0%	0% /10%	5%
Katja Tielbörger	8	60%	0%	0% /20%	5%
Title of paper:		Drought and increased precipitation do not have opposing effects on plant communities in a field experiment			
Status in publication process:		Ready for submission			

Chapter 2 – Drought and increased precipitation do not have opposing effects on plant communities in a field experiment

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Abstract

Climate change is likely to alter plant community structure and function. Since climate change projections include not only directional change of mean temperature and precipitation, but also an increase in the frequency of dry spells and intense rains, it is important to assess the response of ecological communities to both increases as well as decreases in climatic variables. We assessed the influence of the magnitude of climate change on biomass production and species composition (richness, diversity and evenness) by translocating soil and seeds from two climates at a micro-climatic (opposite slopes) and a macro-climatic scale (between climates). We found that plant community structure did not respond to micro-climatic change. However, biomass production was unexpectedly consistently higher on drier slopes than on wetter slopes. Macro-climatic changes triggered several non-intuitive responses, where, similar to the within site translocation, biomass of species from drier origins was lower in the wetter climate. In contrast biomass production did not change significantly when translocated in the opposite direction, i.e. from the wetter origin to a drier climate. Diversity and evenness increased in communities from a wetter origin that were translocated to a drier climate, but did not decrease when communities from a drier origin were translocated to a wetter climate. The non-generality of responses might be an indication that tipping points might occur during drier years, which are not easily recuperated during wetter years, in systems with inter-annual precipitation variability.

Keywords: climate change; plant productivity; reciprocal transplant; Shannon-Wiener index; soil transplant; species evenness; species richness

2.1. Introduction

Climate is changing globally, and extreme climatic events will likely happen more often (IPCC, 2014; Naumann *et al.*, 2018). For example, el Niño southern oscillation (ENSO) have already intensified approximately 20% since 1960, resulting in more frequent extreme la Niña/el Niño events in the last 60 years, i.e. longer droughts and, when occurring, heavier precipitation events (Cai *et al.*, 2021). Furthermore, models predict the occurrence of extreme el Niño/la Niña events to double, and to further enhance their variability (Cai *et al.*, 2021). This intensification will likely affect the structure and function of ecological communities. Climate change impacts on plant communities are abundant and have demonstrated marked shifts in both species composition and biomass production (Tilman and Downing, 1994; Gilman *et al.*, 2010). For example, higher temperatures in cold climates might lead to higher biomass production as it extends the growing season (Garcia *et al.*, 2014), whereas in hot climates, even higher temperatures may exceed the optimum range and be detrimental for plant growth (Hatfield and Prueger, 2015). Decreases in precipitation, however, usually have a consistent negative effect by decreasing biomass production (Peñuelas *et al.*, 2007; Miranda *et al.*, 2011). Generally, effects of climate change on species composition (Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008; Suseela and Tharayil, 2018), are often more complicated to predict, because they are the result of interlinking, biotic (intra- and interspecific) interactions that each respond separately to climate change (Shaver *et al.*, 2000).

When climate changes are small, plants might be able to alter their physiology or morphology in response to changes in environmental conditions. However, this phenotypic plasticity is limited, and constrained to within climate variability (Schlichting, 1986). To inhabit specific climates, plants need system specific adaptations, i.e. to dry conditions or competition, which have specific benefits, but they come at a cost (Orians and Solbrig, 1977). For example, plants with the capacity to cope well with drought are able to resist dry years (Tilman and Downing, 1994; Jump and Peñuelas, 2005), but they might not perform well under more competitive conditions (Grime, 1973; Kneitel and Chase, 2004; Nemer *et al.*, 2021) that can occur during wet years. Therefore, decreases in biomass production due to lower precipitation (Peñuelas *et al.*, 2007), often correlate with increases in species richness and/or diversity and often evenness, due to a decrease in interspecific competition (Craine and Dybzinski, 2013; Alon and Sternberg, 2019; Zhou *et al.*, 2019).

A way to study how increased inter-annual precipitation variability will affect species in the short term, is through reciprocal transplants (Link *et al.*, 2003; Alexander, Diez and Levine, 2015; Liang *et al.*, 2015; Tomiolo, Bilton and Tielbörger, 2020). Translocations allow for mimicking sudden climatic extremes as the studied species is swapped among two or more climates (Maranon and Bartolome, 1993; Alexander, Diez and Levine, 2015). A great advantage of translocation experiments is also that they enable assessing the context-dependency of plant responses to climate changes (Liancourt *et al.*, 2013). Namely, relocated plants are confronted both with different climates, soils, and different biotic interactions within a novel climate. However, translocating species in isolation, and therefore, ignoring the complex interactions between plants and soil, can lead to misleading conclusions about plant adaptations to climate change (Tomiolo, Van Der Putten and Tielbörger, 2015).

Additionally, different processes are likely to respond at different timescales, and might even vary over time (Shaver *et al.*, 2000; Walther *et al.*, 2002). The magnitude of the climatic change, might also affect each feature differently (Garcia *et al.*, 2014), e.g. small changes in climate might shift phenologies of the affected individuals, while extreme events, e.g. storms and drought spells, affect species and their interactions (McCarty, 2001). Interactions between species have a great impact on each other, and some species have a particularly large influence on others (Zarnetske, Skelly and Urban, 2012). When these species are affected by climate change, a cascading effect can occur, affecting other species in the community (Zarnetske, Skelly and Urban, 2012).

However, in contrast, the effect of sudden climate changes can also be buffered by the effect of biotic interactions (Tomiolo, Van Der Putten and Tielbörger, 2015).

Since climatic changes may have opposing effects on plant performance than biotic interactions, reciprocal transplants (i.e. to and from wetter and drier places, respectively) of "small ecosystems", where the interactions are maintained as much as possible, may help to better disentangle the biotic and abiotic components of climate change impacts (Tomiolo, Van Der Putten and Tielbörger, 2015). Interestingly, in such 'whole community transplants' relocation to drier conditions did not necessarily lead to responses that were opposite to relocation to wetter conditions (Zhang *et al.*, 2011; Tomiolo, Bilton and Tielbörger, 2020). These non-opposite responses might occur, due to non-opposite stress factors in either site, i.e. in drier sites water limitation can play a large role, while in wetter sites competition could play an important role (Grime, 1973). Therefore, the impact of the specific stressor (either drought or competition) depends on the climatic conditions in the selected sites (Grime, 1973). For this reason, it is urgently needed to experimentally assess the direction of plant community responses to climate changes in different climates, in order to better predict the implications of climate change locally.

Although translocations of complete ecosystems are used more and more often in restoration ecology, only a handful have been used to understand the impact of climate change (Boyer *et al.*, 2016), and even less used a reciprocal approach. Reciprocal translocations of whole plant communities can be done easily in dryland ecosystems as they often have a permanent seed bank (Holzapfel, Schmidt and Shmida, 1993). This enables the extraction of soil with seeds during the dry season, and the translocation to another ecosystem without major harm to the plants (Tomiolo, Bilton and Tielbörger, 2020).

Here, we translocated soil with seed banks both within (i.e. microclimatic change) as well as between (i.e. macroclimatic change) a semi-arid and mediterranean climate and measured biomass production and diversity. We tested if responses would be smaller for micro-climatic change (within site) and larger for macro-climatic change (between sites), and if increasing humidity and decreasing humidity would have opposite responses. We hypothesized that with decreasing humidity (1) biomass production would decrease and diversity and evenness to increase, and *vice-versa* for transplants to wetter conditions. We furthermore hypothesized (2) a larger response in communities transplanted between than within sites.

2.2. Materials and methods

2.2.1. Study sites

Experiments were situated at two sites in Chile (30° - 33° S), selected to be within the same geographical unit (the coastal cordillera) that share a common bedrock. Their main difference is in their climate, of which precipitation is the most important variable (Table 1). The semi-arid shrub-land site (Reserva privada Quebrada de Talca) had a mean annual soil temperature of 16.6°C (mean annual air temperature: 14.6°C) and a mean annual precipitation of 116mm during the study period (from April 2016 to April 2018). The vegetation cover is 30-40%, consisting of shrubs (mainly Asteraceae), cacti, low trees and geophyte perennials (Squeo, Arancio, *et al.*, 2008). The mediterranean site (Parque Nacional La Campana) had a mean annual soil temperature of 14°C (mean annual air temperature: 14.6°C), and the mean annual precipitation was 218mm during the study period. The sclerophyllous vegetation cover is almost complete and consists of evergreen trees, shrubs, palms, herbs and grasses (Hauenstein, 2012), the latter are not all native (Hauck, Moreira-Muñoz and Nezadal, 2016). See Bernhard, Moskwa, *et al.* (2018) and Oeser *et al.* (2018) for an overview of the species present at the sites. Within each site, five representative, independent dry (north facing) and five representative, independent wet (south facing) slopes were chosen, 20 slopes in total. The independence was secured by choosing slopes with similar aspects that were separated by a distance of at least 100m.

2.2.2 Reciprocal translocations within and between sites

We translocated soil with seed banks between a semi-arid and mediterranean climate with similar average temperatures but differing in precipitation (Figure 2.1b, Table 2.1), to understand the response of dryland plant communities to large (macro) climatic changes. Additionally, we used the local variation of the landscape within the sites to assess the response of these communities to small (micro) climatic changes, and reciprocally transplanted soil with seeds between the dry (north facing) and wet (south facing) expositions.

At each slope one plot (50X50 cm, with four subplots 20x20 cm each was established (Figure 2.1c). In each of these four subplots, five cm of soil (including organic layer) were excavated during the late dry season (March-April 2016), and mixed to gain the best possible homogeneous distribution of soil and seeds per plot. The homogenized soil was split into four equal parts, and each part was placed in a paper bag. One part was taken to the other site (500 km away) and placed in a randomly assigned subplot of the randomly assigned “partner”-plot with the same exposure (“between sites translocation”, Figure 2.1b and c). Two other the parts were taken on a 500 km trip, the distance between sites, as soil aggregates might disintegrate during the translocation between the sites and influence the results. From these two, one part was put back into a randomly assigned subplot (“control”). The second part was placed in a randomly assigned subplot of the randomly assigned “partner”-plot in the same climate but on the opposite exposure (“within site translocation”). We included the methodological hypothesis that biomass production, species richness, diversity and evenness are not influenced by travel. For this we placed a fourth part immediately back into a randomly assigned subplot (“control without travel”). We found no differences between soil that traveled or not in any of our response factors, and therefore pooled the control with and without travel in further analysis (from hereon called: control, supplementary figure S2.1, supplementary table S2.1). All the soils were back in the field before the first winter rains.

Tomst TMS3 sensors were placed next to each plot (20 in total) to monitor soil temperature and soil humidity during the course of the experiment. The soil moisture was calibrated with the calibration tool provided by the manufacturer, based on the sand, silt, clay content of the soil (Bernhard, Moskwa, *et al.*, 2018)

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The transplanted soil was monitored for 2 years, in which the seeds, translocated together with the soil, were allowed to germinate. The germinated plants were considered to have survived if they flowered, and clipped at ground level before they seeded, to avoid the establishment of translocated species at the other site via the dispersal of seeds. They were identified to calculate species richness, and their dry biomass was measured (after at least 48h in the oven at 40°C).

Total biomass production (g) was calculated as the sum of the biomass of all the species per subplot. Species composition was approached with three indices at the subplot level: species richness (S), Shannon Wiener diversity index (H, *sensu* Wilhm, 1968), and species evenness (E, Pielou, 1966). To calculate the Shannon Wiener Index (H), and evenness (E) we used the species biomass instead of number of individuals: $H = -\Sigma[(p_i) \times ln(p_i)]$, where p_i is the proportion of total biomass represented by the species i; and $E = H/H_{max}$, in which $H_{max} = ln(S)$, where S = species richness = number of species.

After 2 years the “non-local” soil was carefully removed and disposed of.

2.2.3 Statistical analyses

We used ANOVAs, with origin (semi-arid vs mediterranean), original exposure (dry *vs*. wet), treatment (control, within site and between site) and all their interactions as fixed factors. Although the experiment was fully reciprocal, we focused the analysis with three planned comparisons among treatments and origin using the data from the three way interaction (origin*original exposure*treatment): I.e. we compared the controls, to analyze the differences between the sites; we then compared the micro- and macro-climatic translocations from dry (semi-arid dry slope) to wetter (semi-arid wet slope) to wet (mediterranean), and from wet (mediterranean wet slope) to drier (mediterranean dry slope) to dry (semi-arid), in order to understand the influence of micro- and macro-climatic changes on biomass production, species richness (S), species diversity (Shannon-Wiener Index, H) and species evenness (E) after two years.

All statistical analyses were performed in the statistical software JMP 15.

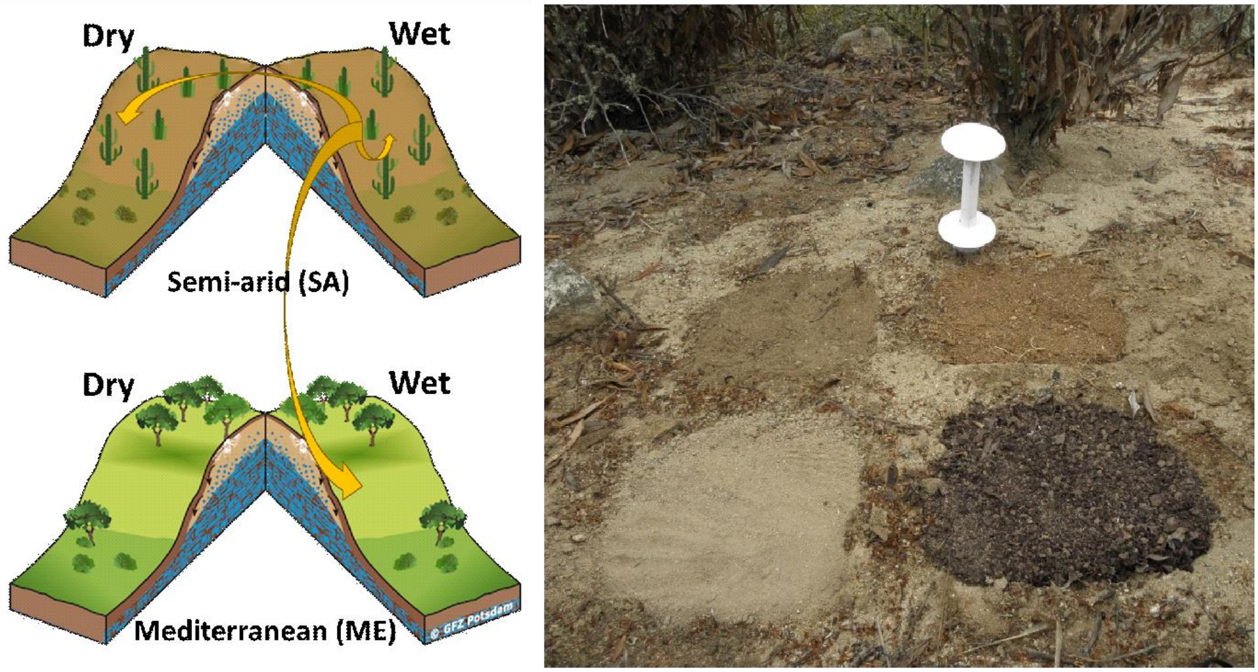

Figure 2.1. *Setup of the experiments at two different sites, each with five dry and five wet slopes (20 in total) in Chile: (left) soil translocations on macro-climatic scale between the semi-arid and mediterranean sites ("between site translocation"), on micro-climatic scale between exposures ("within site translocation") and control ("with" and "without travel"); (right) example of a plot in the semi-arid climate.*

Table 2.1. *Climatic information of the study sites used for the reciprocal translocation experiment along the Coastal Cordillera of Chile, from nearby climate stations and in-situ data loggers (TOMST, 1 per plot, 20 in total), arranged at site level for the study period (April 2016-April 2018). "Min" and "Max" represent the minimum and maximum monthly mean temperature.*

	Sum of Precipitation (mm)[1]	Average precipitation 2014-2021[2]	Average Volumetric Soil Moisture (m^3/m^3)[3]	Average Air temperature (°C) (min-max)[4]	Average soil temperature (°C) 0cm (min-max)[3]	Average Solar radiation (W/m^2)[4]
Semi-arid (WGS84: -30.05, -71.09)		**87**				
Year 1: April 2016-March 2017	43		0.14	15.25 (2.19-31.38)	17.04 (-1.38-44.38)	241
Year 2: April 2017-March 2018	189		0.19	14.22 (0.71-29.69)	16.33 (-1.25-46.13)	240
Overall			**0.17**	**14.63**	**16.62**	**241**
Dry exposure			0.18		17.09	
Wet exposure			0.18		16.21	
Mediterranean (WGS84: -32.95, -71.06)		**191**				
Year 1: April 2016-March 2017	182		0.19	14.9 (-0.2-36.1)	14.4 (0.1-47.6)	211
Year 2: April 2017-March 2018	253		0.18	14.4 (-1.6-35.7)	13.9 (-2.0-46.9)	213
Overall			**0.19**	**14.6**	**14.1**	**213**
Dry exposure			0.17		14.3	
Wet exposure			0.20		13.9	

[1] EarthShape climate station Santa Gracia for Semi-Arid site (Übernickel *et al.*, 2020); Inia climate station La Cruz for Mediterranean site (https://agrometeorologia.cl/)

[2] Inia climate station Gabriela Mistral for semi-arid, La Cruz for mediterranean site (https://agrometeorologia.cl/)

[3] Tomst data loggers

[4] EarthShape climate station Santa Gracia for Semi-Arid site and La Campana for Mediterranean site (Übernickel *et al.*, 2020)

2.3. Results

Planned comparisons among control plots: The full model showed that plant communities growing under semi-arid conditions had a significantly higher species richness than the community growing under mediterranean conditions (F=4.27, p=0.044), but neither biomass nor diversity differed between exposures within each climate (Table S2.2). The planned comparisons showed that the control plots varied in biomass: biomass production was highest on the semi-arid dry exposure and lowest on the wet exposures in the semi-arid and mediterranean climate (figure 2.2a, table 2.2, S2.2 and S2.3). Species richness was highest in the semi-arid climate (no differences between slopes) and lowest on the mediterranean wet slope. Species diversity was highest on the semi-arid wet slope and lowest on the mediterranean wet slope. Evenness showed a hump shaped curve, from lowest on the semi-arid dry slope, to high on the semi-arid wet slope and on the mediterranean dry slope, to low on the mediterranean wet slope (figure 2.2b-d, table 2.2, S2.2 and S2.3).

Planned comparisons between micro- and macro-climatic change: The magnitude of climate change was important for the response to the change. Biomass had the most intriguing response and was the only response factor that was affected by micro-climatic change. Biomass production was highest on the drier slopes. I.e. biomass production for the soil that was translocated from a drier origin to wetter conditions, decreased from dry to wet: biomass production was highest in the semi-arid dry slope, intermediate on the semi-arid wet slope, and lowest in the mediterranean (figure 2.3a left panel, table 2.3, S2.2 and S2.3). However, the biomass for the soil that was translocated from the wetter origin to drier conditions was highest on the mediterranean dry slope, intermediate in the semi-arid, and lowest on the mediterranean wet slope (figure 2.3a right panel, table 2.3, S2.2 and S2.3). Species richness showed a general response and was highest in the semi-arid climate and lowest in the mediterranean climate (figure 2.3b left panel, table 2.3, S2.2 and S2.3). The same pattern was found for the translocation from mediterranean wet slope -> mediterranean dry slope -> semi-arid: species richness was highest in the semi-arid climate and lowest in the mediterranean climate (figure 2.3b right panel, table 2.3, S2.2 and S2.3). So overall the species richness was highest in the semi-arid climate and lowest in the mediterranean independent of the soil origin. Species diversity and evenness did not differ across the soils that were translocated from the dry origin to the wetter climate (figure 2.3c and d left panel, table 2.3, S2.2 and S2.3), but were higher in the drier semi-arid climate than in the mediterranean for the soil that had been translocated from the wetter origin to the drier climate (figure 2.3c and d right panel, table 2.3, S2.2 and S2.3).

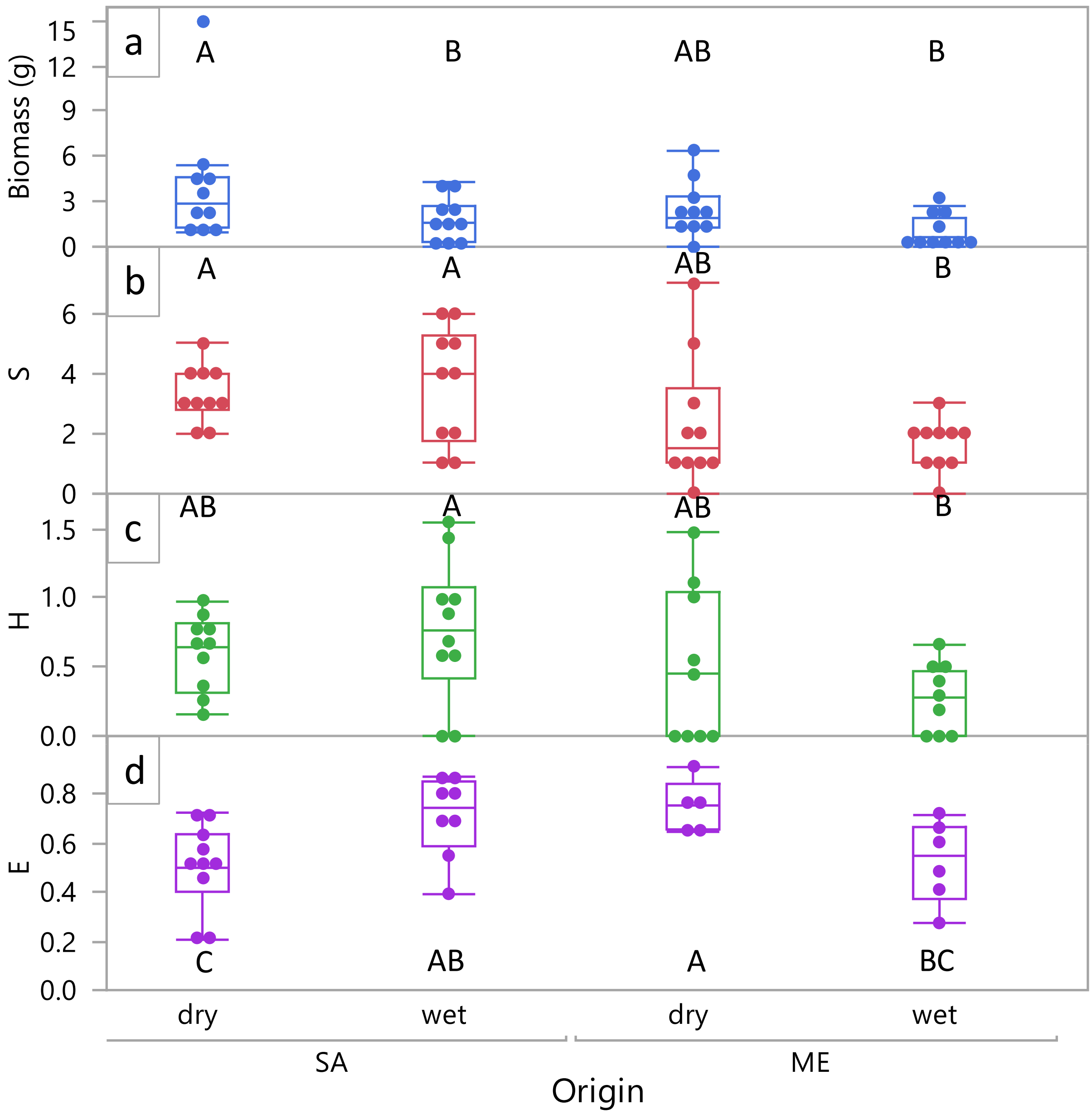

Figure 2.2. *Contrast for control plots for plant (a) biomass (g), (b) species richness (S), (c) Shannon-Wiener index (H) and (d) evenness (E). SA=semi-arid, ME=mediterranean, dry=north facing slope, wet=south facing slope. In the graphs the letters correspond to the planned contrast for the origin ˣ original exposure interaction. See table 2.2 and S2.3 for the corresponding statistics.*

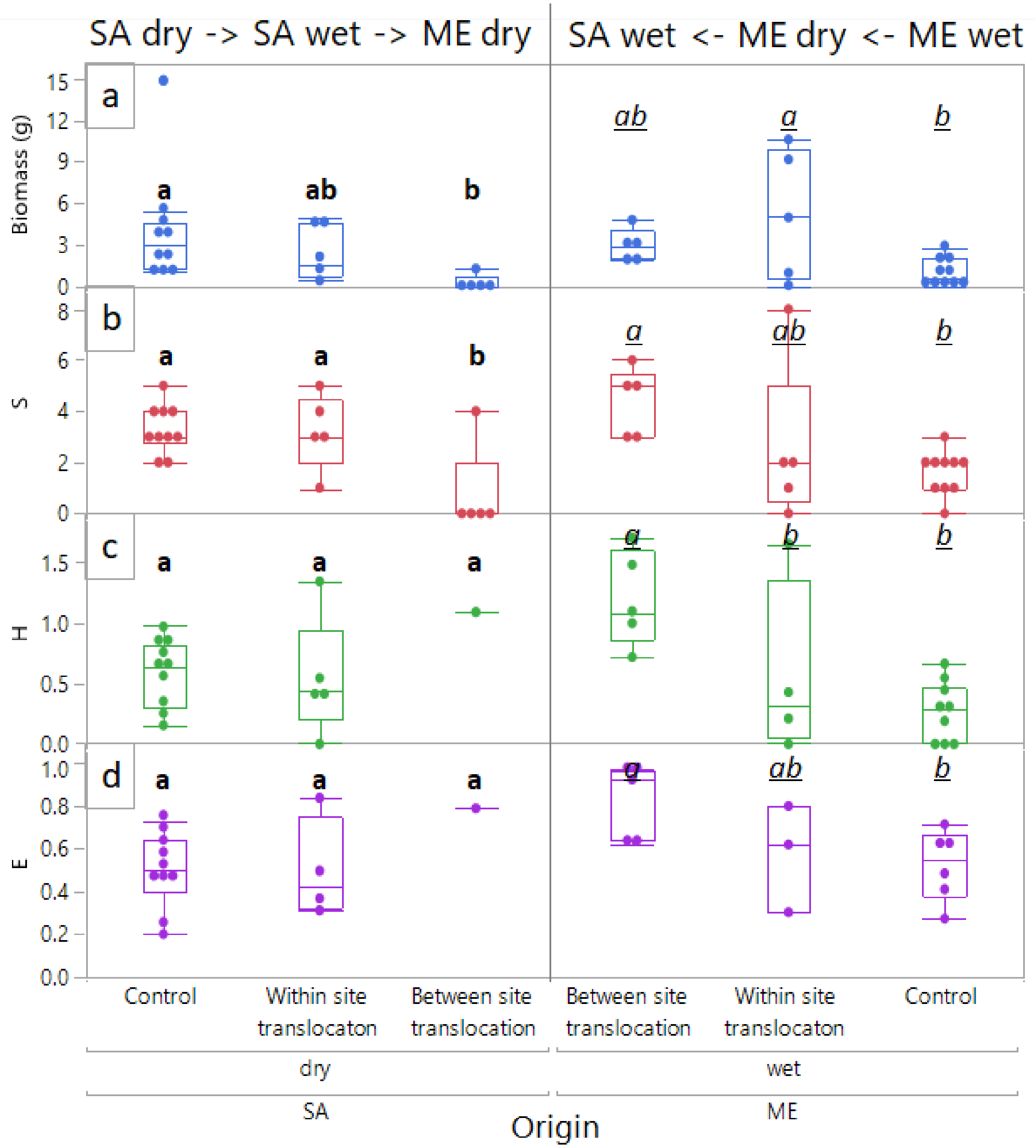

***Figure 2.3**. Contrast for semi-arid dry -> semi-arid wet -> mediterranean and mediterranean wet -> mediterranean dry -> semi-arid translocations on micro-climate scale (within site translocation) and macro-climate scale (between site translocation) for plant (a) biomass (g), (b) species richness (S), (c) Shannon-Wiener index (H), and (d) evenness (E). For easy interpretation the x as is depicted with increasing soil humidity for the translocated soils per origin (SA=semi-arid, ME=mediterranean, dry=north facing slope, wet=south facing slope). In the graphs the letters correspond to the planned contrasts for the origin*original exposure*treatment interaction. See table 2.2 and S2.4 for the corresponding statistics.*

Table 2.2. *Contrast of control plots for biomass, species richness, Shannon-Wiener index and evenness. SS=sum of squares, contrast=specific comparison between two controls. Significant contrasts with bonferroni correction are in bold.*

Y	Effect	Plot	Contrast 1	Contrast 2	Contrast 3	Contrast 4	Contrast 5	Contrast 6
Biomass (g)	O*E*T	SA,dry,Control	1	1	1	0	0	0
		SA,wet,Control	-1	0	0	1	1	0
		ME,dry,Control	0	-1	0	-1	0	1
		ME,wet,Control	0	0	-1	0	-1	-1
		Estimate	2.209	1.608	3.031	-0.601	0.822	1.423
		Std Error	1.043	1.043	1.043	1.043	1.043	1.043
		t Ratio	2.117	1.541	2.905	-0.576	0.788	1.364
		Prob>|t|	**0.038**	0.128	**0.005**	0.567	0.433	0.177
		SS	24.387	12.927	45.930	1.803	3.381	10.124
Species richness	O*E*T	SA,dry,Control	1	1	1	0	0	0
S		SA,wet,Control	-1	0	0	1	1	0
		ME,dry,Control	0	-1	0	-1	0	1
		ME,wet,Control	0	0	-1	0	-1	-1
		Estimate	-0.300	1.000	1.700	1.300	2.000	0.700
		Std Error	0.747	0.747	0.747	0.747	0.747	0.747
		t Ratio	-0.402	1.338	2.275	1.740	2.677	0.937
		Prob>|t|	0.689	0.185	**0.026**	0.086	**0.009**	0.352
		SS	0.450	5.000	14.450	8.450	20.000	2.450
Shannon-Wiener index	O*E*T	SA,dry,Control	1	1	1	0	0	0
H		SA,wet,Control	-1	0	0	1	1	0
		ME,dry,Control	0	-1	0	-1	0	1
		ME,wet,Control	0	0	-1	0	-1	-1
		Estimate	-0.167	0.088	0.322	0.255	0.489	0.234
		Std Error	0.205	0.211	0.211	0.211	0.211	0.216
		t Ratio	-0.813	0.419	1.530	1.210	2.320	1.083
		Prob>|t|	0.420	0.677	0.132	0.231	**0.024**	0.284
		SS	0.139	0.037	0.492	0.308	1.133	0.247
Evenness	O*E*T	SA,dry,Control	1	1	1	0	0	0
E		SA,wet,Control	-1	0	0	1	1	0
		ME,dry,Control	0	-1	0	-1	0	1
		ME,wet,Control	0	0	-1	0	-1	-1
		Estimate	-0.213	-0.255	-0.027	-0.042	0.186	0.228
		Std Error	0.088	0.102	0.096	0.106	0.100	0.112
		t Ratio	-2.412	-2.505	-0.281	-0.400	1.849	2.026
		Prob>|t|	**0.020**	**0.016**	0.780	0.692	0.071	**0.049**
		SS	0.201	0.216	0.003	0.006	0.118	0.142

Table 2.3. *Contrast of dry to wet and wet to dry translocation on micro (within site) and macro (between sites) climatic scales for biomass, species richness, Shannon-Wiener index and evenness. SS=sum of squares, contrast=specific comparison between two treatments. Significant contrasts with bonferroni correction are in bold.*

	Effect	Dry to wetter to wet	Contrast 1	Contrast 2	Contrast 3	Wet to drier to dry	Contrast 1	Contrast 2	Contrast 3
Biomass (g)	O*E*T	SA,dry,Control	1	1	0	ME,wet,Control	1	1	0
		SA,dry,Within site translocation	-1	0	1	ME,wet,Within site translocation	-1	0	1
		SA,dry,Between site translocation	0	-1	-1	ME,wet,Between site translocation	0	-1	-1
		Estimate	1.576	3.794	2.218	Estimate	-4.125	-1.942	2.183
		Std Error	1.278	1.278	1.475	Std Error	1.278	1.278	1.475
		t Ratio	1.234	2.970	1.503	t Ratio	-3.229	-1.520	1.480
		Prob>|t|	0.222	**0.004**	0.137	Prob>|t|	**0.002**	0.133	0.144
		SS	8.280	47.984	12.299	SS	56.727	12.575	11.914
Species richness S	O*E*T	SA,dry,Control	1	1	0	ME,wet,Control	1	1	0
		SA,dry,Within site translocation	-1	0	1	ME,wet,Within site translocation	-1	0	1
		SA,dry,Between site translocation	0	-1	-1	ME,wet,Between site translocation	0	-1	-1
		Estimate	0.100	2.500	2.400	Estimate	-1.000	-2.800	-1.800
		Std Error	0.915	0.915	1.057	Std Error	0.915	0.915	1.057
		t Ratio	0.109	2.732	2.271	t Ratio	-1.093	-3.060	-1.704
		Prob>|t|	0.913	**0.008**	**0.026**	Prob>|t|	0.278	**0.003**	0.093
		SS	0.033	20.833	14.400	SS	3.333	26.133	8.100
Shannon-Wiener index H	O*E*T	SA,dry,Control	1	1	0	ME,wet,Control	1	1	0
		SA,dry,Within site translocation	-1	0	1	ME,wet,Within site translocation	-1	0	1
		SA,dry,Between site translocation	0	-1	-1	ME,wet,Between site translocation	0	-1	-1
		Estimate	0.047	-0.502	-0.548	Estimate	-0.306	-0.929	-0.622
		Std Error	0.251	0.481	0.503	Std Error	0.276	0.256	0.308
		t Ratio	0.186	-1.043	-1.091	t Ratio	-1.111	-3.630	-2.023
		Prob>|t|	0.853	0.301	0.280	Prob>|t|	0.271	**0.001**	**0.048**
		SS	0.007	0.229	0.251	SS	0.260	2.773	0.861
Evenness E	O*E*T	SA,dry,Control	1	1	0	ME,wet,Control	1	1	0
		SA,dry,Within site translocation	-1	0	1	ME,wet,Within site translocation	-1	0	1
		SA,dry,Between site translocation	0	-1	-1	ME,wet,Between site translocation	0	-1	-1
		Estimate	-0.006	-0.292	-0.287	Estimate	-0.051	-0.303	-0.252
		Std Error	0.110	0.195	0.208	Std Error	0.131	0.112	0.136
		t Ratio	-0.052	-1.500	-1.380	t Ratio	-0.388	-2.693	-1.858
		Prob>|t|	0.959	0.141	0.175	Prob>|t|	0.700	**0.010**	0.070
		SS	0.000	0.078	0.066	SS	0.005	0.250	0.119

2.4. Discussion

As expected we found that the magnitude of climate change is important for the response of plant communities. Micro-climatic changes (translocation between slopes) induced a response in plant biomass, with, surprisingly, higher biomass on the drier slopes in the original climate. Macro-climate change, induced by translocation between climates, increased species diversity and evenness when translocated from the wetter origin to the drier climate, but no change occurred when translocated from the drier origin to the wetter climate. Species richness consistently decreased when translocated from the drier origin to the wetter climate, and increased when translocated from the wetter origin to the drier climate.

Biomass production was highest on the drier exposures irrespective of whether the plants originated from drier or wetter conditions. Intriguing, the comparison between controls showed the same pattern. These results are highly surprising, as in both climates the vegetation on the wetter slopes is denser and produces more biomass than on the drier slopes, which is a typical pattern observed when comparing vegetation aspects between slopes (e.g., Sternberg and Shoshany, 2001; Xue *et al.*, 2018; Yang, El-Kassaby and Guan, 2020). There are several factors that might play a role in the higher biomass production of the translocated soil on the drier slopes. On the sun-facing (dry) slope, radiation and temperature are slightly higher than on the shaded slope, which might have led to an increase in biomass production (Pierson, Mack and Black, 1990). Although this usually applies to temperature-limited environments, temperature can explain a small part of biomass production in water-limited regions such as those studied here (Churkina and Running, 1998). More importantly, competition with established vegetation not only for water but for light and nutrients might reduce the survival of seedlings (Lloret, Peñuelas and Estiarte, 2005). Together, this might have led to the interesting and unexpected pattern of higher biomass production on the drier slopes.

Species richness (*S*) (i.e. the amount of species present in a plot) decreased with increasing precipitation in both translocations. This corresponded with the observations of the controls, and confirmed our initial hypothesis. In dry conditions, water stress can select for the most drought-adapted species (Jump and Peñuelas, 2005), while in wetter conditions competition could select for dominant species which might outcompete the others (Kneitel and Chase, 2004). Surprisingly, species diversity (*H*) and evenness (*E*) did only respond in the same manner as richness for the soil that was translocated from wet to dry, where both species diversity and evenness were highest on the drier end of the gradient. The same pattern was observed in the comparison of the controls. However, intriguingly, for the translocation from dry to wet there was no difference in species diversity and evenness across treatments. Our results confirm the uni-model stress-competition model of Grime (1973), who observed a lower diversity (and evenness) in environments with little stress, due to increased competition, than stressful environments. Our results also correspond with the results of Byrne, Adler and Lauenroth (2017) who showed, in a climate manipulation experiment, that drought had an increasing effect on diversity in their wettest site, but not in their drier site. Additionally, they partly correspond to the reciprocal translocation study of Tomiolo, Bilton and Tielbörger (2020), who also found non-consistent patterns in a reciprocal translocation between a semi-arid and mediterranean climate. Similar to our study, only the species diversity of mediterranean origin reacted to the translocation. However, in that study the species diversity decreased when translocated from wet to dry, and the general diversity was lower in the semi-arid climate than in the mediterranean climate. In dry conditions, water stress can select for the most drought-adapted species (Jump and Peñuelas, 2005), while in wetter conditions competition could select for dominant species which might outcompete the others (Kneitel and Chase, 2004). The semi-arid soil probably has a higher amount of drought-tolerant species and little or none competitive species. As drought tolerant species are not well adapted to compete (Grime, 1973), this might explain why species diversity and evenness remained the same in the soil that was translocated from dry to wet. Competition can select for the dominant species (Kneitel and Chase, 2004) in the wetter mediterranean climate, but when there is not enough water for the competitive species to establish in the drier semi-arid climate, there might be better opportunities for drought tolerant species, resulting in an increase in species diversity and evenness (Alon and Sternberg, 2019; Nemer *et al.*, 2021).

During this two-year drought experiment, we observed an intriguing and unexpected change in biomass, i.e. higher on dry slopes, due to small micro-climatic changes, as well as contradicting changes in species diversity and evenness depending on the direction of the large macro-climatic change. The translocation from the dry origin to the wetter climate did not trigger responses, while we expected a decrease in species diversity and evenness. The translocation from the wet origin to the drier climate did, however, increase species diversity and evenness, as expected. Although micro-climate changes did not trigger much response in community composition, they might change plant-soil microbial feedbacks, which can, in the long run, indirectly influence plant composition and productivity (Gundale and Kardol, 2021). The fact that we observed community changes when translocating towards drier conditions, but not when translocating to wetter conditions indicate that the changes induced by drier years might not easily be recuperated during wetter years and that inter-annual variation in precipitation increased drought spells might trigger a tipping point that can shift the whole plant community into a different state.

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2.6. Data availability

Should the manuscript be submitted the data supporting the results will be archived in Dryad.

Contribution statement

Author	Author position	Scientific ideas %	Data generation %	Analysis / interpretation %	Paper writing %
Liesbeth van den Brink	1	20%	80%	60% / 20%	25%
Rafaella Canessa	1	20%	0%	40% / 20%	25%
Harald Neidhardt	2	0%	5%	0% / 3%	5%
Timo Knüver	3	0%	15%	0% / 3%	5%
Rodrigo S. rios	4	0%	0%	0% / 3%	5%
Alfredo Saldaña	5	0%	0%	0% / 3%	5%
Lohengrin A. Cavieres	6	0%	0%	0% / 3%	5%
Yvonne Oelmann	7	20%	0%	0% / 15%	5%
Maaike Y. Bader	7	20%	0%	0% / 15%	10%
Katja Tielbörger	7	20%	0%	0% / 15%	10%
Title of paper:		No home-field advantage in litter decomposition from the desert to temperate forest			
Status in publication process:		Submitted to Functional Ecology			

Chapter 3 – No home-field advantage in litter decomposition from the desert to temperate forest

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Abstract

Litter decomposition rates are determined by the interplay of climate, decomposer organisms and litter quality. It has been suggested that the decomposer community may be locally adapted to litter quality, providing a home-field advantage (HFA) resulting in accelerated decomposition of local compared to non-local litter, after accounting for decomposition differences due to litter quality. Although widely tested in forests, this hypothesis remains controversial and lacks a deep understanding of its generality across climates. We therefore tested the HFA hypothesis for litter decomposition in four contrasting ecosystems along an extensive climatic gradient in Chile, using a translocation experiment involving litter from 20 species. In addition to comparing mass loss, we adopted a novel way to disentangle decomposer effects from climate effects, based on loss rates of decomposable *vs*. leachable nutrient fractions. We used the ratios of N and K losses and P and K losses to unravel the relative role of biotic mineralization (N and P loss) *vs*. physical leaching (K loss, driven by precipitation) along the climate gradient. Thus, at each site, we tested whether litter mass loss, N/K loss and P/K loss presented an additional loss due to a HFA for local compared to non-local litter. Across a wide range of environments and 20 different litter types, our findings unequivocally contradicted the HFA hypothesis. A HFA effect was not found, and litter quality influenced litter decomposition much more strongly than origin or location of the litter. Our study questions the applicability of the HFA for litter decomposition and calls for more studies that include a large range of climatic conditions to understand the context-dependency of the HFA.

Keywords: decomposer ability, climate gradient; decomposition; dryland ecosystem; home-field advantage; litter mass loss; litter quality; local adaptation; nutrient leaching; nutrient loss; reciprocal translocation

3.1. Introduction

Litter decomposition, the breakdown of organic matter and the release of its elements, accounts for about half of the global soil respiration (Raich and Schlesinger, 1992; Couteaux, Bottner and Berg, 1995) and decomposition rates are therefore an important input for climate-change models (Berg and McClaugherty, 2003). Decomposition rates depend on climate, soil biota (Cornwell *et al.*, 2008; Zhang *et al.*, 2008; García-Palacios *et al.*, 2013) and litter quality (Cornwell *et al.*, 2008; Makkonen, Berg, *et al.*, 2012). Among the climatic determinants of decomposition, precipitation, soil moisture and temperature are the most relevant. Decomposition tends to increase with increasing mean annual temperature and precipitation, since warm and moist conditions stimulate decomposer activity (Zhang *et al.*, 2008). However, litter quality (e.g., litter C/N ratio, lignin content) depends on climate as well, and soil characteristics and climate determine the plant and decomposer community composition (Prentice *et al.*, 1992; García-Palacios *et al.*, 2013; Suseela and Tharayil, 2018). Therefore, biotic and abiotic determinants of decomposition are highly interconnected, posing a methodological challenge to dissecting these effects, and to reliably predict geographic patterns in decomposition rates.

A popular hypothesis related to the biotic interactions among plants and microbial decomposers is the home-field advantage (HFA; Gholz *et al.*, 2000; Ayres, Steltzer, Simmons, *et al.*, 2009). This hypothesis states that, because of the close relationship between decomposers and plant litter, decomposer communities are locally adapted to the litter of the associated plant communities (Scheu *et al.*, 2003; Ayres, Dromph and Bardgett, 2006). This “adaptation” should be manifested in accelerated decomposition when litter and decomposer communities come from the same site, compared to the decomposition of non-local litter (Gholz *et al.*, 2000; Ayres, Steltzer, Berg, *et al.*, 2009). The HFA may be one of the factors explaining litter decomposition variability across transplant studies within similar climates (Ayres, Steltzer, Berg, *et al.*, 2009). However, empirical tests of the HFA hypothesis are highly inconsistent (Austin *et al.*, 2014), with some studies confirming (Ayres, Steltzer, Berg, *et al.*, 2009; Veen *et al.*, 2015, 2019) and others contradicting (Gießelman *et al.*, 2011; St. John, Orwin and Dickie, 2011) or remaining inconclusive (Sun and Zhao, 2016; Lu *et al.*, 2017; Palozzi and Lindo, 2018) about the occurrence of a HFA in litter decomposition. These contradictions could indicate that the HFA is highly context-dependent (Veen *et al.*, 2018; Luai, Ding and Wang, 2019) and/or does not apply to all plant species and functional types. Studies on HFA usually translocate one or two litter species between different study sites within similar ecosystems or climates (e.g. Wallenstein *et al.*, 2013; Yuan *et al.*, 2019), limiting our understanding of HFA effects across ecosystems (Keiser *et al.*, 2014). Studies contrasting different climates with fully reciprocal transplant studies and using a large diversity of species to test for the HFA are rare (Veen *et al.*, 2015), yet needed to determine under which conditions a HFA occurs (Austin *et al.*, 2014).

Most of the research on litter decomposition in general and on the HFA for litter decomposition, in particular, has focused on temperate and tropical forests (e.g. Wallenstein *et al.*, 2013; Wang, Zhong and He, 2013; Veen *et al.*, 2015; Lin *et al.*, 2020). In contrast, dry ecosystems remain particularly underrepresented in litter decomposition and HFA studies, even though their documentation is key to predict ecosystem responses to global warming (Shaver *et al.*, 2000). In arid environments, strong environmental filtering creates a stabilizing selection for particular plant species and functional traits, which results in a highly homogeneous and predictable litter (e.g., sclerified or succulent leaves: Cunningham, Summerhayes and Westoby, 1999; Wright *et al.*, 2004; Griffiths and Males, 2017). This low diversity of litter types (Schlesinger and Pilmanis, 1998; Carrera and Bertiller, 2010), along with a patchy vegetation distribution and with harsh environmental conditions (e.g., low moisture availability and high radiation), could function as environmental filters that also favor a specialized soil microbial community, capable of efficiently decomposing local litter. In contrast, wet and diverse ecosystems (e.g., rainforests) produce a more variable litter, which together with fewer environmental filters, can lead to less specialized microbial communities (Gießelman *et al.*, 2011; Moskwa, Oses and Wagner, 2020), that can decompose a narrow range of litter types (Keiser *et al.*, 2014). Alternatively, one could also expect that in diverse areas with variable litter, a higher competition could lead to more specialized decomposer communities.

Local adaptation has been widely tested in plant evolutionary studies by using intraspecific reciprocal transplants of plants or seeds among sites with different environmental conditions (Macel *et al.*, 2007; Leimu and Fischer, 2008). In litter decomposition, local "adaptation" is related to an interaction between two communities of organisms, both of which are directly and indirectly affected by abiotic and biotic factors of interest. This makes studies of the HFA challenging, as confounding between several abiotic and biotic components may be expected. For example, litter quality among and within sites is highly variable, therefore the decomposability of both local and non-local species may vary drastically, independent of a possible HFA (Freschet, Aerts and Cornelissen, 2012; Makkonen, Berg, *et al.*, 2012; He *et al.*, 2016). Additionally, litter decomposition depends on the inherent ability of the microbial community of a specific site (*sensu* Keiser *et al.*, 2014), with higher ability (and thus, faster decomposition) in sites where the functional breadth of the microbial community is large (Keiser *et al.*, 2014). Moreover, decomposition also varies according to abiotic factors, which, combined, can confound possible HFA effects. Therefore, differences between litter decomposition at "home" and "away" could be dominated by climatic or general site conditions, especially when they differ substantially. An approach that is able to separate the microbial breakdown (driven by climate and HFA effects) from the purely physico-chemical leaching (driven by climate) of organic matter would allow for a comparison across different climates.

Here, we propose a novel approach to address the above-mentioned problems of detecting a HFA in different climates that makes use of the differences among elements in the way they are released from litter during decomposition. On the one hand, there are easily leachable elements, not covalently bound to organic compounds (e.g., potassium, K), and their loss is independent of microbial activity but depends on precipitation (Xu, Shibata and Enoki, 2006; Schreeg, Mack and Turner, 2013). On the other hand, structural elements such as nitrogen (N) and phosphorus (P) are lost by some physical leaching (a proportion is present as dissolved ions), but predominantly by biological decomposition, driven by the local decomposer community (Laskowski, Niklińska and Maryański, 2013; Berg, 2014). We suggest that a "local advantage" for species placed within their home site (HFA) could be detectable by an over-proportional release of the decomposer-dependent elements relative to leachable cations compared to non-local litter. Although this approach has limitations (e.g. Jasieński and Bazzaz, 1999) we think this is the only way to separate climatic and biotic influence on litter decomposition.

To address the occurrence of HFA across ecosystems, an ideal study system includes an environmental gradient, i.e. a setting with clearly different environmental conditions using highly dissimilar litter types (Veen *et al.*, 2015), in order to have large effect sizes. In this study, we conducted a fully reciprocal litterbag translocation experiment, with litter of 20 different plant species, along a very strong climatic gradient in Chile (with an almost 100-fold difference in precipitation between both ends) to test whether a HFA is prevalent across different ecosystems. In addition to calculating HFA values for litter mass loss (as used in Ayres, Steltzer, Berg, *et al.* 2009 and Keiser *et al.*, 2014), we used the proportional loss of leachable and biologically degradable elements. We expected the relative loss of K to be similar among local and non-local litter within a site, but to increase towards wetter sites because this element is mainly leached. Additionally, we tested the hypotheses that (1) local litter shows a HFA through accelerated mass loss, but particularly through accelerated N/K loss and P/K loss, and (2) the HFA is stronger on the arid end of the gradient.

3.2. Materials and methods

3.2.1 Study sites

The study was conducted at four sites along a climatic gradient in the Coastal Cordillera of Chile, spanning from the arid Atacama Desert in the north, to the humid temperate forest in the south (26°-38° S; Table 3.1, Fig. S3.1). The study sites share a homogeneous granitoid parent material but differ in micro and macro-climatic conditions (Table 3.1, Oeser *et al.* 2018): along the gradient, from north to south, mean annual temperatures during the study period decreased slightly from the (semi-)arid (18°C) to the mediterranean site (14°C) and then more sharply towards the temperate site (7°C), whereas annual precipitation during the study period increased from 22 mm in the north to 2158 mm in the south (Table 3.1). Rainfall occurs during the austral winter, between May and August. The arid site ("AR", Pan de Azúcar National Park) has a sparse cover (<5%) of desert vegetation (cacti and small succulent shrubs), the semi-arid site ("SA", Quebrada de Talca Private Reserve) presents shrubby vegetation with 30-40% cover, the mediterranean site ("ME", La Campana National Park) exhibits a sclerophyllous forest with almost full cover, and the temperate site ("TE", Nahuelbuta National Park) presents a fully covered mixed evergreen and deciduous *Nothofagus*-dominated forest. Further information on vegetation and geomorphology of the study sites can be found in Bernhard, Moskwa, *et al.* (2018) and Oeser *et al.*, (2018). At each site, six independent, representative plots were selected for the experiments, assuring a distance of 100 m or a separation by ravines.

3.2.2 Plant species and litterbag experiment

Five abundant and representative plant species per site were selected for the experiment (Table S3.1). At the temperate site, one lichen species was chosen, as it was highly abundant on trees and present in the litter layer. Freshly senesced leaves were handpicked, while still attached to the plants during the dry season preceding the experiment (December 2016-January 2017). Litter was oven-dried at only 45°C for 48h, to avoid strongly modifying the phyllosphere (Fanin *et al.*, 2021), and the dry weight of the litter that went into each litter bag was recorded separately and the bag labeled. Depending on leaf size, weight and availability of the dried litter, 1, 2 or 2.5 (±0.005) g of litter were bagged in a 2-mm polyester mesh. For those species with small leaf sizes, we used a second layer (same mesh size) to prevent losses. A pilot study indicated that there was no difference in decomposition measured when different numbers of layers were used for one species (van den Brink *et al.*, 2021).

Litter from all species was fully reciprocally translocated along the gradient and placed within each plot at each site (20 species * 6 replicate plots * 4 sites) in early May 2017 (late autumn in the southern hemisphere). The experiment was protected against animals with a poultry-wire mesh cage. All litterbags were retrieved after 12 months, placed in individual paper bags and the remaining litter was weighed after drying at 45°C for 48 h or until constant dry weight. For each sample, the percentage of litter mass loss was calculated as $100*(M_0-M_t)/M_0$, where M_0 is the initial dry mass of a sample and M_t is the remaining dry mass after 12 months of decomposition. The remaining litter from each litter bag was stored in individual paper bags and used for elemental analyses.

Table 3.1. *Information about the study sites used for our litter decomposition experiment along the Coastal Cordillera of Chile, including climatic (nearby climate stations) and in situ microclimatic data (Tomst data loggers), averaged at the site level for the study period (May 2017-May 2018). "Min" and "Max" represent the minimum and maximum monthly mean temperature.*

Climate and site coordinates	**Mean Soil Temperature (˚C) at ground level Average (min-max)**	**Annual Precipitation[1] (mm)**	**Mean Soil Moisture 0-15 cm depth (m^3/m^3)**	**Elevation (m asl)**
Arid (AR) -25.95S, -70.61W	17.6 (13.5 - 23.6)	22.0	0.12	523-529
Semi-Arid (SA) -30.05S, -71.10W	17.8 (12.4 - 22.9)	74.8	0.20	624-690
Mediterranean (ME) -32.95S, -71.10W	13.7 (7.5 - 20.3)	136	0.20	493-778
Temperate (TE) -37.81S, -73.01W	7.1 (0.7 - 14.0)	2158	0.31	1195-1290

[1] Übernickel *et al.* (2020) for arid, semi-arid and temperate; INIA (2020, (https://agrometeorologia.cl/) for mediterranean (La Cruz weather station).

3.2.3 Elemental analyses

Five subsamples per species were separated from the initial litter and analyzed to determine initial element contents per species (Table S3.1). After 12 months of decomposition, the remaining litter from each litter bag (480 in total) was analyzed to determine the remaining element contents. Each litter sample was homogenized with a planet ball mill (Pulverisette 5, Fritsch Idar-Oberstein, Germany). The samples were not washed prior to the analysis to avoid loss of leachable elements such as K. Total C and N concentrations were measured by a CNS elemental analyser (Vario EL III, Elementar Analysensysteme GmbH, Langenselbold, Germany), and were used to calculate C/N mass ratios. For details regarding detection limits and quality controls, see Table S3.2. To determine the concentrations of potassium (K) and phosphorus (P), litter samples were dissolved by an acid pressure digestion system (Loftfield PDS-6, Loftfield Analytical Solutions, Neu Eichenberg, Germany). All vessels used were soaked in 10% HCl overnight and rinsed with Millipore water prior to use. Homogenized sample material (target weight: 0.05g) was transferred into Teflon pressure beakers before adding 4mL HNO_3 conc. (65%, Merck KGaA, p.a. ≥ 98%). After heating for seven hours at 180°C, digestion solutions were filtered (MN 619 G¼ Ø185 mm, Macherey-Nagel, Düren, Germany) and diluted with Millipore water (Synergy UV ultrapure, Millipore) to a final volume of 50 ml. Digestions were analyzed by an inductively coupled plasma optical emission spectrometer (ICP-OES Optima 5300 DV, PerkinElmer, Wellesley USA) according to EN ISO 11885. Concentrations of P and K (mg kg^{-1}) were calculated and corrected for recovery rates of the certified reference material BCR®-129 (hay powder, Institute for Reference Materials and Measurements; Table S3.3). Similarly, the final element mass (mg) of a sample was calculated from the respective element concentration and the sample weight. The initial element concentration was averaged at the species level.

The percentage of relative change in element content (K loss (%), N loss (%) and P loss (%)) for a sample was calculated as 100*(averaged initial element mass - final element mass) / averaged initial element mass. Later, the relative N/K loss and relative P/K loss ratios were calculated (i.e. N loss (%)/K loss (%) and P loss (%)/K loss (%)). With K loss representing pure leaching effects and N and P losses representing partially leaching, partially biological decomposition, the relative N/K loss and relative P/K loss, therefore, give an estimate of biological decomposition, as they standardize N and P losses for leaching effects. Across sites (i.e., across the precipitation gradient), an increase in the ratios represents higher biological decomposition, as the ratios are standardized for climatic influence by the climate-dependent element (K).

Because litter of high quality is decomposed faster by the microbial decomposer community than that of low quality (Zhou, Wang et al. 2018) we additionally analyzed the influence of litter quality, grouping species into three categories based on the C/N ratios: high (C/N ratio <30), medium (C/N ratio 30-50) and low (C/N ratio >50, levels according to Zhou, Huang et al 2018, Supporting information Fig. S3.2). N/K loss and P/K loss were only weakly correlated with C/N ($r=0.19$, $p<0.001$ and $r=0.12$, $p<0.001$, respectively), and thus we assume that differences in nutrient ratios were not related to litter quality.

3.2.4 HFA calculations and statistical analyses

To calculate the HFA, we used two models published by Ayres, Steltzer, Berg, *et al.* (2009) and Keiser *et al.* (2014). The first model allows calculation of the additional decomposition at home when several species are translocated simultaneously. The second model allows distinguishing if this additional decomposition at home results from HFA, litter quality and the ability of the soil microorganisms.

Thus, we calculated the HFA as the percent of additional litter mass loss when decomposing at home versus away (Ayres, Steltzer, Berg, *et al.*, 2009) using

$\mathrm{ADHi} = \mathrm{HDDi} - \mathrm{ADDi} - \mathrm{H}$

$\mathrm{HDDi} = (\mathrm{DiI} - \mathrm{DjI}) + (\mathrm{DiI} - \mathrm{DkI}) + (\mathrm{DiI} - \mathrm{DmI})$

$\mathrm{ADDi} = (\mathrm{DiJ} - \mathrm{DjJ}) + (\mathrm{DiK} - \mathrm{DkK}) + (\mathrm{DiM} - \mathrm{DmM})$

$\mathrm{H} = \sum \mathrm{HDDi} / (\mathrm{N} - 1)$

where ADHi is the additional decomposition at home for species i; i, j, k and m are litters derived from plant species i, j, k and m, respectively; I, J, K and M are areas dominated by species i, j and k, and m respectively; D is a measure of decomposition (e.g. litter mass loss or in our study, biological decomposition via N/K and P/K losses); HDD and ADD represent home decomposition difference and away decomposition difference, respectively; H represents the total HFA for all species combined; and N represents the number of species. This method allows to determine the magnitude of additional decomposition at home for each species (or site) when more than two species (or sites) are involved in the reciprocal transplants (Ayres, Steltzer, Berg, *et al.*, 2009).

Additionally, we calculated if the additional decomposition at home is a result from litter quality, soil community ability or HFA using the model proposed by Keiser *et al.* (2014):

$$Yi = \alpha + \sum_{l=1}^{N} \boldsymbol{\beta} l \mathbf{Litter} li + \sum_{s=1}^{M} \boldsymbol{\gamma} s \mathbf{Soil} si + \sum_{h=1}^{K} \boldsymbol{\eta} h \mathbf{Home} hi + \varepsilon$$

were Y_i is the decomposition (or N/K and P/K losses) for observation i, β*l* is the litter quality of litter species l (for species 1 to N), γ*s* is the ability of the soil community s (for community 1 to M), and η*h* is the HFA of h (for home combination 1 to K). Home*h* = Litter*l* * Soil*s* when *l* and *s* are home-field pairings. Litter*l*, Soil*s* and Home*h* are dummy variables that equal 1 or 0 depending on the presence or absence of the litter species, soil community or home combination, respectively. The parameters to be estimated are β*l* for the effect of litter quality, *γs* for the effect of decomposer ability and η*h* for the effect of HFA (Keiser *et al.*, 2014).

To analyze the general patterns of litter decomposition and nutrient losses across sites and species, we used linear mixed models with least-squares means testing the response of litter mass loss (%), K loss (%) (to estimate leaching differences among species) as well as relative N/K loss and relative P/K loss to litter origin, site of decomposition (i.e. differences among ecosystems), and litter quality. We used site, origin, litter quality (all as categorical variables) and the interactions site * origin and site * litter quality as fixed factors, and species as a random factor, with Tukey HSD post-hoc tests per site.

To analyze the home-field advantage hypothesis along the gradient, we calculated the additional decomposition at home (ADH) across sites according to Ayres, Steltzer, Berg, *et al.* (2009) and then calculated which part of the ADH could be explained by the effect of the litter quality, the micro-organism ability and HFA according to Keiser *et al.* (2014), for mass loss, the relative N/K loss and relative P/K loss. *Araucaria araucana* (Molina) K. Koch was excluded from the relative N/K loss and relative P/K loss analyses, as its initial K content was very low and this led to extreme values of these ratios (i.e. relative N/K loss: -2.24 to 21.7; relative P/K loss: -18.7 to 1.59).

3.3. Results

3.3.1 Decomposition across sites

Overall, litter mass loss (%) increased from the arid (AR) to the temperate (TE) site, i.e. along the precipitation gradient (Fig. S3.3a). However, at each site, species with arid origin decomposed significantly faster than species from the mediterranean and the TE, whereas species from the semi-arid (SA) decomposed faster than species from TE. Species originating from the mediterranean and temperate sites consistently decomposed the slowest (Fig. S3.3a).

3.3.2 Litter nutrient loss

Potassium (K) loss (%) after 12 months of decomposition was considerable and proportionally higher than overall mass loss (88% averaged over species and sites), with higher losses at the wetter than at the drier sites (96% at TE; 90% at ME; 83% at semi-arid and 79% at AR). Losses were similar among litter from all origins at the arid and semi-arid sites, while at the mediterranean and temperate sites the loss of K was significantly lower for litter from the temperate site, compared to litter from other origins (Fig. S3.3b). These results, i.e. the increased loss of K towards wetter sites independently of the litter origin, is an indication that this element is indeed mainly leached. Nitrogen (N) and phosphorus (P) loss (32 and 58% on average across species and sites, respectively) also varied among sites and with litter quality (Fig. S3.3c and d, Table S3.3).

Relative N/K loss and P/K loss ratios were significantly higher at the temperate compared to the other climates, indicating that microbial decomposition was highest at this wettest site, as expected (Fig. S3.3e, f, Table S3.2). Additionally, we observed a non-significant but consistent pattern along the gradient of high relative N/K loss ratios in the litter from the dry site to lower ratios in litter from the wetter site (Fig. S3.3f).

3.3.3 Additional decomposition at home, litter quality, soil community ability and home-field advantage

The combined litter from each site did not show any additional decomposition at home (ADH) in terms of mass loss, N/K loss or P/K loss (Fig. 3.1). ADH values were even negative at all sites when using litter mass loss as a decomposition variable (Fig. 3.1a). For relative N/K loss, the arid and the temperate sites showed negative ADH values, whereas the semi-arid and the mediterranean sites did not differ from zero (Fig. 3.1b). When using the relative P/K loss, the ADH value at the temperate site was also negative, whereas at all other sites they did not differ from zero (Fig. 3.1c).

When the ADH was calculated based on individual species mass loss, 16 of 19 species (84%) showed faster decomposition away than at home (Fig. S3.4a). The three species that decomposed faster at home than away were *Senna cumingii* (from the semi-arid site) and *Aristeguietia salvia* and *Cestrum parqui* from the mediterranean site. The ADH of species calculated based on N loss/K loss ratios yielded more variable results, with 12 species (63%) decomposing faster away than at home (Fig. S3.4b). All species from the arid site showed this pattern, whereas some species from the semi-arid and mediterranean sites showed a small ADH effect. *Quillaja saponaria* from the mediterranean site showed the highest ADH effect. One species from the temperate site presented a small ADH effect. ADH of species calculated based on P loss/K loss ratios exhibited that 15 of 19 species (79%), decomposition faster away compared to at home (Fig. S3.4c). One species from the arid, one of the semi-arid and three from the mediterranean showed ADH effects, although the ADH in the mediterranean species was small.

Using the model of Keiser *et al.* (2014), we observed no HFA along the gradient (Fig. 3.1d-f, Table 3.2). Interestingly, according to this model, the arid and temperate sites showed that their litter decomposed significantly better away from home when litter mass loss was used as a proxy of decomposition (Fig. 3.1d, Table 3.2). The relative N/K and P/K losses also showed no evidence of HFA, indicated by either negative or null values of HFA (Fig. 3.1e and f). Litter quality had a large influence on the decomposition along the gradient: significantly positive for both the arid and semi-arid site, but significantly negative for the litter from the mediterranean and temperate site (Fig. 3.1g, Table 3.2). The C/N ratios of the litter show that along this gradient there is a consistent decrease in initial litter quality (Fig. S3.2). When using the same model as for the mass loss but using the relative N/K loss as a response variable, litter quality effects (*sensu* Keiser *et al.*, 2014) showed the same pattern as for mass loss (i.e. a higher litter quality effect at the arid and semi-arid sites, and lower at the mediterranean and temperate sites, Fig. 3.1h). When we evaluated the relative P/K loss, the effect of litter quality for the arid and mediterranean litter seemed lower, and for the temperate litter higher (Fig. 3.1i). The ability of the soil community increased along the gradient, and was negative in the arid and semi-arid sites (where litter quality is high) and positive in the temperate site (where the litter is more recalcitrant) (Fig. 3.1j-l, Table 3.2).

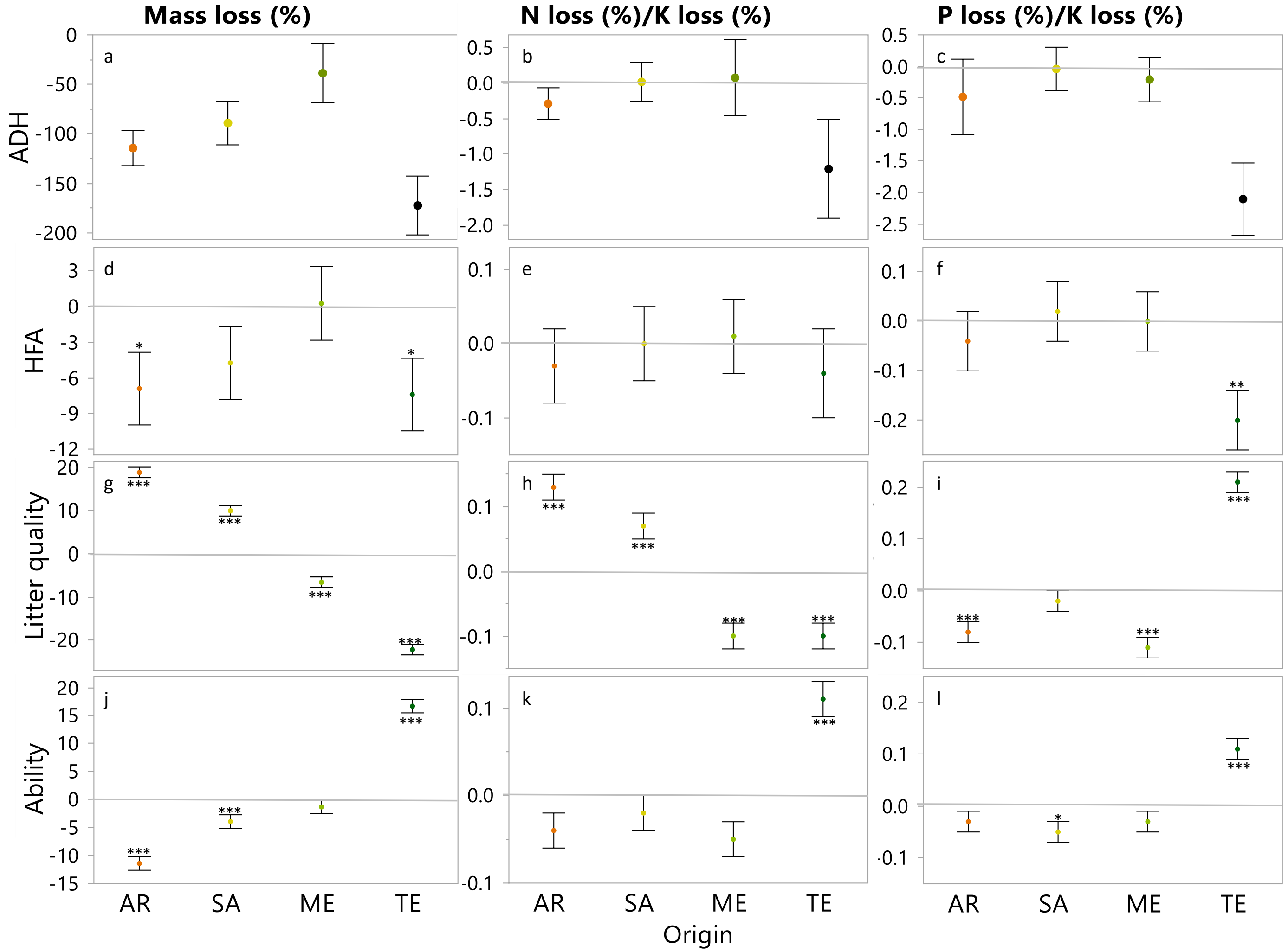

Figure 3.1. *Home-field advantage (HFA) parameter estimates (mean ±SE), calculated according to Ayres, Steltzer, Berg, et al. (2009) (ADH, panels a, b and c) and Keiser et al. (2014) (HFA, panels d, e, f; litter quality, panels g, h, i; and ability, panels j, k, l) with mass loss (left), N loss (%)/K loss (%) (middle) and P loss (%)/K loss (%) (right). Stars indicate significance according to the derived model (p<0.05 *; p<0.001 ***). Data represent values of 20 species at each site for mass loss, and 19 species for N loss (%)/K loss and P loss (%)/K loss.*

Table 3.2. *Parameter estimates (mean ±SE) calculated according* Keiser et al. (2014). *Significant values are bold.*

	Mass loss		N loss/K loss		P loss/K loss	
Variable	Parameter Estimate	P-value	Parameter Estimate	P-value	Parameter Estimate	P-value
Intercept	40.55 ± 0.65	**<.0001**	0.37 ± 0.01	**<.0001**	0.65 ± 0.01	**<.0001**
Litterquality: AR	18.83 ± 1.20	**<.0001**	0.13 ± 0.02	**<.0001**	-0.08 ± 0.02	**0.0005**
Litterquality: SA	9.94 ± 1.20	**<.0001**	0.07 ± 0.02	**0.0006**	-0.02 ± 0.02	0.4229
Litterquality: ME	-6.57 ± 1.21	**<.0001**	-0.10 ± 0.02	**<.0001**	-0.11 ± 0.02	**<.0001**
Litterquality: TE	-22.21 ± 1.20	**<.0001**	-0.10 ± 0.02	**<.0001**	0.21 ± 0.02	**<.0001**
Ability: AR	-11.42 ± 1.20	**<.0001**	-0.04 ± 0.02	0.0615	-0.03 ± 0.02	0.2611
Ability: SA	-3.93 ± 1.21	**0.0012**	-0.02 ± 0.02	0.2413	-0.05 ± 0.02	**0.0354**
Ability: ME	-1.32 ± 1.20	0.2719	-0.05 ± 0.02	**0.0330**	-0.03 ± 0.02	0.1698
Ability: TE	16.68 ± 1.20	**<.0001**	0.11 ± 0.02	**<.0001**	0.11 ± 0.02	**<.0001**
HFA: AR	-6.91 ± 3.06	**0.0246**	-0.03 ± 0.05	0.6156	-0.04 ± 0.06	0.5090
HFA: SA	-4.75 ± 3.07	0.1223	0.00 ± 0.05	0.9638	0.02 ± 0.06	0.7442
HFA: ME	0.27 ± 3.10	0.9315	0.01 ± 0.05	0.8564	0.00 ± 0.06	0.9602
HFA: TE	-7.41 ± 3.06	**0.0158**	-0.04 ± 0.06	0.4737	-0.20 ± 0.06	**0.0015**

3.4. Discussion

We tested the home-field advantage (HFA) hypothesis for litter decomposition across four different ecosystems along a long climate gradient in Chile, using 20 species of different litter quality. By using two common models for studying HFA effects in litter decomposition (Ayres, Steltzer, Berg, *et al.*, 2009; Keiser *et al.*, 2014), we found no support for the HFA hypothesis for litter decomposition along our climatic gradient. Neither traditional litter mass loss nor our proxy for biological decomposition showed that local litter decomposed faster than expected in its home site, in accordance with several previous studies (e.g. Gholz *et al.*, 2000; Ayres, Dromph and Bardgett, 2006; St. John, Orwin and Dickie, 2011; Makkonen, Berg, *et al.*, 2012; Wallenstein *et al.*, 2013; Veen *et al.*, 2015; Sun and Zhao, 2016; Lu *et al.*, 2017; Fujii *et al.*, 2018). Instead, most litter decomposed faster with increasing precipitation along the gradient.

3.4.1 Additional decomposition at home and home-field advantage across ecosystems

Previous studies have mainly tested the HFA hypothesis using translocations of litter within similar climates (e.g. Gholz *et al.*, 2000; Ayres, Dromph and Bardgett, 2006; St. John, Orwin and Dickie, 2011; Wallenstein *et al.*, 2013; Veen *et al.*, 2015; Sun and Zhao, 2016; Lu *et al.*, 2017 but see Makkonen, Berg, *et al.*, 2012; Fujii *et al.*, 2018). While this design has the advantage that there is no confounding between climate and home-site effects, it implies that the "home advantage" cannot be compared across largely different environments. Our study addressed this aspect, as it covered a wide range of ecosystems, including semi-arid and arid sites which have rarely been studied to test a HFA (Austin *et al.*, 2014). We found that all litter types exhibited a consistent ranking in decomposition across all the studied ecosystems, i.e. litter decomposed faster towards wetter climates, as reported in many other across-ecosystem studies (e.g. Aerts, 1997; Zhang *et al.*, 2008). Along this gradient, we expected to find, if existing, a decreasing HFA, considering the stressful conditions of the arid climates, that could force a strong selection of decomposers. Our results showed, however, no support for a HFA in litter decomposition along our climate gradient, similar to other studies (e.g. Makkonen, Berg, *et al.*, 2012; Fujii *et al.*, 2018). Although a HFA may occur in specific situations or for specific species, our study suggests that it is not a prevalent phenomenon across ecosystems. HFAs seem to specifically occur in mono-dominant stands (Ayres, Steltzer, Berg, *et al.*, 2009; Ayres, Steltzer, Simmons, *et al.*, 2009), and likely only occur if a specific decomposer is present, e.g. specific fungi (Veen *et al.*, 2019). However, in most ecosystems litter is provided by a mix of plant species, where decomposer communities likely contain decomposers for all litter types and are therefore more generalistic (Gießelman *et al.*, 2011; Moskwa, Oses and Wagner, 2020). This was the situation at all our sites except the arid site, where single-species plant patches were dominant, but we did not find support for a HFA there either. In this type of ecosystem, a pronounced microsite variation is possible and thus, to capture this soil heterogeneity within a site we used six plots per site. Even though there might be differences between the plots due to microclimatic differences (Bradford *et al.*, 2017), these are much smaller than the differences between the sites.

Precipitation can be a confounding factor in studies of HFA along gradients, as litter mass loss increases not only through organic decomposition but also through leaching (Gholz *et al.*, 2000; Powers *et al.*, 2009). Therefore, to better evaluate the HFA hypothesis, it is helpful to disentangle the effects of climate and decomposers on litter decomposition. We did this by contrasting losses of leachable elements (here: K) against losses of elements released by biological decomposition (here: N and P). This approach is, to our knowledge, implemented for the first time here. The increasing loss of potassium (K) along the precipitation gradient was constant among species within sites and thus nicely depicts that this element was mainly lost by physical leaching (Xu, Shibata and Enoki, 2006; Schreeg, Mack and Turner, 2013), a process less affected by litter quality than biological decomposition. We expected that, if a HFA is prevalent, the relative N/K loss and relative P/K loss would be higher than expected for local species (i.e. an accelerated biological decomposition at home, ADH), and that this would show as a positive HFA in the analysis *sensu* Keiser *et al.* (2014). However, this was not the case, which shows the lack of HFA in our climatic gradient, while it supports the idea that HFA effects on litter decomposition are species specific (Sun and Zhao, 2016; Lu *et al.*, 2017; Palozzi and Lindo, 2018).

Another climatic factor that could influence decomposition and varies along our gradient is solar radiation. At our arid sites, photodecomposition could have played a role besides biological decomposition (Austin, 2011). However, Canessa *et al.* (2021) showed that photodecomposition plays a minor role compared to biological decomposition at these sites, as lignin-rich litter did not decompose faster than expected without photodecomposition (Austin and Ballaré, 2010). Thus, we consider that our results, which consistently showed no evidence to support the HFA hypothesis at any of our sites, were not strongly affected by this factor.

3.4.2 Ability of decomposers and litter quality effects on decomposition

The lack of a HFA could be attributed to the ability of the microbial community to rapidly shift in species composition or to adjust physiologically or evolutionarily in the presence of different resources (e.g., functionally different litter; MacLean, 2005; Gießelman *et al.*, 2011; St. John, Orwin and Dickie, 2011), even in mono-dominant vegetation patches like at our arid site. Given the high colonization and diversification rates of microorganisms, it is thought that microbial communities are ubiquitous ("everything is everywhere", Becking, 1934 in Martiny *et al.*, 2006) and that a certain environment selects only temporarily for a particular microbial assemblage (De Wit and Bouvier, 2006). Our findings support this hypothesis and indicate that decomposer communities (especially the bacterial community) can quickly re-adjust when alternative resources are available.

Our results show that the species rankings based on mass loss, relative N/K loss and relative P/K loss were highly consistent along our climate gradient. Makkonen, Berg, *et al.* (2012), in their reciprocal translocation experiment, also found that the ranking of plant species, based on their mass loss, remained the same in all climates. Moreover, litter quality had a significant effect on litter decomposition in the calculations *sensu* Keiser *et al.* (2014). Thus, our results support the hypothesis that, instead of a HFA, there is a litter-quality advantage (i.e. high-quality litter decomposes faster).

Although decomposer ability to break down recalcitrant litter increases with precipitation along our gradient, recalcitrant litter might still decompose better in nutrient-rich away sites, while litter with high quality can be decomposed everywhere (Palozzi and Lindo, 2018). We would have expected a higher HFA for low-quality litter types, which was not particularly the case in our study (i.e. most of the species that showed a positive HFA are not of low quality, see Fig. S3.2 and S3.4). We found that the ability correlated negatively with litter quality, i.e. low ability of the decomposer community at the site where the litter was of the highest quality, and high ability at the site where the litter was of the lowest quality. This might be explained by the functional breadth hypothesis, i.e. the functional ability of decomposer organisms is wider when litter is more recalcitrant (Keiser *et al.*, 2014).

In our study, local litter was not favored by local decomposer communities but was instead decomposed as expected based on climate (slow at the arid site, quick at the temperate site) and litter quality (slow for low-quality and quick for high-quality litter). The large range of environmental conditions, together with the fact that we separated decomposition into leachable and decomposer-dependent fractions, allowed us to rigorously test for a HFA. It has been shown before that HFA in litter decomposition is very context-dependent (Sun and Zhao, 2016; Lu *et al.*, 2017; Palozzi and Lindo, 2018). Although Ayres, Steltzer, Berg, *et al.* (2009) and Keiser *et al.* (2014) have developed useful models to quantify the HFA for litter decomposition, we think that the additional distinction between biological and leaching processes can help future studies of litter decomposition to gain more insights in these differences. Ongoing shifts in climate and land use will cause direct changes in decomposition conditions as well as changes in plant and decomposer communities. For example, the introduction of foreign litter could naturally occur when plant species invade new ecosystems (Simberloff, 2015). Therefore, a deeper understanding of the relative importance of biotic versus abiotic controls on decomposition is needed to correctly predict the feedback from litter decomposition to atmospheric CO_2 concentrations and climate. In the light of our findings, we expect decomposer communities to adjust to climate-change, litter quality or species composition shifts, resulting in changes in decomposition rates and carbon and nutrient cycles. However, the direction of these changes might not be as easily predictable as assumed by the general HFA hypothesis.

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3.6. Data availability

Data will be made publicly available at the Dryad Digital Repository should the manuscript be accepted.

Contribution statement

Author	Author position	Scientific ideas %	Data generation %	Analysis / interpretation %	Paper writing %
Liesbeth van den Brink	1	20%	85%	100% / 25%	60%
Rafaella Canessa	2	0%	0%	0% /10%	8%
Maaike Y. Bader	3	5%	0%	0% /10%	5%
Harald Neidhardt	4	5%	15%	0% /10%	5%
Yvonne Oelmann	5	20%	0%	0% /10%	5%
Lohengrin A. Cavieres	6	0%	0%	0% /10%	2%
Katja Tielbörger	7	50%	0%	0% / 25%	15%
Title of paper:		Space cannot substitute for time – an integrated experimental assessment of climate-change effects on litter decomposition			
Status in publication process:		Ready for submission (reviewed in Ecology Letters)			

Chapter 4 – Space cannot substitute for time – an integrated experimental assessment of climate-change effects on litter decomposition

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Abstract

Litter decomposition, a key component of the global carbon cycle, is greatly affected by climate. Unfortunately, our current understanding of climate-change effects on decomposition stems mainly from space-for-time studies along climate gradients, where biotic and climatic effects on litter decomposition are confounded. Experimental studies separating indirect from direct climate effects are needed that test the validity of the space-for-time approach. Here, we combined large- and small scale reciprocal litter translocations, *in situ* precipitation manipulation, and a prominent climate gradient for studying drought effects on litter decomposition. Interestingly, all experiments indicated clear positive effects of precipitation on decomposition, but the space-for-time approach indicated the opposite, due to indirect climate effects on litter quality. This indicates that space cannot substitute for time and highlights the need for experimental evidence in litter decomposition studies. Such evidence would improve predictions of models of the global carbon cycle that include interactions between climate and vegetation.

Keywords: Carbon cycling, climate change, drought, litter mass loss, precipitation, reciprocal translocation, rainout shelters, space-for-time.

4.1. Introduction

Climate is changing alarmingly quick with possibly dramatic consequences for single species to global biogeochemical cycles (IPCC, 2014; Ripple *et al.*, 2020). The global carbon cycle is strongly affected by both anthropogenic and natural processes. Litter decomposition, for example, releases roughly the same amount of CO_2 into the atmosphere as anthropogenic CO_2 production (Raich and Schlesinger, 1992; Couteaux, Bottner and Berg, 1995), and is therefore highly important for the understanding of global carbon and nutrient cycles (Berg and McClaugherty, 2003). However, since biological processes themselves are affected by climate change directly and indirectly (Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008; Suding *et al.*, 2008), modeling the carbon cycle is highly complex and uncertain (Ostle *et al.*, 2009). Direct effects have been studied a lot, mostly with respect to precipitation (or humidity) and temperature (Couteaux, Bottner and

Berg, 1995). These studies reveal unequivocally that in wet (Aerts, 1997; Yahdjian, Sala and Austin, 2006; Suseela and Tharayil, 2018) and warm climates (Couteaux, Bottner and Berg, 1995) decomposition is faster than in dry and cold environments (Stark and Firestone, 1995; Chapin III, Matson and Vitousek, 2011; Baker *et al.*, 2018). Indirect effects of climate on decomposition operate via the vegetation, e.g. via growth rates, litter quality, or plant species composition (Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008; Suseela and Tharayil, 2018).

An important indirect effect of climate on decomposition is via plant litter quality, i.e. the combination of chemical (holocellulose:lignin ratio, carbon (C)/nitrogen (N) content, and phosphorus (P) concentration; Cornwell *et al.*, 2008; Graça and Poquet, 2014) and physiognomic traits (leaf dry matter content, specific leaf area (SLA), and leaf toughness; Meentemeyer, 1978; Couteaux, Bottner and Berg, 1995; Hobbie, 1996; Aerts, 1997; Cornwell *et al.*, 2008; Andresen *et al.*, 2010; Melillo, Aber and Muratore, 2014). Because many of these leaf traits may also represent specific adaptations to climatic conditions, they strongly vary among different climates (Graça and Poquet, 2014). For example, small, tough leaves with thick cuticulae represent well-known adaptations to drought and are thus common in plants inhabiting arid environments (Anonymous, 1932; Cunningham, Summerhayes and Westoby, 1999; Wright *et al.*, 2004). Therefore, plants in dry climates usually have a lower litter quality (Wright *et al.*, 2004; Graça and Poquet, 2014; Pugnaire *et al.*, 2019; Xu *et al.*, 2020) which inhibits break down by the decomposer community (Pérez-Harguindeguy *et al.*, 2000; Zhang *et al.*, 2008). *Vice-versa*, in wetter climates, plant species often exhibit 'soft' leaves, low C/N-ratio, and high SLA (Wright *et al.*, 2004) because costly adaptations to drought are not needed, however, the vegetation is denser, and light is scarcer, which results in leaves with high SLA to increase photosynthetic ability (Kunstler *et al.*, 2016; Gruntman *et al.*, 2017). Overall, it has been repeatedly concluded that along climatic gradients from dry to wet conditions, leaf traits should change, from small, spiny, tough leaves with low SLA and low litter quality with high lignin and carbon content and low phosphorus content to soft leaves with opposite traits (Wright, Reich and Westoby, 2001; Wright *et al.*, 2004). This suggests that direct and indirect climate effects on litter decomposition amplify each other, i.e. decomposition will be slower in dry climates due to lower litter quality (Aerts, 1997) and to less precipitation (Austin and Vitousek, 2000).

However, while these assumptions are backed up by many previous studies (Aerts, 1997; Zhang *et al.*, 2008) exceptions to this rule have been found, too (Pérez-Harguindeguy *et al.*, 2007). This is because plant litter quality is also determined by factors that operate independently of climate, like biogeographic history, biotic interactions, nutrient availability, or disturbance (Woodward and Diament, 1991; Chapman *et al.*, 2003; Wiens and Donoghue, 2004; Chapman, 2006; Bhalawe *et al.*, 2012; Zhu *et al.*, 2016). Despite these exceptions, dynamic vegetation models (e.g. LPJ, MC1, HYBRID, ORCHIDEE and TRIFFID) or terrestrial carbon cycle models (e.g. ED, CTEM), and their derivatives assume that conditions in climatically similar ecosystems have selected for plants with similar traits (and therefore similar decomposition) and that they therefore will respond similarly to climate change. These models have commonly assumed increasing litter decomposition rates with wetter climates (Patton, 1996; Friend *et al.*, 1997; Cox, 2001; Smith, 2001). If not backed up by solid evidence, the generalization used in the models can cause serious dissimilarities between the modeled and the real climate-change effects, especially as decomposition accounts for approximately half of the CO_2 release into the atmosphere (Raich and Schlesinger, 1992; Couteaux, Bottner and Berg, 1995).

Ecological climate impact studies have used several different approaches, and each has advantages and disadvantages:

Space-for-time approach: observations along climatic gradients. This approach is commonly applied and is based on the same assumption as the above models. It uses observations along natural gradients as a proxy for environmental change over time. For example, observations along a temperature gradient are supposed to reflect the response of single sites to increasing temperatures in time. Several litterbag experiments have used natural climatic gradients (mostly temperature) to focus on differences in decomposition of local litter (Meentemeyer, 1978; Berg *et al.*, 1993; Couteaux, Bottner and Berg, 1995; Aerts, 1997; Fan *et al.*, 2014), and found that climate was very important for litter decomposition. However, the species, and therefore the litter, in each climate differed, making a comparison among sites extremely challenging (Parton *et al.*, 2007; Cornwell *et al.*, 2008; Currie *et al.*, 2010; Makkonen, Berg, *et al.*, 2012; Suseela and Tharayil, 2018). To overcome this inequality of native litter, standard litter (e.g. tea or wooden dowels) can be decomposed in different climates (e.g. Pérez-Harguindeguy *et al.*, 2007; Djukic *et al.*, 2018). However, this method only addresses short-term climate effects without considering the role of litter quality. A "common garden" approach (Dorrepaal *et al.*, 2005; Cornwell *et al.*, 2008; T. Freschet, Aerts and Cornelissen, 2012), using litter from different sites decomposing in one standardized climate, can confirm the influence of litter quality on decomposition, but does not reflect the decomposition of that litter in their local habitat ("at home"). Overall, the space-for time approach is intuitive and can be applied for many species and over large scales, but as it is based on correlations, it does not yield causal relationships between decomposition rates and climate change. Most importantly, climate effects are confounded with other environmental or evolutionary processes.

Experiment-for-time: reciprocal translocations along gradients. Reciprocal translocations along climate gradients (litter collected at each site is decomposed at each site of a climate gradient) combine common gardens with the space-for-time approach, overcoming most of the drawbacks of both. For example, by using litter from different origins at different climates, the effect of litter identity (i.e. species) and climate can be separated by testing whether litter origin or climate is more important. Such studies are relatively abundant, albeit less than the space-for-time approach. Reciprocal translocations have been used to test how climatic effects (e.g. precipitation, temperature, or actual evapotranspiration) and litter chemistry influence decomposition (e.g. Aerts, 1997; Makkonen, Berg, *et al.*, 2012; Araujo and Austin, 2015; Portillo-Estrada *et al.*, 2016). These studies confirmed that climate and litter quality are the major drivers of decomposition, although their relative importance varies over time (Canessa *et al.*, 2021). While such studies are highly valuable, they do not control for the specific microbial community which can mediate litter quality and climate effects (García-Palacios *et al.*, 2013), or climatic variables (i.e. not direct manipulation).

Experiment-for-time approach: *in situ* climate manipulations. Field experiments can manipulate the climate factor of interest (e.g. precipitation, temperature) while the response of the ecological factor (e.g. decomposition) is studied. *In situ* climate experiments of litter decomposition are not very common, and have studied the effect of manipulated precipitation (e.g. Yahdjian, Sala and Austin, 2006; Andresen *et al.*, 2010; Zhou *et al.*, 2018) or temperature (e.g. Andresen *et al.*, 2010). Most of these studies found that reduced precipitation significantly reduced litter decomposition (Yahdjian and Sala, 2002; Brandt, King and Milchunas, 2007; Andresen *et al.*, 2010; Santonja *et al.*, 2017; Zheng *et al.*, 2017; Zhou *et al.*, 2018), and due to the experimental approach, these relationships are causal However, their mechanistic insight comes at a cost. As they usually manipulate only one factor, they may have side effects (Leuzinger *et al.*, 2011; Kreyling *et al.*, 2017) and be less 'realistic' than observations. They are also costly and often restricted to one site. Furthermore, it is unclear whether short-term mechanistic relationships between independent (e.g. climate) and dependent (e.g. ecosystem process) variables can be extrapolated to longer time scales.

Tielbörger *et al.* (2014) developed an approach that combines the best of all the above-mentioned approaches and that directly tests for the validity of the space-for-time approach. This approach requires a multi-site setup along a climate gradient. The rationale of the approach is that by manipulating climate at a given site and including an adjacent site with similar specific climatic conditions as within the manipulation, the gradient can be used directly as a hypothesis for the direction and magnitude of change within the climate manipulations. Thus, this approach has two controls, an *in situ* control where all environmental conditions, except for the manipulated one, are similar, and a spatial control where specific climatic conditions are similar. By applying this approach to an aridity gradient in Israel, Tielbörger et al. (2014) showed a large mismatch between space (plant communities differed largely among sites) and experimental drought (no effect in species composition, abundance or productivity).

Here, we expanded this approach with reciprocal transplants to study climate change effects on litter decomposition along an even more extreme climate gradient. We combined the space-for-time observations with a) a fully reciprocal translocation of native and a standard litter, b) a small-scale humidity gradient by comparing drier with wetter expositions, and c) *in situ* drought treatments, simulating precipitation conditions of the adjacent drier site. This allowed us to directly and experimentally test for the applicability of space-for-time approaches in carbon cycle studies, and to separate the effects of climate alone from the indirect climatic effects on litter quality.

We used a prominent climate gradient ranging from extremely arid to wet temperate conditions in the Chilean coastal cordillera. Because litter decomposition correlates very weakly to air temperature above 6.7 °C (Bradford *et al.*, 2016), and because regional climate scenarios predict a decrease in precipitation (IPCC, 2014) we focused on the influence of drought on litter decomposition. Our gradient encompasses a 100-fold difference in precipitation, ensuring a large effect size.

We tested the overarching hypothesis that space can substitute for time. Namely, we assumed that *in situ* litter decomposition accelerates from arid to humid climates due to a) climatic conditions (i.e. more humidity) and b) higher litter quality at wetter sites. We expected that the higher decomposition under wetter conditions would be reflected in the decomposition of translocated litter among sites, between expositions within sites, as well as in the experimentally manipulated plots.

4.2. Materials and methods

4.2.1. Study sites

Our study was conducted in Chile at four sites along a large climate gradient that runs from the arid Atacama Desert to the humid temperate forest (26° - 38° S, Table S4.1, Figure 4.1). The sites were selected to be within the same geographical unit (the Chilean coastal cordillera) and share a common granitoid bedrock (Oeser *et al.*, 2018). Thus, the main difference between the four sites is the climate, with increasing precipitation from north to south. With the exception of the (cooler) temperate site, average temperatures were relatively similar, whereas annual precipitation (AP) increased along the gradient and differed approximately 100-fold between the wettest (2158 mm y^{-1}) and the driest (22 mm y^{-1}) site (Figure 4.1a, Table 4.1, for additional information see: Bernhard et al., 2018; Oeser et al., 2018).

In the northernmost, arid site (Parque Nacional Pan de Azúcar), vegetation cover is low (<5%) and dominated by succulent species and shrubs, though during years with rain events an important cover of annuals and perennial geophytes emerges (Rundel, Dillon and Palma, 1996). The second site is a semi-arid shrub-land (Reserva Privada Quebrada de Talca) which has a vegetation cover of 30-40%, consisting of shrubs (mainly Asteraceae), cacti, low trees and geophyte perennials (Squeo, Tracol, *et al.*, 2008). In the third site, the mediterranean dry sclerophyllous shrub-land/forest (Parque Nacional La Campana), vegetation cover is almost 100% and contains evergreen trees, shrubs, palms, herbs and grasses (Hauenstein, 2012). The most southern site is situated in a humid temperate forest (Parque Nacional Nahuelbuta), with a full vegetation cover dominated by tall trees (mainly *Araucaria araucana* (Molina) K. Koch and *Nothofagus* species), bamboo, shrubs, grasses and annual herbs (Bernhard et al., 2018; Oeser et al., 2018; Wolodarsky-Franke & Diaz Herrera, 2011).

Within each site, three dry (north facing) and three wet (south facing) representative expositions were chosen to study the influence of differences in soil moisture on litter decomposition. Their independence was ensured by a distance of at least 100m between plots with a similar aspect or by separation by small ravines.

4.2.2. Drought manipulation with rainout shelters

We installed drought treatments (*sensu* Yahdjian and Sala, 2002) on wet and the dry expositions at the semi-arid and mediterranean sites. At the semi-arid site, where plants were small, the shelters covered representative sections of the overall vegetation. At the mediterranean site, the shelters were erected between large trees, but included small shrubs and herbaceous vegetation.

The treatment reduced the precipitation by 75%, approximating both the mean annual precipitation of the adjacent drier site (arid and semi-arid, respectively. Figure 4.1b) and scenarios for future extreme droughts events in the region (Quintana and Aceituno, 2012; Garreaud *et al.*, 2017). Continuous soil moisture measurements indicated that the treatments were highly effective in reducing soil moisture (i.e. 15-35%) and that these drought conditions were similar to soil moisture at the adjacent drier site (Supplementary data: Figure S4.1, Table

S4.2). Our data also showed very small side-effects of the shelters on soil temperature (on average +0.1°C compared to controls).

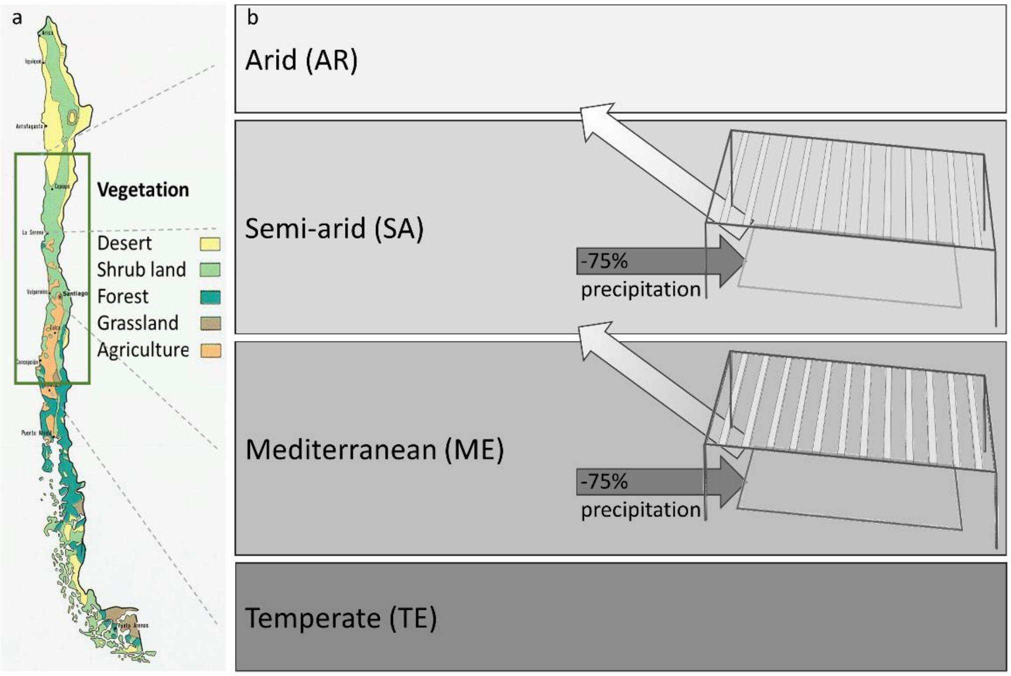

Figure 4.1. *Climate gradient and experimental drought setup. Shown is a land-cover map showing the study site locations (a) (U.S. Central Intelligence Agency, 1972), and the experimental setup of the drought experiment (b). The rainout shelters reduce the percentage of rain which reaches the plot under the rainout shelter (dark arrow) by 75%, which mimics the average annual precipitation that falls in the adjacent drier site (light arrows). The drought treatment therefore has two controls: one at the same site, where climate is the same, and one at the drier adjacent site, where precipitation is similar as under the rainout shelter, but other aspects of the climate and environment are different. The setup included three replicate plots (three control and three experimental drought treatments) at both exposures (dry and wet) at each climate (semi-arid and mediterranean).*

4.2.3. Species selection and litter bag preparation

At each site, we selected five abundant and representative native species. Senescent leaves, attached to the plant to minimize contamination with on-site soil microbes (Stone, 1987), were collected during the dry season (December 2016 - January 2017, Table S4.3). For evergreen species, green leaves were collected. In addition, Lipton® green tea (*Camellia sinensis*, EAN Nr.: 8 722700 055525, from here on “tea”) was used as a standard litter (Keuskamp *et al.*, 2013; Djukic *et al.*, 2018) to help separating litter origin and climate effects. The collected litter and tea bags were dried to a stable weight for 72 hours at 40°C, and depending on leaf size, leaf weight and availability of dry litter 1, 2 or 2.5 g (± 0.005 g the exact initial weight was recorded) were bagged in 2 mm polyester mesh. When leaves were very small, brittle, or had the tendency to pass through the mesh, an additional layer of 2 mm mesh was used. No significant differences in decomposition were detected when both types of bags were used (Supplementary data: Table

S4.4). Litterbags and teabags were placed at ground level in the field between 11 and 29 May 2017, just before the first rains of the season (May – August).

4.2.4. Reciprocal translocations along the gradient (between and within sites)

Litterbags of all species were fully reciprocally distributed along the climate gradient and placed in the independent plots on dry and wet exposition (20 species * 3 replicates * 3 retrievals * 3 plots * 2 expositions * 4 sites), together with two tea bags per plot (2 replicates * 3 retrievals * 3 plots * 2 expositions * 4 sites). Litter and tea bags were collected at three points in time to account for the temporal dynamics of decomposition: after 3, 6, and 12 months (93±1; 195±4; 366±5 days), respectively. Due to a snow event at the temperate site, the 3-month batch was retrieved after 9 months (280.5±0.5 days). Overall, 4320 litterbags and 144 tea bags were used in the reciprocal translocations.

4.2.5 Decomposition in in situ climate manipulations

Only local species (species occurring at the manipulated sites) were used for this experiment. Litterbags (5 species * 3 replicates * 3 retrievals * 3 plots * 2 treatments * 2 expositions * 2 sites), as well as tea bags (2 replicates * 3 retrievals * 3 plots * 2 treatments * 2 expositions * 2 sites) were placed in drought- and control plots and collected after 3-, 6-, and 12 months (93±1; 195±4; 366±5 days), respectively. Overall, 1080 litterbags and 144 tea bags were used.

All retrieved bags were dried at 40°C for at least 72 hours until stable weight, after which the remaining litter was weighed. Mass loss was calculated as a proportion of the initial weight: (dry $\text{weight}_{\text{initial}}$ - dry $\text{weight}_{\text{end}}$)/dry $\text{weight}_{\text{initial}}$.

4.2.6. Litter quality

Total carbon (C_t, detection limit 0.1 weight percent (wt %)) and nitrogen (N_t, detection limit 0.03 (wt %)) contents of homogenized (planetary ball mill, Pulverisette 5, Fritsch) initial litter samples (i.e. before decomposition) were analyzed with an Element Analyzer (Vario EL III, Elementar Analysensysteme GmbH). The outcomes were used to calculate C/N mass ratios of the respective litter as proxy for litter quality (i.e., low values are expected to decompose fast, high values slow). For details regarding detection limits and quality control see Table S4.5 in the supplementary data.

4.2.7. Statistics

To analyze differences in initial C/N ratios among litter from different origins a linear mixed model (LMM) with least squares means and a Tukey HSD post-hoc test were used. Litter origin was used as a fixed factor and species as a random factor.

The same type of LMM and post-hoc test were used to analyze the proportion of mass loss of the native litter along the gradient. Location of decomposition, litter origin (for decomposition along the gradient) or treatment (for decomposition under drought condition) and exposition (fixed factors), with all their interactions were used in the model. Non-significant interactions were removed if they did not improve the model according to AIC values. Species, plot and their interaction were used as random factors. The models were run for each retrieval time (3, 6, 12 months). The same models (without origin or species) were used to analyze the decomposition of tea. The pairwise differences from the post-hoc tests were used to analyze three experimental substitutes for climate change:

Space-for-time: observations along the gradient. The effect of space was analyzed by comparing decomposition of local litter at its home site (5 species per site, from here on "local litter") and by comparing litter quality among origins.

Experiment-for-time: reciprocal translocations along the gradient (between and within sites). The effects of climate and origin of the litter (20 reciprocally translocated species at each site, from here on "litter") on decomposition were analyzed at two scales: among sites along the climate gradient and between dry and wet expositions, within each site.

Experiment-for-time: *in situ* climate manipulations. The effect of experimental drought was analyzed by comparing drought with non-manipulated control plots at each of the two central sites.

All statistical analyses were performed in JMP 14.

4.3. Results

As the qualitative patterns of all retrievals were similar, we only show the decomposition after 12 months. For remaining results see supplementary material (Figures S4.2-5, Tables S4.6-S4.8).

Space-for-time: observations along the gradient (decomposition of local litter at home). After six months, litter decomposition rates of local litter, "at home", decreased with increasing precipitation ($p=0.02$, supplementary data: Table S4.6 (space-for-time) and Figure S4.2a, c and e). After 12 months, this pattern remained, but was not statistically significant anymore ($p=0.11$, Figure 4.2, Table 4.1: space-for-time).

Space-for-time: litter quality. Analyses of carbon and nitrogen concentrations showed that average initial litter quality gradually decreased, i.e. increasing C/N ratios (from 31 to 98), from the driest to the wettest site ($p<0.05$, Figure 4.3; Table 4.3, S4.9, S4.10)

Experiment-for-time: reciprocal translocations along the gradient (decomposition among climates). The mass loss of litter from the 20 species and that of tea increased markedly with increasing precipitation ($p<0.01$, Figure 4.2 and 4.4, Table 4.1). The mass loss in the temperate site was twice as high as in the arid site. This pattern was confirmed for all litter origins (Figure 4.2: bars with similar colors, Table 4.1). Furthermore, the litter from the two driest sites decomposed faster than the litter from the temperate site in each site, and the litter from the mediterranean climate always fell in between.

Experiment-for-time: reciprocal translocations within climates. Litter mass loss was generally higher on the wetter exposition, though this difference was only significant ($p<0.001$) at the semi-arid site. The mass loss of tea did not differ between exposition (Figure 4.4; Table 4.2.).

Experiment-for-time: *in situ* climate manipulations (decomposition in drought treatments). Decomposition of local litter (five local species at each of the sites with drought treatment) and tea was markedly lower in drought plots compared to controls ($p<0.01$). With one exception (dry exposition at the semi-arid site), these differences were significant. For tea, the drought treatment decreased mass loss significantly only on the dry exposition (semi-arid $p<0.01$, mediterranean $p<0.05$; Figure 4.4; Table 4.2.).

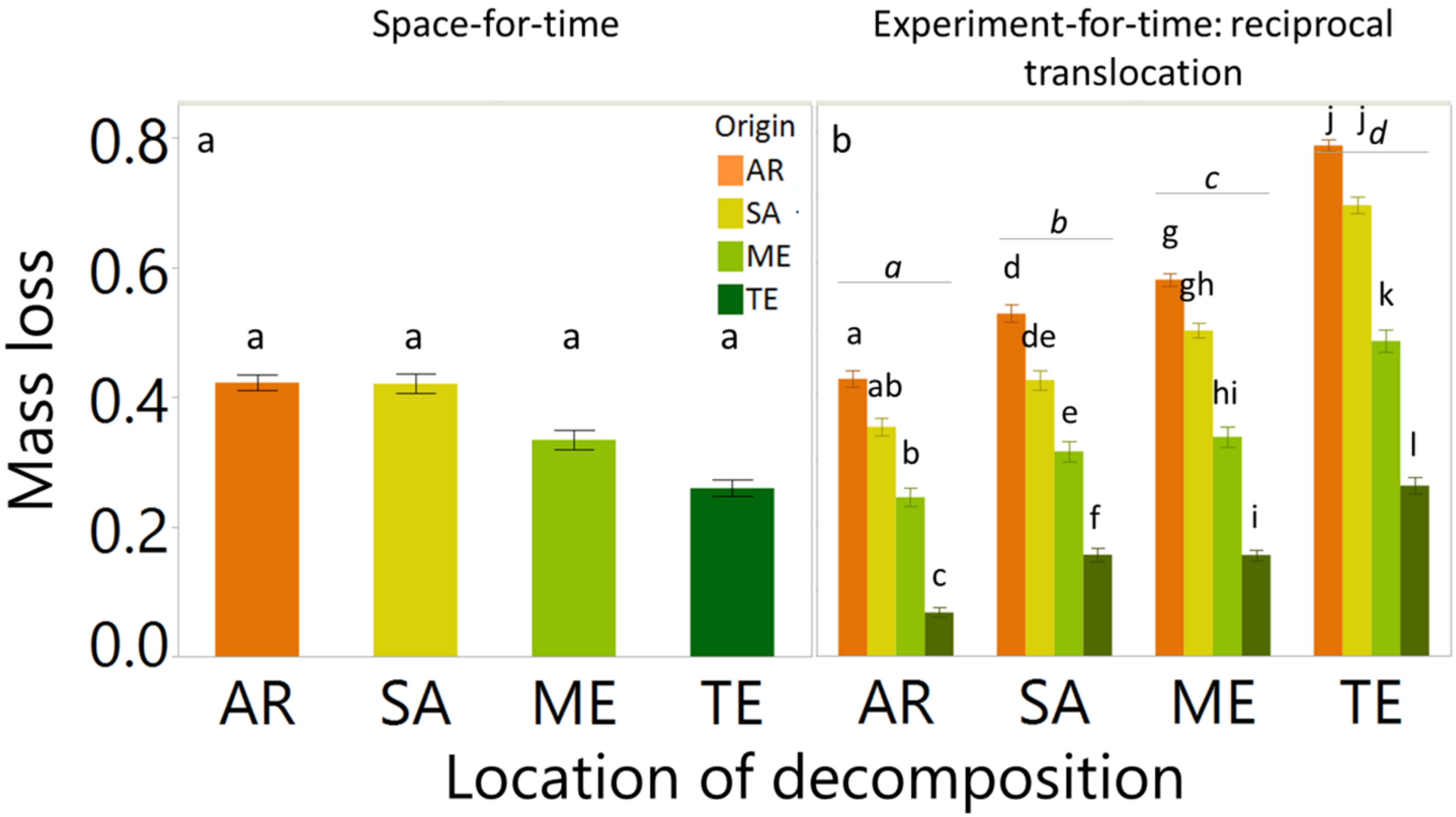

Figure 4.2. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight, in proportion) of 20 species from 4 climates (Origin, different colors) along a climate gradient in Chile after 12 months shown in each climate (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate). The left panel (a) represent litter mass loss of local litter at the home site (i.e. space-for-time). Significant differences (p<0.05) of litter decomposing at home were not found, as indicated above the bars (n=3). The right panel (b) represents the litter mass loss of reciprocally translocated litter (i.e. experiment for time) and is broken up into bars from each origin (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing precipitation from left to right. Significant differences in mass loss (p<0.05) between climates are indicated above the bars in underlined italic letters (n=3), significant differences between origins of litter are indicated directly above the bars (n=3) (NOTE: letters of significance can only be compared within climates, not between). See Table 4.1. for corresponding statistics.*

Table 4.1. *Results of linear mixed models (Least Squares) on mass loss of litter decomposing at home and initial C/N ratio (space-for-time, local litter, 5 species per site) for the effect of origin, and for litter translocated to all sites (experiment-for-time, native litter, 20 species per site and standard litter (green tea)) after 12 months for the effects of origin (only for litter), location, exposition and their interactions, including species, plot and their interaction as random factors when applicable. Significant results are in bold.*

	Local litter (at home)			**Initial C/N ratio**		
Space-for-time	**DF**	**F-ratio**	**p**	**DF**	**F-ratio**	**p**
Origin (O)	3; 22	2.21	0.116	3; 16	4.45	**0.019**
		Wald Z	**p**		**Wald Z**	**p**
Species (S)		2.52	**0.006**		5.14	**0.007**
Plot (P)		0.77	**0.005**		NA	NA
S × P		0.18	0.165		NA	NA
	Litter (translocation)			Tea		
Experiment-for-time	**DF**	**F-ratio**	**P**	**DF**	**F-ratio**	**p**
Origin (O)	3; 16	20.54	**<0.001**	NA	NA	NA
Location (L)	3; 16	218.63	**<0.001**	3; 16	85.04	**<0.001**
Exposition (E)	1; 16	32.36	**<0.001**	1; 16	3.05	0.100
O × L	9; 423	10.46	**<0.001**	NA	NA	NA
O × E	3; 423	8.60	**<0.001**	NA	NA	NA
L × E	3; 16	6.42	**0.005**	3; 16	0.56	0.651
		Wald Z	**p**		**Wald Z**	**p**
Species (S)		2.45	**0.006**		NA	NA
Plot (P)		0.06	0.201		0.21	0.478
S × P		0.96	**<0.001**		NA	NA

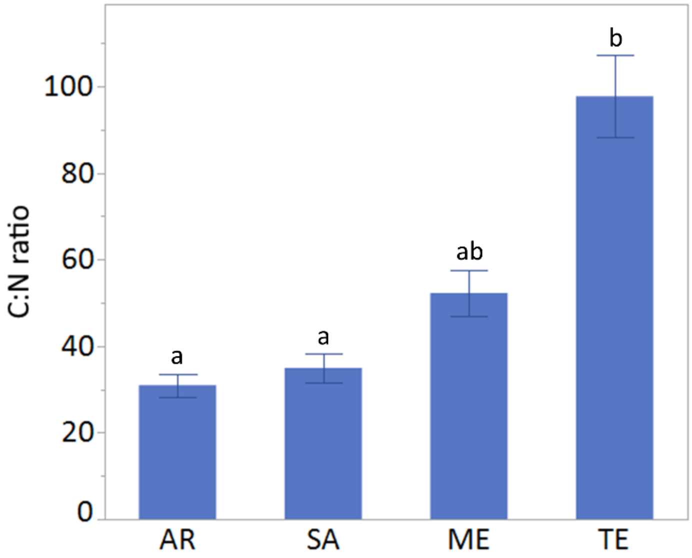

Figure 4.3. *Mean ± SE C/N of the initial litter (five species per site, n=5) per origin (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate). Significant differences in initial C/N ratio (p<0.05) between the origins of the litter are indicated above the bars in letters. See Table S4.10 for corresponding statistics and C and N values.*

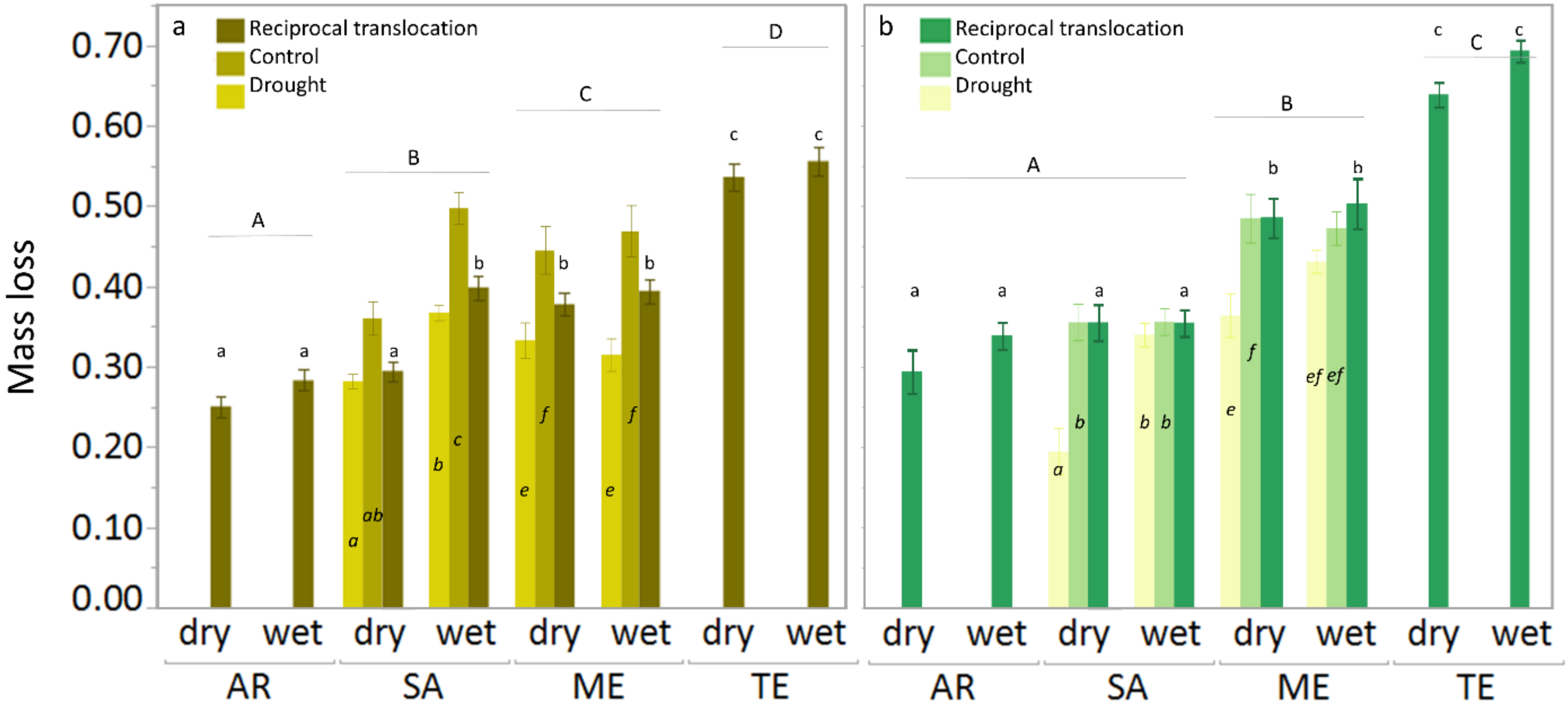

Figure 4.4. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight) along a climate gradient in Chile after 12 months shown in each climate (Location of decomposition, AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing precipitation from left to right for all native litter combined (a) and standard litter (Lipton green tea, b). Dark bars show the mass loss from the reciprocal translocation of 20 species (n=3), or tea (n=2) along the climate gradient (significant differences in uppercase) at both expositions (dry vs wet: significant differences, p<0.05, in lowercase). Lighter bars in the SA and ME climate show the mass loss of the 5 local species (n=3) and tea (n=2) in the drought experiment (significant differences between drought and control plots, p<0.05, in italic. NOTE: letters of significance can only be compared within climates, not between). See Table 4.2. for corresponding statistics.*

Table 4.2. *Results of linear mixed models on decomposition fraction of local litter (5 species) and standard litter (green tea) after 12 months for the effects of treatment (drought vs. control), location (semi-arid vs. mediterranean), exposition (dry vs. wet) and all their interactions, including species, plot and their interaction as random factors. Significant results are in bold.*

		Litter			***Tea***	
	DF	**F-ratio**	**P**	**DF**	**F-ratio**	**p**
Treatment (T)	1,18	86.29	**<0.001**	1,18	26.88	**<0.001**
Location (L)	1,8	0.05	0.826	1,18	58.94	**<0.001**
Exposition (E)	1,18	27.56	**<0.001**	1,18	8.37	**0.010**
T × E	1,18	5.07	**0.037**	1,18	11.97	**0.003**
L × E	1,18	21.89	**<0.001**	1,18	2.18	0.157
		Wald Z	**p**		**Wald Z**	**p**
Species (S)		4.575	**0.049**		2.448	…
Plot (P)		0.068	0.447		0.055	0.155
S × P		0.580	**<0.001**		0.963	…

4.4. Discussion

Our findings indicate that a simple space-for time approach for inferring climate-change effects (i.e. using natural gradients to represent future climate scenarios) on litter decomposition may yield opposing results to those generally assumed. Namely, decomposition of local litter at its home site decreased in a clinal fashion with increasing precipitation. However, the experiments (reciprocal translocations and *in situ* drought experiments) clearly indicated an increase in decomposition with increasing rainfall, i.e. the opposite of the local litter decomposition pattern.

Space-for-time: observations along the gradient. Decomposition of local litter decreased with increasing precipitation, and these differences decreased with increasing decomposition time. This is surprising, given that climate has been suggested to be the main predictor of litter decomposition among ecosystems, with wetter climates promoting faster decomposition (Fan *et al.,* 2014; Aerts, 1997). With precipitation being the most important predictor (Walse, Berg and Sverdrup, 1998; Austin, 2002), and a 100-fold difference in precipitation between the arid and the temperate site, we expected a much larger mass loss of the local species at the wetter than at the drier site. In our arid site, the lack of moisture could partially have been compensated by photo-degradation, which can account for up to 50% of carbon loss in arid and semi-arid ecosystems (Montaña *et al.*, 1988; Moorhead and Reynolds, 1989; Steinberger, Shmida and Whitford, 1990; Austin and Vivanco, 2006; Day *et al.*, 2018), thus increasing litter decomposition. However, Canessa *et al.* (2021), who worked at the same sites, showed that the effect photodecomposition in the arid sites was marginal. Also, this phenomenon cannot explain the lowest decomposition rates of local litter at the wettest site. There, lower temperatures could play a role (Couteaux, Bottner and Berg, 1995; Wu *et al.*, 2020), but in subtropical and temperate areas (with temperatures > 6.7°C) like our study sites, decomposition does not strongly depend on temperature (Bradford *et al.*, 2016). These explanations can also only explain differences between the most extreme sites, but not the consistent trend from dry to wet sites.

The consistent order in decomposition rates among the litter from different origins when translocated to other sites might be explained by the species- and site-specific litter quality. Namely, the quality (evaluated by the C/N ratio) of local litter decreased gradually with increasing precipitation. Species with soft succulent leaves dominated at the arid site and species with hard sclerophyllous leaves at the temperate site as well as at the mediterranean (Canessa *et al.*, 2021). This gradient in leaf litter quality and leaf toughness translated directly into origin-specific litter decomposition rates, i.e. when looking only at decomposition within a single site (or exposition, or experiment), there was a clear cline of increasing decomposition from the litter of the wettest to the driest origin. Interestingly, these trends for local decomposition were strong in early stages (i.e. 6 months) and ceased towards later stages (i.e. 12 months). This is consistent with recent findings of Canessa *et al.* (2021) who found that litter quality is important in the first phase of decomposition, but that climate becomes more important in later stages.

Initial nutrient composition is important for the decomposition rate (Couteaux, Bottner and Berg, 1995; Andresen *et al.*, 2010; Manzoni, 2008), and can be linked with climate (Chen *et al.*, 2013; Graça and Poquet, 2014). It is commonly thought that species from temperate, humid climates produce high quality litter (but see Santiago and Mulkey, 2005) and decompose quickly (Aerts, 1997), while species from arid climates produce low quality litter (tough and waxy leaves; Anonymous, 1932), as a response to drought (Schulze *et al.*, 1998; Niinemets, 2001; Wright, Reich and Westoby, 2001; Wright *et al.*, 2004; Graça and Poquet, 2014; Pugnaire *et al.*, 2019). This was confirmed in several studies showing that local litter in humid sites decomposed quicker than local litter in dry sites (Meentemeyer, 1978; Berg *et al.*, 1993; Couteaux, Bottner and Berg, 1995; Aerts, 1997; Fan *et al.*, 2014). Our counterintuitive findings could be explained by e.g. biogeographic, phylogenetic history and biotic interactions, which all influence litter quality and therefore local litter decomposition (Woodward and Diament, 1991; Chapman *et al.*, 2003; Wiens and Donoghue, 2004; Chapman, 2006; Bhalawe *et al.*, 2012; Zhu *et al.*, 2016). Also, along our gradient the soil pH decreases with increasing precipitation (Bernhard et al., 2018) and a decrease in soil pH increases leaf dry matter content (Laughlin *et al.*, 2015), which negatively affects litter decomposition (Cortez *et al.*, 2007). Additionally, the succulent and soft-leaved species at the arid site reflects an alternative adaptation to aridity and enables persistence through highly irregular arid conditions (Griffiths and Males, 2017). Overall, while litter quality probably explains the unexpected findings of local litter decomposition, it is still remarkable that this biotic factor could override a climate gradient with a 100-fold difference in precipitation. The experimental approaches enabled us to separate these unexpected biotic effects from the direct effect of precipitation.

Experiment-for-time: reciprocal translocations. Decomposition rates of tea and individual litter of the 20 species clearly followed the expected trend from low rates in the arid environments to high rates in wet environments. It is not surprising that decomposition rates of tea and litter were highest under wetter conditions, especially if we consider that three out of the four ecosystems studied are highly water limited, especially in summer. Previous studies also show that the decomposition of standard litter (e.g. teabags, cellulose disks, wooden dowels or litter from the same species) is quicker on wetter ends of a climate gradient (e.g. Berg *et al.*, 1993; Gallardo and Merino, 1993; Pérez-Harguindeguy *et al.*, 2007; Powers *et al.*, 2009; Jentsch *et al.*, 2011; Djukic *et al.*, 2018). Interestingly, the litter mass loss observed at our arid and semi-arid sites was almost twice as high as in Israeli (semi-)arid climates which receive similar mounts of precipitation (Steinberger, Shmida and Whitford, 1990), or a Mexican (semi-)arid site that receives five times more precipitation than our sites (Vanderbilt *et al.*, 2008). As explained above, while photo-degradation, (Austin and Vivanco, 2006; Day *et al.*, 2018) could play a role, Canessa *et al.* (2021) showed that it is of low importance compared to microbial decomposition. Another explanation of the rather high decomposition rates may be the fog deposition in the most arid site, which can locally produce a superficial moisture, which can amount to 125 mm m^{-2} day^{-1} (Lehnert *et al.*, 2018; Jung *et al.*, 2020) and potentially increase decomposition rates.

Interestingly, the clear trend of higher decomposition at wetter sites observed along the climate gradient was not prominently reflected in local-scale differences in decomposition between dry and wet exposition. This might be explained by the fact that compared to the steep climate gradient, differences in soil moisture between expositions were rather small.

Experiment-for time - *in situ* climate manipulations. Our experimental drought experiments confirmed the causal relationship between litter decomposition and moisture. Namely, decomposition in the drought treatment was markedly lower in drought plots compared to controls. This corresponds with previous studies that looked at litter decomposition under experimental drought (e.g. Andresen et al., 2010; Jentsch et al., 2011; Wu et al., 2020; L. Yahdjian et al., 2006). The results of our drought experiment, designed to manipulate precipitation, confirmed the results from the reciprocal translocation experiment: decomposition was slower under the drought treatments and similar to the decomposition in the adjacent drier site. This indicates that, despite the fact that decreasing litter quality decreases decomposition of local litter decreased towards the wetter sites, precipitation was still a main driver of decomposition rates along our gradient.

The combination of a fully reciprocal translocation experiment with litter of 20 common species from four distinct ecosystems and one standard litter, using dry and wet exposition within the sites, with an additional on-site drought treatment in two ecosystems, is a comprehensive approach to study the influence of climate, and single climatic factors (i.e. precipitation or soil moisture), on litter decomposition. Only with this approach, combining space-for-time observations with experiments and manipulations, we could disentangle the indirect climate effects from direct effects of precipitation. We found a clear causal and positive relationship between precipitation and decomposition, but this pattern disappeared when we used the space-for-time approach only. Therefore, we suggest that space-for-time observations in litter decomposition should be treated with caution, as has been suggested for plant traits, species distributions or bioclimatic envelope models (e.g. Sandel *et al.* 2010; Sternberg *et al.* 2011; Pliscoff *et al.* 2012; Tielbörger *et al.* 2014), especially when used to predict responses to climate change. This conclusion is important because the space-for-time assumption is also fundamental for global vegetation models that attempt to simulate the carbon cycle (Scheiter, Langan and Higgins, 2013) and could be biased for a large fraction of South American vegetation. We thus strongly advocate an experimental approach, combined with 'space' or 'time', to study climate change effects on biogeochemical processes and the global carbon and nutrient cycle and separate biotic effects from climate-only effects.

4.5. Acknowledgements

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4.6. Data availability

Should the manuscript be submitted the data supporting the results will be archived in Dryad.

Chapter 5 – Synthesis and outlook

5.1. The resistance of dryland plant communities to inter-annual precipitation variance

Micro-climatic changes (translocations of “small ecosystems” within sites) showed little effect on plant community structure and litter decomposition. Only plant biomass showed an unexpected response to micro-climatic change with higher biomass production when soils were translocated to the drier slope within sites. This might be explained by higher radiation, as the vegetation cover was lower on the drier slopes (personal observations). The difference in soil moisture between slopes was small within sites (Chapter 2) and was probably not large enough to trigger responses. Central Chile, where our study took place, is influenced by El Niño southern oscillation, and exhibits a large inter-annual variation in precipitation (Aceituno, 1988), resulting in large inter-annual variation in soil moisture (Chapter 2). This can create dynamic but resistant plant communities that can withstand these yearly variations in precipitation (Jaksic, 2001). The use of plant communities that are used to strong inter-annual precipitation variation likely explains why they performed and decomposed similarly on opposite slopes within the same climate.

5.2. Responses to climate change

Macro-climatic changes (translocations of “small ecosystems” between sites) triggered several responses in plant communities, although not always in the same direction. I.e. the translocation from wet to dry sites triggered responses in the plant community, with higher diversity and evenness at the dry site, but when translocated from dry to wet sites there was no decrease in diversity and evenness. These results show that the effect of climate change on plant communities might depend on the direction of the climate change. These results are important, as climate change is affecting the variance in inter-annual precipitation, resulting in longer dry periods, but also more rain during the occasional rain events (IPCC, 2014). Although small climate changes did not trigger much response on plant communities, they will likely change plant-soil microbial feedbacks, which can, in the long run, indirectly influence plant composition and productivity and nutrient availability (Gundale and Kardol, 2021).

By reciprocally translocating litter from different sites, we evaluated how a specific litter decomposes along a climate gradient and thus, tested for decomposition responses to precipitation and soil community changes. Increasing precipitation can increase decomposition in arid ecosystems, but too much precipitation can slow down decomposition in waterlogged environments, as it creates an anaerobic environment in the soil, which creates the need for specific microbial decomposers (Gao *et al.*, 2016) or inhibit it completely (Prescott, 2010). Microbial communities differ in their activity across climates (Jansson and Hofmockel, 2020) as well as in species, functional group composition and abundance (Evans, Wallenstein and Burke, 2014; Moskwa, Oses and Wagner, 2020). Climate changes can directly select for specific microorganisms, and to understand their influence on decomposition, I actively changed plant-soil microbial feedbacks in chapter 3, testing the home-field advantage hypothesis (HFA) in litter decomposition. The home-field advantage hypothesis states that, because of the close relationship between decomposers and plant litter, decomposer communities are locally adapted to the litter of the associated plant communities (Scheu *et al.*, 2003; Ayres, Dromph and

Bardgett, 2006). When testing home-field advantage effects, precipitation can be a confounding factor when translocating litter between different climates. It is therefore usually tested within similar climates (e.g. Gholz *et al.*, 2000; Ayres, Dromph and Bardgett, 2006; St. John, Orwin and Dickie, 2011; Wallenstein *et al.*, 2013; Veen *et al.*, 2015; Sun and Zhao, 2016; Lu *et al.*, 2017, but see Makkonen, Berg, *et al.*, 2012; Fujii *et al.*, 2018). However, we accounted for the differences in precipitation by contrasting the biologically decomposable fraction (nitrogen or phosphorus) and the leachable fraction (potassium). We found that litter decomposed faster with increasing precipitation and litter quality, and had no home-field advantage (Chapter 3). This result confirms the idea that home-field advantage is system- and even species specific (Sun and Zhao, 2016; Lu *et al.*, 2017; Palozzi and Lindo, 2018; Veen *et al.*, 2018; Luai, Ding and Wang, 2019) even when different biomes are used and climatic factors (in this case, precipitation) are accounted for. Our results fall within the many studies which did not find a home-field advantage (e.g. Gholz *et al.*, 2000; Ayres, Dromph and Bardgett, 2006; St. John, Orwin and Dickie, 2011; Makkonen, Berg, *et al.*, 2012; Wallenstein *et al.*, 2013; Veen *et al.*, 2015; Sun and Zhao, 2016; Lu *et al.*, 2017; Fujii *et al.*, 2018).

The lack of a home-field advantage could be attributed to two factors: the inherent ability of the microbial community to decompose litter and the litter quality. The ability of the microbial community is higher in sites where the functional breadth of the microbial community is large (Keiser *et al.*, 2014). But even if the functional breadth of a decomposer community increases with decreasing litter quality (Keiser *et al.*, 2014), recalcitrant litter might still be decomposed better in a nutrient-rich “away” site, while litter of high quality will decompose everywhere (Palozzi and Lindo, 2018). Instead of having a home-field advantage, litter decomposition followed the prediction based on climate (slow at the arid site, quick at the temperate site) and litter quality (slow for low-quality and quick for high-quality litter). The consistent order in decomposition rates among the litter from all origins in each site is likely explained by the species- and site-specific litter quality (Makkonen, Berg, *et al.*, 2012), which is especially influential in the first phase of decomposition (Canessa *et al.*, 2021). Additionally, we expect that the microbial community has the capability to rapidly shift in species and/or functional composition or to adjust physiologically in the presence of different resources (e.g., functionally different litter; MacLean, 2005; Gießelman *et al.*, 2011; St. John, Orwin and Dickie, 2011).

When considering the litter from all species and sites together, decomposition rates of litter were highest under wetter conditions (Chapter 4). An increasing decomposition rate under wetter conditions was expected given that three out of the four ecosystems studied are highly water limited, especially in summer. We showed with in-situ precipitation manipulations in the semi-arid and mediterranean sites that climate and not the differences among soil microbial communities across sites induced changes in decomposition rates. These manipulations confirmed the results from the reciprocal translocation experiment: decomposition was slower under the drought treatments and similar to the decomposition in the adjacent drier site (Chapter 4). This indicates that precipitation is a main driver of decomposition rates along the studied precipitation gradient, together with litter quality.

5.3. Usefulness of experiments combined with observational studies

The decomposition of local litter at their “home” site (i.e. arid litter in the arid site, semi-arid litter in the semi-arid site, mediterranean litter in the mediterranean site, and temperate litter in the temperate site) did, however, vary between sites and unexpectedly decreased with increasing precipitation. This pattern is surprising, given that climate has been suggested to be the main predictor of litter decomposition among ecosystems, with wetter climates promoting faster decomposition (Aerts, 1997; Fan *et al.*, 2014). And we did find that precipitation increased leaching and microbial decomposition (Chapter 3), probably due to an increase in the microbial abundance along the gradient (Moskwa, Oses and Wagner, 2020). Two factors might explain the unexpected results of the litter that decomposed “at home”: fog and litter quality. These factors require a closer look into the specifics of the ecosystems involved. Fog is a large contributor that sustains life in the arid, and in lesser amounts in the semi-arid and mediterranean sites used in this thesis (Lehnert *et al.*, 2018). Fog can increase soil moisture, which can in turn increase microbial activity and therefore litter decomposition. Additionally, the litter quality of plant species at the arid end of the gradient was very high. In contrast to the general assumption that litter quality increases with increasing precipitation (Wright, Reich and Westoby, 2001; Wright *et al.*, 2004; Díaz *et al.*, 2016), the litter quality of the species used in this study decreased with increasing precipitation (Chapter 4). We found sclerophyllous, hard to decompose, leaves at the wet end of the gradient used in this thesis, while the climate in the arid site selected for succulent, easy to decompose plant forms, with foliar structures that can store water and tolerate high salinity and temperature conditions (Griffiths and Males, 2017). These succulent leaves are rich in nutrients, and decompose fast in comparison to the leaves from the other study sites (Chapter 3 and 4). Thus, even though there is a strong water limitation on the arid end of this gradient, the influence of the fog, in combination with the high litter quality produced by the succulent species, likely resulted in high decomposition of the arid species in the arid climate. The opposite happened for the temperate end of the gradient, where sclerophyllous plants and conifers produced litter of low quality, which resulted in low decomposition of temperate species in the temperate climate (Chapter 3 and 4). The differences in decomposition along the gradient decreased over time and were only significant in the beginning of the decomposition (after 6 months). After twelve months, the decomposition pattern was similar, but the differences between sites were smaller. This result is consistent with recent findings of Canessa *et al.* (2021) who found that litter quality is more important in the first phase of decomposition, after which climate becomes more important. This stresses the need to study litter decomposition as a time series, but also the need to study the underlying mechanisms that provoke the inconsistency with general rules, as they give a deeper insight into the possible future impacts of climate change (Parmesan and Hanley, 2015). The counterintuitive litter quality pattern might be explained by e.g. biogeography, phylogenetic history and/or biotic interactions, which all influence litter quality and therefore local litter decomposition (Woodward and Diament, 1991; Chapman *et al.*, 2003; Wiens and Donoghue, 2004; Chapman, 2006; Bhalawe *et al.*, 2012; Zhu *et al.*, 2016). Litter quality probably explains the unexpected findings of local litter decomposition, and it is remarkable that this biotic factor could override a climate gradient with a 100-fold difference in precipitation.

Our findings indicate that a simple observational approach to infer climate-change effects (i.e. using natural gradients to represent future climate scenarios) on litter decomposition may yield opposing results from experimental climate manipulation. Decomposition of local litter at its home site showed a decrease with increasing precipitation. However, the experiments (reciprocal translocations and in situ manipulations) clearly indicated an increase in decomposition with increasing rainfall, i.e. the opposite of the local litter decomposition pattern.

Only when we combined observations with experiments and manipulations, we could disentangle the indirect climate effects from direct effects of precipitation (Chapter 4). We found a clear causal and positive relationship between precipitation and decomposition in both the drought treatment and reciprocal translocation of the litter, but this pattern disappeared when we used the observational approach only. Therefore, we suggest that space-for-time observations in litter decomposition should be treated with caution, as has been suggested for plant traits, species distributions or bioclimatic envelope models (e.g. Sandel *et al.*, 2010; Sternberg *et al.*, 2011; Pliscoff, Arroyo and Cavieres, 2012; Tielbörger *et al.*, 2014). This is especially so when space-for-time observations are used to predict responses to climate change. Although in the long run, climate change might impose changes in ecosystem processes that correspond to those observed along the gradient in our study, long term monitoring and manipulative experiments are important to give insight into the changes that can be expected for the coming decades (Elmendorf *et al.*, 2015). Additionally, it is important to disentangle apparent dissimilarities between observation, theory and prediction when faced with counter-intuitive results, as they give a deeper insight into the possible future impacts of climate change (Parmesan and Hanley, 2015). We thus strongly advocate combining an experimental approach with observations along a climate gradient, while including several aspects of ecosystems to study climate change effects on biogeochemical processes and the global carbon and nutrient cycle. This approach will also help to separate biotic effects from climate-only effects, and to be able to better predict responses to future climate change.

5.4. Consequences of climate change for nutrient cycling

The influence of precipitation, litter quality and their interaction on decomposition is highly relevant to correctly predict the consequences of climate change on carbon and nutrient cycling. An increase in temperature (especially in combination with a decrease in rainfall, as predicted for our study region by climate change scenarios, IPCC, 2014) can decrease litter quality (e.g. increase in carbon/nitrogen ratio), reduce decomposition rates and increase nitrogen immobilization (Prieto *et al.*, 2019). Furthermore, climate change will affect several aspects of ecosystems at the same time, but not necessarily in the same time period. It can alter species richness and diversity (Chapter 2; (Chapin III *et al.*, 2000), and thereby modify the litter input, which can in turn change decomposition rates (Chapter 3 and 4). As all biological processes are affected directly and indirectly by climate change (Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008; Suding *et al.*, 2008), modeling the carbon cycle is complex and uncertain (Ostle et al., 2009), but can be done if litter decomposition data from experiments and manipulations are available.

For northern Chile, the predictions for climate change include more extreme climate events, a raise in temperature and a decrease in precipitation (IPCC, 2014). Even though an increase in temperature could potentially have an increasing effect on litter decomposition, the effect of temperature on decomposition is minimal in mild temperature ranges, i.e. 10-20°C (Bradford *et al.*, 2016), which is the case of the gradient used in this thesis. A reduction in precipitation, however, will probably have a hampering effect on nutrient cycling as it slows down decomposition and nutrient cycling (Chapter 4).

This thesis provides important insights in litter decomposition in arid and semi-arid environments. Until recently, litter decomposition studies focused mainly on boreal and temperate ecosystems (Berg and McClaugherty, 2003), which made predicting the effect of climate change on litter decomposition on a global scale almost impossible. The gradient used in this study is highly valuable as it combines underrepresented sites with a well-known ecosystem, namely temperate forest. Thus, it is possible to compare the results of this study with the former studies and then systematically extend these findings to mediterranean, semi-arid and arid ecosystems.

Precipitation is a large driver of decomposition along this gradient (Chapter 4), together with litter quality (Chapter 3 and 4). Even though plant communities and soil properties seem relatively robust to cope with inter-annual precipitation variability, the predicted precipitation reduction for the next decades will most likely alter decomposition rates, which will affect carbon and nutrient cycling. The precipitation reduction might additionally decrease the ability of the decomposer community (Chapter 3), but, if species composition shifts according to the observed pattern along the gradient, might also increase the litter quality and with that increase the decomposability of the litter (Chapter 3 and 4). The combination of increased decomposability with decreasing precipitation might indicate that nutrient cycling is not much slower in arid systems than in forests (Chapter 4). However, it should be taken into consideration that the litter production on the arid side of the gradient is much less, due to a sparser vegetation cover (Bernhard, L. M. Moskwa, *et al.*, 2018). To better predict the influence of climate change on the nutrient cycle, future studies should quantify litter production and plant community changes. A combination of a detailed quantification of plant community litter production with observations, translocations and manipulations of litter decomposition, will make it possible to correctly estimate the effect of future climate change on the nutrient cycle.

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References

Aceituno, P. (1988) ‘On the functioning of the Southern Oscillation in the South American Sector. Part I: Surface Climate’, *Monthly Weather Review*, 116, pp. 505–524.

Aerts, R. (1997) ‘Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship’, *Oikos*, 79(3), pp. 439–449.

Alexander, J. M., Diez, J. M. and Levine, J. M. (2015) ‘Novel competitors shape species’ responses to climate change’, *Nature*, 525(7570), pp. 515–518.

Alon, M. and Sternberg, M. (2019) ‘Effects of extreme drought on primary production, species composition and species diversity of a Mediterranean annual plant community’, *Journal of Vegetation Science*, 30(6), pp. 1045–1061.

Andresen, L. C. *et al.* (2010) ‘Plant nutrient mobilization in temperate heathland responds to elevated CO2, temperature and drought’, *Plant and Soil*, 328(1), pp. 381–396.

Anonymous (1932) ‘Xeromorphic adaptations in plants’, *Nature*, 129(3245), pp. 47–48.

Araujo, P. I. and Austin, A. T. (2015) ‘A shady business: Pine afforestation alters the primary controls on litter decomposition along a precipitation gradient in Patagonia, Argentina’, *Journal of Ecology*, 103(6), pp. 1408–1420.

Austin, A. T. (2002) ‘Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii’, *Ecology*, 83(2), pp. 328–338.

Austin, A. T. (2011) ‘Has water limited our imagination for aridland biogeochemistry?’, *Trends in Ecology and Evolution*. Elsevier Ltd, 26(5), pp. 229–235.

Austin, A. T. *et al.* (2014) ‘There’s no place like home? An exploration of the mechanisms behind plant litter – decomposer affinity in terrestrial ecosystems’, *New Phytologist*, 204, pp. 307–314.

Austin, A. T. and Ballaré, C. L. (2010) ‘Dual role of lignin in plant litter decomposition in terrestrial ecosystems’, *Proceedings of the National Academy of Sciences*, 107(10), pp. 4618–4622.

Austin, A. T. and Vitousek, P. M. (2000) ‘Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai’i’, *Journal of Ecology*, 88, pp. 129–138.

Austin, A. T. and Vivanco, L. (2006) ‘Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation’, *Nature*, 442(7102), pp. 555–558.

Ayres, E., Steltzer, H., Simmons, B. L., *et al.* (2009) ‘Home-field advantage accelerates leaf litter decomposition in forests’, *Soil Biology and Biochemistry*. Elsevier Ltd, 41(3), pp. 606–610.

Ayres, E., Steltzer, H., Berg, S., *et al.* (2009) ‘Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them’, *Journal of Ecology*, 97(5), pp. 901–912.

Ayres, E., Dromph, K. M. and Bardgett, R. D. (2006) ‘Do plant species encourage soil biota that specialise in the rapid decomposition of their litter?’, *Soil Biology and Biochemistry*, 38(1), pp. 183–186.

Baker, N. R. *et al.* (2018) ‘Microbial decomposers not constrained by climate history along a Mediterranean climate gradient in southern California’, *Ecology*, 99(6), pp. 1441–1452.

Becking, B. (1934) *Geobiologie of inleiding tot de milieukunde*. Edited by D. E. Canfield. The Hague: W.P. van Stockum & Zoon.

Berg, B. *et al.* (1993) ‘Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality’, *Biogeochemistry*, 20, pp. 127–159.

Berg, B. (2014) ‘Decomposition patterns for foliar litter - A theory for influencing factors’, *Soil Biology and Biochemistry*, 78, pp. 222–232.

Berg, B. and McClaugherty, C. (2003) *Plant litter - Decomposition, humus formation, carbon sequestration*. 1st edn.

Edited by B. Berg and C. McClaugherty. Berlin Heidelberg: Springer-Verslag.

Bernhard, N., Moskwa, L.-M. M., *et al.* (2018) ‘Pedogenic and microbial interrelations to regional climate and local topography: New insights from a climate gradient (arid to humid) along the Coastal Cordillera of Chile, supplement’, *GFZ Data Services*. Elsevier.

Bhalawe, S. *et al.* (2012) ‘Leaf litter decomposition rate in different multipurpose trees’, *Journal of Tropical Forestry*, 28(3), pp. 1–12.

Bocock, K. L. *et al.* (1960) ‘Changes in leaf litter when placed on the surface of soils with contrasting humus types. I. Losses in dry weight of oak and ash leaf litter’, *Journal of Soil Science*, 11(1), pp. 1–9.

Boyer, S. *et al.* (2016) ‘Can ecosystem-scale translocations mitigate the impact of climate change on terrestrial biodiversity? Promises, pitfalls, and possibilities’, *F1000Research*, 5(May), pp. 1–12.

Bradford, M. A. *et al.* (2016) ‘Understanding the dominant controls on litter decomposition’, *Journal of Ecology*, 104, pp. 229–238.

Bradford, M. A. *et al.* (2017) ‘A test of the hierarchical model of litter decomposition’, *Nature Ecology and Evolution*. Springer US, 1(12), pp. 1836–1845.

Brandt, L. A., King, J. Y. and 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, pp. 2193–2205.

Byrne, K. M., Adler, P. B. and Lauenroth, W. K. (2017) ‘Contrasting effects of precipitation manipulations in two Great Plains plant communities’, *Journal of Vegetation Science*, 28(2), pp. 238–249.

Cai, W. *et al.* (2021) ‘Changing El Niño–Southern Oscillation in a warming climate’, *Nature Reviews Earth and Environment*. Springer US, 2(9), pp. 628–644.

Canessa, R. *et al.* (2021) ‘Relative effects of climate and litter traits on decomposition change with time, climate and trait variability’, *Journal of Ecology*, 1, pp. 447–458.

Carrera, A. L. and Bertiller, M. B. (2010) ‘Relationships among plant litter, fine roots, and soil organic C and N across an aridity gradient in northern Patagonia, Argentina’, *Ecoscience*, 17(3), pp. 276–286.

Chapin III, F. S. *et al.* (2000) ‘Consequences of changing biodiversity’, *Nature*, 405(May), pp. 234–242.

Chapin III, F. S., Matson, P. A. and Vitousek, P. M. (2011) ‘Terrestrial decomposition’, in Chapin III, F. S., Matson, P. A., and Vitousek, P. M. (eds) *Principles of Terrestrial Ecosystem Ecology*. 2nd edn. New York: Springer Science+Business Media, LLC, pp. 151–175.

Chapman, S. K. *et al.* (2003) ‘Insect herbivory increases litter quality and decomposition: An extension of the acceleration hypothesis’, *Ecology*, 84(11), pp. 2867–2876.

Chapman, S. K. (2006) ‘Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees’, *Oikos*, 114(3), pp. 566–574.

Chen, Y. *et al.* (2013) ‘Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form’, *Ecography*, 36(2), pp. 178–184.

Churkina, G. and Running, S. W. (1998) ‘Contrasting climatic controls on the estimated productivity of global terrestrial biomes’, *Ecosystems*, 1(2), pp. 206–215.

Cornelissen, Johannes H. C. *et al.* (2007) ‘Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes’, *Ecology Letters*, 10(7), pp. 619–627.

Cornelissen, Johannes H C *et al.* (2007) ‘Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes’, *Ecology Letters*, 10, pp. 619–627.

Cornwell, W. K. *et al.* (2008) ‘Plant species traits are the predominant control on litter decomposition rates within biomes worldwide’, *Ecology Letters*, 11(10), pp. 1065–1071.

Cortez, J. *et al.* (2007) ‘Plant traits, litter quality and decomposition in a Mediterranean old-field succession’, *Plant and Soil*, 296, pp. 19–34.

Couteaux, M.-M., Bottner, P. and Berg, B. (1995) ‘Litter decomposition, climate and litter quality’, *Trends in Ecology and Evolution*, 10(2), pp. 63–66.

Cox, P. M. (2001) *Description of the ‘TRIFFID’ dynamic global vegetation model.*, *Hadley Center technical note 24*. Berks: Hadley Center, Met Office.

Craine, J. M. and Dybzinski, R. (2013) ‘Mechanisms of plant competition for nutrients, water and light’, *Functional Ecology*, 27(4), pp. 833–840.

Cunningham, S. A., Summerhayes, B. and Westoby, M. (1999) ‘Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients’, *Ecology*, 69(4), pp. 569–588.

Currie, W. S. *et al.* (2010) ‘Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale’, *Global Change Biology*, 16, pp. 1744–1761.

Day, T. A. *et al.* (2018) ‘Desert leaf litter decay: Coupling of microbial respiration, water-soluble fractions and photodegradation’, *Global Change Biology*, 24(August), pp. 5454–5470.

Díaz, S. *et al.* (2016) ‘The global spectrum of plant form and function’, *Nature*. Nature Publishing Group, 529(7585), pp. 167–171.

Djukic, I. *et al.* (2018) ‘Early stage litter decomposition across biomes’, *Science of the Total Environment*, 628–629(July), pp. 1369–1394.

Dorrepaal, E. *et al.* (2005) ‘Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient?’, *Journal of Ecology*, 93(4), pp. 817–828.

Elmendorf, S. C. *et al.* (2015) ‘Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns’, *Proceedings of the National Academy of Sciences*, 112(2), pp. 448–452.

Evans, S. E., Wallenstein, M. D. and Burke, I. C. (2014) ‘Is bacterial moisture niche a good predictor of shifts in community composition under long-term drought?’, *Ecology*, 95(1), pp. 110–122.

Fan, J. *et al.* (2014) ‘Leaf litter decomposition in three subalpine forests along an elevation gradient in Tibet’, *Polish Journal of Environmental Studies*, 23(4), pp. 1137–1146.

Fanin, N. *et al.* (2021) ‘Home-field advantage of litter decomposition: from the phyllosphere to the soil’, *New Phytologist*, 231(4), pp. 1353–1358.

Freschet, G. T., Aerts, R. and Cornelissen, J. H. C. (2012) ‘A plant economics spectrum of litter decomposability’, *Functional Ecology*, 26(1), pp. 56–65.

Freschet, T., Aerts, R. and Cornelissen, J. H. C. (2012) ‘A plant economics spectrum of litter decomposability’, *Functional Ecology*, 26, pp. 56–65.

Friend, A. D. *et al.* (1997) ‘A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3 . 0)’, *Ecological Modelling*, 95, pp. 249–287.

Fujii, S. *et al.* (2018) ‘Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient’, *Functional Ecology*, 32, pp. 840–852.

Gallardo, A. and Merino, J. (1993) ‘Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality’, *Ecology*, 74(1), pp. 152–161.

Gao, H. *et al.* (2016) ‘Decomposition dynamics and changes in chemical composition of wheat straw residue under anaerobic and aerobic conditions’, *PLoS ONE*, 11(7), pp. 1–17.

García-Palacios, P. *et al.* (2013) ‘Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes’, *Ecology Letters*, 16(8), pp. 1045–1053.

Garcia, R. A. *et al.* (2014) 'Multiple dimensions of climate change and their implications for biodiversity', *Science*, 344(1247579), pp. 1–10.

Garreaud, R. D. *et al.* (2017) 'The 2010 – 2015 megadrought in central Chile: impacts on regional hydroclimate and vegetation', *Hydrology and Earth System Sciences*, 21, pp. 6307–6327.

Gholz, H. L. *et al.* (2000) 'Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition', *Global Change Biology*, 6, pp. 751–765.

Gießelman, C. U. *et al.* (2011) 'Lack of home-field advantage in the decomposition of leaf litter in the Atlantic Rainforest of Brazil', *Applied Soil Ecology*, 49, pp. 5–10.

Gilman, S. E. *et al.* (2010) 'A framework for community interactions under climate change', *Trends in Ecology and Evolution*. Elsevier Ltd, 25(6), pp. 325–331.

Glassman, S. I. *et al.* (2018) 'Decomposition responses to climate depend on microbial community composition', *Proceedings of the National Academy of Sciences*, 115(47), p. 201811269.

Graça, M. A. S. and Poquet, J. M. M. (2014) 'Do climate and soil influence phenotypic variability in leaf litter, microbial decomposition and shredder consumption?', *Oecologia*, 174(3), pp. 1021–1032.

Griffiths, H. and Males, J. (2017) 'Succulent plants', *Current Biology*, 27(17), pp. R890–R896.

Grime, J. P. (1973) 'Competitive exclusion in herbaceous vegetation', *Nature*, 242, pp. 344–347.

Gruntman, M. *et al.* (2017) 'Decision-making in plants under competition', *Nature Communications*. Springer US, 8(2235), pp. 1–8.

Gundale, M. J. and Kardol, P. (2021) 'Multi-dimensionality as a path forward in plant-soil feedback research', *Journal of Ecology*, 109(10), pp. 3446–3465.

Hatfield, J. L. and Prueger, J. H. (2015) 'Temperature extremes: Effect on plant growth and development', *Weather and Climate Extremes*, 10, pp. 4–10.

Hauck, L., Moreira-Muñoz, A. and Nezadal, W. (2016) 'La flora exótica ruderal del Parque Nacional La Campana, Región de Valparaíso, Chile central The exotic ruderal flora of La Campana National Park, Valparaíso Region, central Chile', *Gayana Botánica*, 73(2), pp. 206–219.

Hauenstein, E. (2012) 'Wealth of flora and vegetation in the La Campana-Peñuelas Biosphere Reserve, Valparaiso Region, Chile', in Ishwaren, N. (ed.) *The Biosphere*. 1st edn. Rijeka: InTech, pp. 215–244.

He, Z. *et al.* (2016) 'Litter decomposition, residue chemistry and microbial community structure under two subtropical forest plantations: A reciprocal litter transplant study', *Applied Soil Ecology*. Elsevier B.V., 101, pp. 84–92.

Hobbie, S. E. (1996) 'Temperature and plant species control over litter decomposition in Alaskan tundra', *Ecological Monographs*, 66(4), pp. 503–522.

Holzapfel, C., Schmidt, W. and Shmida, A. (1993) 'The role of seed bank and seed rain in the recolonization of disturbed sites along an aridity gradient', *Phytocoenologia*, 23(1–4), pp. 561–580.

Huang, J. *et al.* (2016) 'Accelerated dryland expansion under climate change', *Nature Climate Change*, 6(2), pp. 166–171.

IPCC (2014) *Climate change 2014 - Synthesis report*, *IPCC*. Edited by The Core Writing Team, R. K. Pachauri, and L. Meyer. Geneva.

Jaksic, F. M. (2001) 'Ecological effects of El Niño in terrestrial ecosystems of western South America', *Ecography*, 24, pp. 241–250.

Jansson, J. K. and Hofmockel, K. S. (2020) 'Soil microbiomes and climate change', *Nature Reviews Microbiology*. Springer US, 18(1), pp. 35–46.

Jasieński, M. and Bazzaz, F. A. . (1999) ‘The fallacy of ratios and the testability of models in biology’, *Oikos*, 84(2), pp. 321–326.

Jentsch, A. *et al.* (2011) ‘Climate extremes initiate ecosystem-regulating functions while maintaining productivity’, *Journal of Ecology*, 99(3), pp. 689–702.

St. John, M. G., Orwin, K. H. and Dickie, I. A. (2011) ‘No “home” versus “away” effects of decomposition found in a grassland-forest reciprocal litter transplant study’, *Soil Biology and Biochemistry*. Elsevier Ltd, 43(7), pp. 1482–1489.

Jump, A. S. and Peñuelas, J. (2005) ‘Running to stand still: Adaptation and the response of plants to rapid climate change’, *Ecology Letters*, 8(9), pp. 1010–1020.

Jung, P. *et al.* (2020) ‘Desert breath—How fog promotes a novel type of soil biocenosis, forming the coastal Atacama Desert’s living skin’, *Geobiology*, 18(1), pp. 113–124.

Keiser, A. D. *et al.* (2014) ‘Disentangling the mechanisms underlying functional differences among decomposer communities’, *Journal of Ecology*, 102(3), pp. 603–609.

Keiser, A. D. and Bradford, M. A. (2017) ‘Climate masks decomposer influence in a cross-site litter decomposition study’, *Soil Biology and Biochemistry*. Elsevier Ltd, 107, pp. 180–187.

Keuskamp, J. A. *et al.* (2013) ‘Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems’, *Methods in Ecology and Evolution*, 4(11), pp. 1070–1075.

Kneitel, J. M. and Chase, J. M. (2004) ‘Trade-offs in community ecology: Linking spatial scales and species coexistence’, *Ecology Letters*, 7(1), pp. 69–80.

Kreyling, J. *et al.* (2017) ‘Drought effects in climate change manipulation experiments: quantifying the influence of ambient weather conditions and rain-out shelter artifacts’, *Ecosystems*. Springer US, 20(2), pp. 301–315.

Kunstler, G. *et al.* (2016) ‘Plant functional traits have globally consistent effects on competition’, *Nature*. Nature Publishing Group, 529(7585), pp. 204–207.

Laskowski, R., Niklińska, M. and Maryański, M. (2013) ‘The dynamics of chemical elements in forest litter’, *Ecology*, 76(5), pp. 1393–1406.

Laughlin, D. C. *et al.* (2015) ‘Environmental filtering and positive plant litter feedback simultaneously explain correlations between leaf traits and soil fertility’, *Ecosystems*. Springer US, 18(7), pp. 1269–1280.

Lehnert, L. W. *et al.* (2018) ‘A case study on fog/low stratus occurrence at las lomitas, atacama desert (Chile) as a water source for biological soil crusts’, *Aerosol and Air Quality Research*, 18(1), pp. 254–269.

Leimu, R. and Fischer, M. (2008) ‘A meta-analysis of local adaptation in plants’, *PLoS ONE*, 3(12), p. e4010.

Leuzinger, S. *et al.* (2011) ‘Do global change experiments overestimate impacts on terrestrial ecosystems?’, *Trends in Ecology and Evolution*, 26(5), pp. 236–241.

Liancourt, P. *et al.* (2013) ‘Plant response to climate change varies with topography, interactions with neighbors, and ecotype’, *Ecology*, 94(2), pp. 444–453.

Liang, Y. *et al.* (2015) ‘Long-term soil transplant simulating climate change with latitude significantly alters microbial temporal turnover’, *ISME Journal*. Nature Publishing Group, 9(12), pp. 2561–2572.

Lin, D. *et al.* (2020) ‘Home-field advantage of litter decomposition differs between leaves and fine roots’, *New Phytologist*, 227(4), pp. 995–1000.

Link, S. O. *et al.* (2003) ‘A reciprocal transplant experiment within a climatic gradient in a semiarid shrub-steppe ecosystem: Effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen’, *Global Change Biology*, 9(7), pp. 1097–1105.

Lloret, F., Peñuelas, J. and Estiarte, M. (2005) ‘Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland’, *Journal of Vegetation Science*, 16(1), pp. 67–76.

Lu, W. *et al.* (2017) ‘Impact of vegetation community on litter decomposition: Evidence from a reciprocal transplant study with 13 C labeled plant litter’, *Soil Biology and Biochemistry*. Elsevier Ltd, 112, pp. 248–257.

Luai, V. B., Ding, S. and Wang, D. (2019) ‘The effects of litter quality and living plants on the home-field advantage of aquatic macrophyte decomposition in a eutrophic urban lake, China’, *Science of the Total Environment*. Elsevier B.V., 650, pp. 1529–1536.

Macel, M. *et al.* (2007) ‘Climate vs. soil factors in local adaptation of two common plant species’, *Ecology*, 88(2), pp. 424–433.

MacLean, R. C. (2005) ‘Adaptive radiation in microbial microcosms’, *Journal of Evolutionary Biology*, 18(6), pp. 1376–1386.

Makkonen, M., Berg, M., *et al.* (2012) ‘Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient_appendixs1’, *Ecology Letters*, 15(9), pp. 1033–1041.

Makkonen, M., Berg, M. P., *et al.* (2012) ‘Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient’, *Ecology Letters*, 15(9), pp. 1033–1041.

Manzoni, S. (2008) ‘The global stoichiometry of litter nitrogen mineralization’, *Science*, 321, pp. 684–686.

Maranon, T. and Bartolome, J. W. (1993) ‘Reciprocal transplants of herbaceous communities between Quercus agrifolia woodland and adjacent grassland’, *The Journal of Ecology*, 81(4), pp. 673–682.

Martiny, J. B. H. *et al.* (2006) ‘Microbial biogeography: Putting microorganisms on the map’, *Nature Reviews Microbiology*, 4(2), pp. 102–112.

McCarty, J. P. (2001) ‘Ecological Consequences of Recent Climate Change’, *Conservation Biology*, 15(2), pp. 320–331.

Meentemeyer, V. (1978) ‘Macroclimate and lignin control of litter decomposition rates’, *Ecology*, 59(3), pp. 465–472.

Melillo, J. M., Aber, J. D. and Muratore, J. F. (2014) ‘Nitrogen and lignin control of hardwood leaf litter decomposition dynamics’, *Ecology*, 63(3), pp. 621–626.

Miranda, J. D. *et al.* (2011) ‘Climatic change and rainfall patterns: Effects on semi-arid plant communities of the Iberian Southeast’, *Journal of Arid Environments*. Elsevier Ltd, 75(12), pp. 1302–1309.

Montaña, C. *et al.* (1988) ‘The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments’, *Journal of Arid Environments*, 14(February 1987), pp. 55–60.

Moorhead, D. L. and Reynolds, J. F. (1989) ‘Mechanisms of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation’, *Journal of Arid Environments*. Academic Press Limited, 16(2), pp. 157–163.

Moskwa, L.-M., Oses, R. and Wagner, D. (2020) ‘Distribution of microbial generalists and habitat specialists in soils along a climate gradient in the Chilean Coastal Cordillera’, *Researchsquare Preprint*.

Naumann, G. *et al.* (2018) ‘Global changes in drought conditions under different levels of warming’, *Geophysical Research Letters*, 45(7), pp. 3285–3296.

Nemer, D. *et al.* (2021) ‘Species stress tolerance and community competitive effects drive differences in species composition between calcareous and siliceous plant communities’, *Journal of Ecology*, 109(12), pp. 4132–4142.

Niinemets, Ü. (2001) ‘Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs’, *Ecology*, 82(2), pp. 453–469.

Oeser, R. A. *et al.* (2018) ‘Chemistry and microbiology of the Critical Zone along a steep climate and vegetation gradient in the Chilean Coastal Cordillera’, *Catena*. Elsevier, 170(June), pp. 183–203.

Orians, G. H. and Solbrig, O. T. (1977) ‘A cost-income model of leaves and roots with special reference to arid and semiarid areas’, *The American Naturalist*, 111(980), pp. 677–690.

Ostle, N. J. *et al.* (2009) ‘Integrating plant – soil interactions into global carbon cycle models’, *Journal of Ecology*, 97, pp. 851–863.

Palozzi, J. E. and Lindo, Z. (2018) ‘Are leaf litter and microbes team players? Interpreting home-field advantage decomposition dynamics’, *Soil Biology and Biochemistry*. Elsevier, 124(January), pp. 189–198.

Parmesan, C. and Hanley, M. E. (2015) ‘Plants and climate change: Complexities and surprises’, *Annals of Botany*, 116(6), pp. 849–864.

Parton, W. *et al.* (2007) ‘Global-scale similarities in nitrogen release patterns during long-term decomposition’, *Science*, 315, pp. 361–364.

Patton, W. (1996) ‘The CENTURY model’, in Powlson, D. S., Smith, P., and Smith, J. U. (eds) *Evaluation of Soil Organic Matter Models. NATO ASI series (Series I: Global Environmental Change)*. Berlin, Heidelberg: Springer.

Peñuelas, J. *et al.* (2007) ‘Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: Reductions in primary productivity in the heat and drought year of 2003’, *Global Change Biology*, 13(12), pp. 2563–2581.

Pérez-Harguindeguy, N. *et al.* (2000) ‘Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina’, *Plant and Soil*, 218, pp. 21–30.

Pérez-Harguindeguy, N. *et al.* (2007) ‘Direct and indirect effects of climate on decomposition in native ecosystems from central Argentina’, *Austral Ecology*, 32(7), pp. 749–757.

Pielou, E. C. (1966) ‘The measurement of diversity in different types of biological collections’, *Journal of Theoretical Biology*, 13(C), pp. 131–144.

Pierson, E. A., Mack, R. N. and Black, R. A. (1990) ‘The effect of shading on photosynthesis, growth, and regrowth following defoliation for Bromus tectorum’, *Oecologia*, 84, pp. 534–543.

Pliscoff, P., Arroyo, M. T. K. and Cavieres, L. (2012) ‘Changes in the main vegetation types of Chile preliminary study: Models, uncertainties and adapting research to a dynamic biodiversty world’, *Anales Instituto Patagonia*, 40(1), pp. 81–86.

Portillo-Estrada, M. *et al.* (2016) ‘Climatic controls on leaf litter decomposition across European forests and grasslands revealed by reciprocal litter transplantation experiments’, *Biogeosciences*, 13, pp. 1621–1633.

Pörtner, H. O. and Farrell, A. P. (2008) ‘Physiology and climate change’, *Science*, 322(October), pp. 690–692.

Powers, J. S. *et al.* (2009) ‘Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient’, *Journal of Ecology*, 97, pp. 801–811.

Prentice, I. C. *et al.* (1992) ‘Special Paper: A global biome model based on plant physiology and dominance, soil properties and climate’, *Journal of Biogeography*, 19(2), pp. 117–134.

Prescott, C. E. (2010) ‘Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils?’, *Biogeochemistry*, 101(1), pp. 133–149.

Prieto, I. *et al.* (2019) ‘Altered leaf litter quality exacerbates the negative impact of climate change on decomposition’, *Journal of Ecology*, 107(5), pp. 2364–2382.

Pugnaire, F. I. *et al.* (2019) ‘Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems’, *Science Advances*, 5(eaaz1834), pp. 1–12.

Quintana, J. M. and Aceituno, P. (2012) ‘Changes in the rainfall regime along the extratropical west coast of South America (Chile): 30-43^{o} S’, *Atmosfera*, 25(1), pp. 1–22.

Raich, J. W. and Schlesinger, W. H. (1992) ‘The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate’, *Tellus*, 44B, pp. 81–99.

Ripple, W. J. *et al.* (2020) ‘World scientists’ warning of a climate emergency’, *BioScience*, 70(1), pp. 8–12.

Rundel, P. W., Dillon, M. O. and Palma, B. (1996) ‘Flora and vegetation of Pan de Azucar National Park in the Atacama desert of northern Chile', *Gayana Botanica*, 53(2), pp. 295–315.

Sandel, B. *et al.* (2010) 'Contrasting trait responses in plant communities to experimental and geographic variation in precipitation', *New Phytologist*, 188(2), pp. 565–575.

Santiago, L. S. and Mulkey, S. S. (2005) 'Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem', *Trends in Ecology and Evolution*, 19, pp. 349–356.

Santonja, M. *et al.* (2017) 'Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest', *Journal of Ecology*, 105(3), pp. 801–815.

Scheiter, S., Langan, L. and Higgins, S. I. (2013) 'Next-generation dynamic global vegetation models: learning from community ecology', *New Phytologist*, 198, pp. 957–969.

Scheu, S. *et al.* (2003) 'The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces', *Oikos*, 101(2), pp. 225–238.

Schlesinger, W. H. and Pilmanis, A. (1998) 'Plant-soil interactions in deserts', *Biogeochemistry*, 42, pp. 169–187.

Schlichting, C. D. (1986) 'The evolution of phenotypic plasticity in plants', *Annual Review of Ecology, Evolution, and Systematics*, 17, pp. 667–683.

Schreeg, L. A., Mack, M. C. and Turner, B. L. (2013) 'Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species', *Ecology*, 94(1), pp. 94–105.

Schulze, E. D. *et al.* (1998) 'Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia', *Australian Journal of Plant Physiology*, 25(4), pp. 413–425.

Shaver, G. R. *et al.* (2000) 'Global warming and terrestrial ecosystems: A conceptual framework for analysis', *BioScience*, 50(10), pp. 871–882.

Simberloff, D. (2015) 'Non-native invasive species and novel ecosystems', *F1000Prime Reports*, 7(April).

Smith, B. (2001) 'LPJ-GUESS – an ecosystem modelling framework', *Department of Physical Geography and Ecosystems Analysis. INES. Sölvegaten*, 12, p. 22362.

Squeo, F. A., Arancio, G., *et al.* (2008) *Flora amenazada de la Región de Atacama y estrategias para su conservación*. ULS. La Serena: Universidad de La Serena, La Serena, Chile.

Squeo, F. A., Tracol, Y., *et al.* (2008) 'Vegetación nativa y variación temporal de su productividad en la Provincia de Elqui', in Cepeda, P. (ed.) *Los sistemas naturales de la cuenca del Río Elqui (Región de la Coquimbo, Chile): Vulnerabilidad y cambio del clima.* La Serena: Universidad de la Serena, pp. 168–191.

Stark, J. M. and Firestone, M. K. (1995) 'Mechanisms for soil moisture effects on activity of nitrifying bacteria', *Applied and Environmental Microbiology*, 61(1), pp. 218–221.

Steinberger, Y., Shmida, A. and Whitford, W. G. (1990) 'Decomposition along a rainfall gradient in the Judean desert, Israel', *Oecologia*, 82, pp. 322–324.

Sternberg, M. *et al.* (2011) 'The use and misuse of climatic gradients for evaluating climate impact on dryland ecosystems - an example for the solution of conceptual problems', in *Climate Change - Geophysical foundations and Ecological Effects*. InTech, pp. 361–374.

Sternberg, M. and Shoshany, M. (2001) 'Influence of slope aspect on Mediterranean woody formations: Comparison of a semiarid and an arid site in Israel', *Ecological Research*, 16(2), pp. 335–345.

Stone, J. K. (1987) 'Initiation and development of latent infections by Rhabdocline parkeri on Douglas-fir', *Canadian Journal of Botany*, 65, pp. 2614–2621.

Suding, K. N. *et al.* (2008) 'Scaling environmental change through the framework for plants', *Global Change Biology*, 14, pp. 1125–1140.

Sun, Y. and Zhao, S. (2016) 'Leaf litter decomposition in urban forests: test of the home-field advantage hypothesis', *Annals of Forest Science*. Annals of Forest Science, 73(4), pp. 1063–1072.

Suseela, V. and Tharayil, N. (2018) ‘Decoupling the direct and indirect effects of climate on plant litter decomposition: Accounting for stress-induced modifications in plant chemistry’, *Global Change Biology*, 24(4), pp. 1428–1451.

Tielbörger, K. *et al.* (2014) ‘Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment’, *Nature Communications*. The Author(s), 5(5102), pp. 1–9.

Tilman, D. and Downing, J. A. (1994) ‘Biodiversity and stability in grasslands’, *Nature*, 367(6461), pp. 363–365.

Tilman, D., Kilham, S. S. and Kilham, P. (1982) ‘Phytoplankton community ecology: the role of limiting nutrients.’, *Annual review of ecology and systematics. Volume 13*, pp. 349–372.

Tomiolo, S., Bilton, M. C. and Tielbörger, K. (2020) ‘Plant community stability results from shifts in species assemblages following whole community transplants across climates’, *Oikos*, 129(1), pp. 70–80.

Tomiolo, S., Van Der Putten, W. H. and Tielbörger, K. (2015) ‘Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change’, *Ecology*, 96(5), pp. 1298–1308.

Übernickel, K. *et al.* (2020) *Time series of meteorological station data in the EarthShape study areas in the Coastal Cordillera, Chile*.

van den Brink, L. *et al.* (2021) ‘Space cannot substitute for time – an integrated experimental assessment of climate-change effects on litter decomposition’, *Authorea Preprint*.

Vanderbilt, K. L. Ã. *et al.* (2008) ‘Aboveground decomposition in arid environments: Results of a long-term study in central New Mexico’, *Journal of Arid Environments*, 72(2008), pp. 696–709.

Veen, G. F. (Ciska. *et al.* (2018) ‘Variation in home-field advantage and ability in leaf litter decomposition across successional gradients’, *Functional Ecology*, 32(6), pp. 1563–1574.

Veen, G. F. (Ciska. *et al.* (2019) ‘Relationships between fungal community composition in decomposing leaf litter and home-field advantage effects’, *Functional Ecology*, 33(8), pp. 1524–1535.

Veen, G. F. C. *et al.* (2015) ‘Litter quality and environmental controls of home-field advantage effects on litter decomposition’, *Oikos*, 124(2), pp. 187–195.

Wallenstein, M. D. *et al.* (2013) ‘Litter chemistry changes more rapidly when decomposed at home but converges during decomposition - transformation’, *Soil Biology and Biochemistry*. Elsevier Ltd, 57, pp. 311–319.

Walse, C., Berg, B. and Sverdrup, H. (1998) ‘Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity’, *Environmental Reviews*, 6, pp. 25–40.

Walther, G. *et al.* (2002) ‘Ecological response to recent climate cnahge’, *Nature*, 416, pp. 389–395.

Wang, Q., Zhong, M. and He, T. (2013) ‘Home-field advantage of litter decomposition and nitrogen release in forest ecosystems’, *Biology and Fertility of Soils*, 49(4), pp. 427–434.

Wiens, J. J. and Donoghue, M. J. (2004) ‘Historical biogeography, ecology and species richness’, *Trends in Ecology and Evolution*, 19(12), pp. 639–644.

Wilhm, J. L. (1968) ‘Use of biomass units in Shannon’ s formula’, *Ecology*, 49(1), pp. 153–156.

De Wit, R. and Bouvier, T. (2006) ‘“Everything is everywhere, but, the environment selects”; what did Baas Becking and Beijerinck really say?’, *Environmental Microbiology*, 8(4), pp. 755–758.

Wolodarsky-Franke, A. and Diaz Herrera, S. (2011) *Cordillera de Nahuelbuta - Reserva Mundial de Biodiversidad*. Valdivia, Chile: WWF.

Woodward, F. I. and Diament, A. D. (1991) ‘Functional approaches to predicting the ecological effects of global change’, *Functional Ecology*, 5(2), pp. 202–212.

Wright, I. J. *et al.* (2004) ‘The worldwide leaf economics spectrum’, *Nature*, 12428, pp. 821–827.

Wright, I. J., Reich, P. B. and Westoby, M. (2001) ‘Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats’, *Functional Ecology*, 15(4), pp. 423–434.

Wu, Q. *et al.* (2020) ‘Differential responses of litter decomposition to warming, elevated CO2, and changed precipitation regime’, *Plant and Soil*. Plant and Soil, 455(4).

Xu, M. and Shang, H. (2016) ‘Contribution of soil respiration to the global carbon equation’, *Journal of Plant Physiology*. Elsevier GmbH., 203, pp. 16–28.

Xu, S. *et al.* (2020) ‘Variations in foliar carbon:nitrogen and nitrogen:phosphorus ratios under global change: a meta-analysis of experimental field studies’, *Scientific Reports*. Nature Publishing Group UK, 10(12156), pp. 1–11.

Xu, X., Shibata, H. and Enoki, T. (2006) ‘Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: dynamics of mineral nutrients’, *Journal of Forestry Research*, 17(1), pp. 1–6.

Xue, R. *et al.* (2018) ‘Slope aspect influences plant biomass, soil properties and microbial composition in alpine meadow on the Qinghai-Tibetan Plateau’, *Journal of Soil Science and Plant Nutrition*, 18(1), pp. 1–12.

Yahdjian, L. and Sala, O. E. (2002) ‘A rainout shelter design for intercepting different amounts of rainfall’, *Oecologia*, 133, pp. 95–101.

Yahdjian, L., Sala, O. E. and Austin, A. T. (2006) ‘Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe’, *Ecosystems*, 9, pp. 128–141.

Yang, J., El-Kassaby, Y. A. and Guan, W. (2020) ‘The effect of slope aspect on vegetation attributes in a mountainous dry valley, Southwest China’, *Scientific Reports*. Nature Publishing Group UK, 10(1), pp. 1–11.

Yuan, X. *et al.* (2019) ‘Litter decomposition in fenced and grazed grasslands: A test of the home-field advantage hypothesis’, *Geoderma*. Elsevier, 354(November 2018), p. 113876.

Zarnetske, P. L., Skelly, D. K. and Urban, M. C. (2012) ‘Biotic multipliers of climate change’, *Science*, 336(6088), pp. 1516–1518.

Zhang, D. *et al.* (2008) ‘Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors’, *Journal of Plant Ecology*, 1(2), pp. 85–93.

Zhang, F. *et al.* (2011) ‘Response of alpine plant community to simulated climate change: two-year results of reciprocal translocation experiment (Tibetan Plateau)’, *Polish Journal of Ecology*, 59(4), pp. 741–751.

Zheng, J. *et al.* (2017) ‘Nitrogen addition, drought and mixture effects on litter decomposition and nitrogen immobilization in a temperate forest’, *Plant and Soil*. Plant and Soil, 416(1–2), pp. 165–179.

Zhou, C. *et al.* (2019) ‘Extreme-duration drought impacts on soil CO2 efflux are regulated by plant species composition’, *Plant and Soil*, 439(1–2), pp. 357–372.

Zhou, S. *et al.* (2018) ‘Effects of reduced precipitation on litter decomposition in an evergreen broad-leaved forest in western China’, *Forest Ecology and Management*. Elsevier, 430(211), pp. 219–227.

Zhu, W. *et al.* (2016) ‘Changes in litter quality induced by nutrient addition alter litter decomposition in an alpine meadow on the Qinghai-Tibet Plateau’, *Scientific Reports*. Nature Publishing Group, 6(34290), pp. 1–10.

Supporting information

Appendix chapter 2 – Drought and increased precipitation do not have opposing effects on plant communities in a field experiment

Table S2.1. *ANOVAs for biomass, species richness, Shannon-Wiener index and evenness for traveled vs non-traveled soil. DF = degrees of freedom, F = F statistic,* p *= statistical significance, significant values in bold.*

Response	Variable	DF	SS	F Ratio	Prob > F
Biomass (g)	Origin (O)	1	0.43	0.08	0.780
	Original exposure (E)	1	7.09	1.30	0.258
	O*E	1	6.18	1.14	0.291
	Treatment (T)	2	30.04	2.76	0.070
	O*T	2	38.48	3.54	**0.035**
	E*T	2	84.09	7.73	**0.001**
	O*E*T	2	2.61	0.24	0.788
Species richness S	Origin (O)	1	0.72	0.26	0.613
	Original exposure (E)	1	7.22	2.59	0.112
	O*E	1	0.72	0.26	0.613
	Treatment (T)	2	3.04	0.54	0.583
	O*T	2	69.64	12.47	**<.001**
	E*T	2	8.04	1.44	0.244
	O*E*T	2	5.74	1.03	0.363
Shannon-Wiener Index H	Origin (O)	1	0.10	0.50	0.483
	Original exposure (E)	1	0.01	0.06	0.807
	O*E	1	0.29	1.38	0.246
	Treatment (T)	2	0.68	1.62	0.207
	O*T	2	0.51	1.21	0.306
	E*T	2	0.31	0.74	0.481
	O*E*T	2	1.32	3.14	0.051
Evenness E	Origin (O)	1	0.06	1.74	0.194
	Original exposure (E)	1	0.01	0.38	0.543
	O*E	1	0.07	2.17	0.148
	Treatment (T)	2	0.21	3.06	0.057
	O*T	2	0.02	0.30	0.742
	E*T	2	0.01	0.11	0.898
	O*E*T	2	0.11	1.62	0.211

Table S2.2. *ANOVAs for biomass, species richness, Shannon-Wiener index. DF = degrees of freedom, F = F statistic,* p *= statistical significance, significant values in bold.*

Response	Variable	DF	F Ratio	Prob > F
Biomass (g)	Origin (O)	1	0.07	0.7950
	Original exposure (E)	1	0.31	0.5783
	O*E	1	0.24	0.6280
	Treatment (T)	2	1.62	0.2087
	O*T	2	0.54	0.5875
	E*T	2	1.16	0.3236
	O*E*T	2	0.35	0.7086
Species richness S	Origin (O)	1	4.27	**0.0441**
	Original exposure (E)	1	0.02	0.9016
	O*E	1	0.94	0.3374
	Treatment (T)	2	0.13	0.8782
	O*T	2	1.10	0.3399
	E*T	2	0.14	0.8719
	O*E*T	2	2.91	0.0642
Shannon-Wiener Index H	Origin (O)	1	0.73	0.3969
	Original exposure (E)	1	0.09	0.7609
	O*E	1	0.20	0.6550
	Treatment (T)	2	1.13	0.3328
	O*T	2	1.08	0.3501
	E*T	2	0.38	0.6879
	O*E*T	2	2.76	0.0765
Evenness E	Origin (O)	0		
	Original exposure (E)	0		
	O*E	0		
	Treatment (T)	1	5.21	**0.0309**
	O*T	1	0.96	0.3374
	E*T	1	0.65	0.4270
	O*E*T	1	0.14	0.7115

Table S2.3. *Mean ± SE for biomass, species richness, Shannon-Wiener index and evenness.*

			Biomass (g)	**Species richness**	**Shannon-Wiener index**	**Evenness**
Origin	**Exposure**	**Treatment**	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Semi-arid	dry	Control	4.035 ± 1.302	3.3 ± 0.3	0.591 ± 0.087	0.496 ± 0.055
		Micro	2.459 ± 0.908	3.2 ± 0.663	0.545 ± 0.221	0.502 ± 0.118
		Macro	0.241 ± 0.241	0.8 ± 0.8	1.093 ± NA	0.789 ± NA
	wet	Control	1.827 ± 0.454	3.6 ± 0.618	0.758 ± 0.163	0.709 ± 0.059
		Micro	4.46 ± 1.267	4 ± 0.707	0.766 ± 0.247	0.533 ± 0.114
		Macro	0.575 ± 0.339	1 ± 0.447	0.329 ± 0.182	0.711 ± 0.197
Mediterranean	dry	Control	2.428 ± 0.592	2.3 ± 0.684	0.503 ± 0.187	0.751 ± 0.048
		Micro	0.829 ± 0.609	1 ± 0.548	0.275 ± 0.275	0.75 ± NA
		Macro	2.184 ± 0.4	2.8 ± 0.735	0.688 ± 0.198	0.825 ± 0.064
	wet	Control	1.005 ± 0.305	1.6 ± 0.267	0.269 ± 0.081	0.523 ± 0.067
		Micro	5.13 ± 2.13	2.6 ± 1.4	0.575 ± 0.372	0.574 ± 0.145
		Macro	2.947 ± 0.53	4.4 ± 0.6	1.198 ± 0.177	0.826 ± 0.077

Travel effects on biomass production and diversity:

We found no differences between travelled and non-travelled soil in biomass production, species diversity, Shannon-Wiener Index and evenness, in none of the sites (Figure S1a). However, as before, the species richness and Shannon-Wiener index were higher in the semi-arid climate than in the mediterranean climate (Figure 4a).

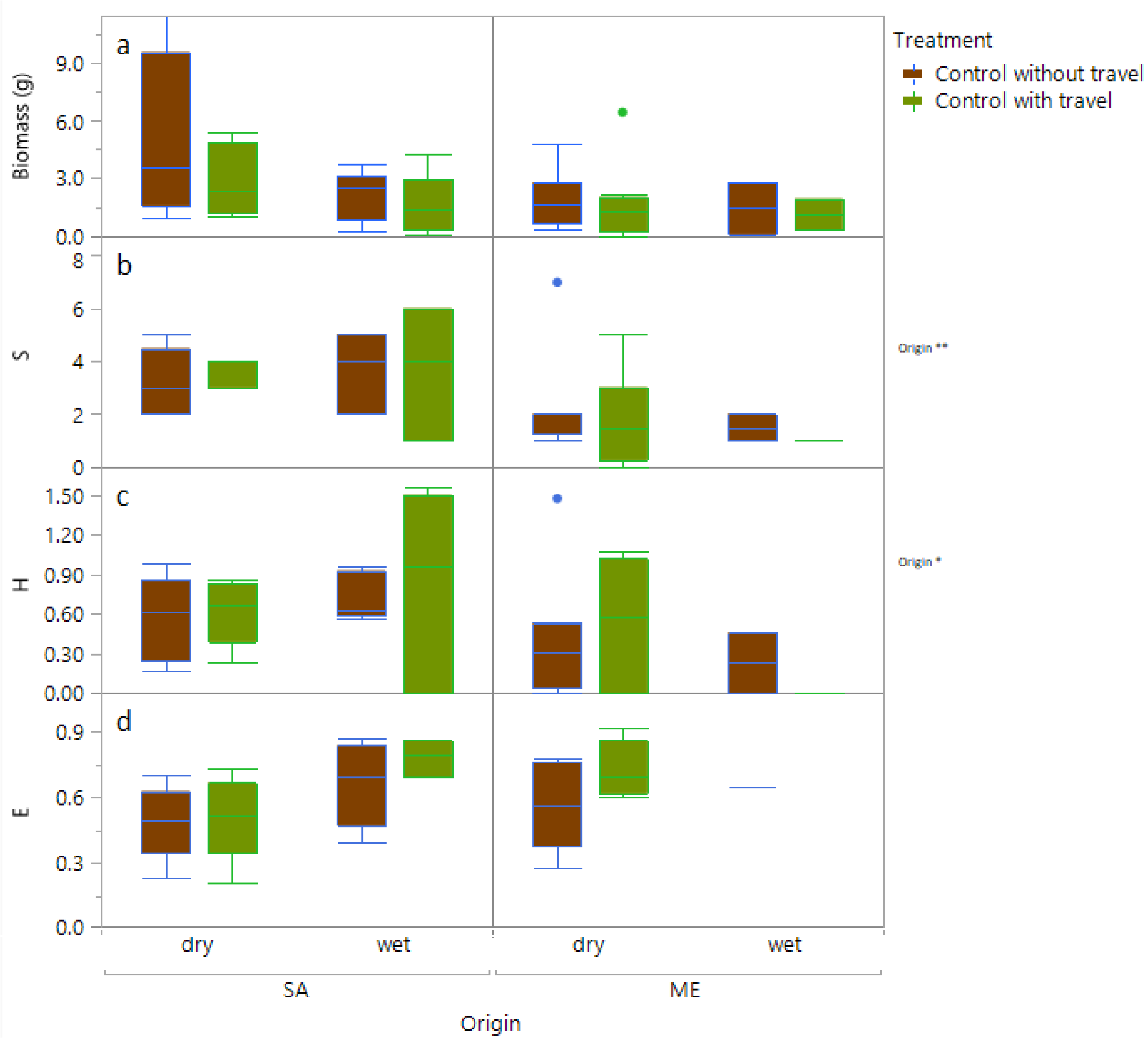

Figure S2.1. *Box-plot of a) Biomass (g), species richness (S), Shannon-Wiener index (H), and evenness (E) of soil that travelled ("control with travel") or not ("control without travel") before it was placed back in its original plot at its original exposure (dry vs wet) in its original climate (SA=semi-arid, ME=mediterranean). Significant differences of the factors are indicated on the right of the figure (* for p<0.05; ** for p<0.01; *** for p<0.001). The graph corresponds to the origin ˣ original exposure ˣ treatment interaction. There were no significant differences in this interaction. See supplementary table S2 for the corresponding statistics.*

Appendix chapter 3 – No home-field advantage in litter decomposition from the desert to temperate forest

Table S3.1. *Overview of the 19 plant species and one lichen used in a translocation experiment along a large climatic gradient in Chile, including their ecosystem origin and initial leaf litter chemistry.*

Origin	**Species**	**Growth form**	**K [mg/g]**	**P [mg/g]**	**C [mg/g]**	**N [mg/g]**	**C/N**
arid	*Heliotropium pycnophyllum* Phil.	Perennial succulent shrub	20.3	0.49	252	11.0	22.9
	Nolana crassulifolia Poepp.	Perennial succulent shrub	12.7	0.57	284	8.99	31.5
	Nolana mollis I.M. Johnst.	Perennial succulent shrub	9.79	0.19	207	3.96	52.3
	Ophryosporus triangularis Meyen	Perennial succulent shrub	19.6	1.54	415	18.9	22.0
	Tetragonia maritima Barnéoud	Perennial succulent shrub	22.9	0.87	26	11.2	23.5
semi-arid	*Cordia decandra* Hook. & Arn.	Deciduous shrub	21.3	1.23	389	19.6	19.9
	Flourensia thurifera (Molina) DC	Deciduous shrub	22.5	0.64	444	8.73	50.9
	Lobelia tupa Hook. & Arn.	Deciduous shrub	28.8	3.35	435	10.3	42.0
	Maytenus boaria Molina	Evergreen shrub	15.2	1.89	407	17.7	22.9
	Senna cumingii (Hook. & Arn.) H.S. Irwin	Evergreen or deciduous shrub	16.5	1.94	414	18.4	22.5
mediterranean	*Aristeguietia salvia* (Colla) R.M. King & H. Rob.	Deciduous shrub	23.7	1.38	426	13.3	32.0
	Cestrum parqui (Lam.) L`Hér.	Deciduous shrub	46.5	1.29	420	12.8	32.8
	Jubaea chilensis (Molina) Baill.	Palm	6.83	0.59	492	9.65	51.0
	Podantus mitiqui Lind.	Deciduous shrub	28.4	1.47	434	9.49	45.7
	Quillaja saponaria Molina	Evergreen tree	6.85	0.55	441	4.85	90.8
temperate	*Araucaria araucana* (Molina) K.Koch	Evergreen conifer	0.47	0.35	471	4.63	102
	Chusquea culeou É. Desv	Perennial grass	11.2	1.40	429	14.6	29.5
	Festuca sp.	Perennial grass	8.34	1.16	447	3.12	143
	Notofagus antarctica (G. Forst.) Oerst.	Deciduous tree	5.41	0.94	482	10.9	44.5
	Usnea sp.	Lichen	2.59	0.67	438	3.96	111

Table S3.2. *Detection limits and quality control (Certified Standard IVA 33802150, sediment high organic, lot: 155656, 144137) for C and N measurements. idl= instrumental detection limit (for a sample weight of 0.04 g), wt%= weight percentage, RSD= relative standard deviation.*

element	N [wt%]	C [wt%]
idl [wt%]	0.03	0.1
IVA 33802150 (n= 196)		
Average:	0.65	8.03
RSD [%]:	4.57	3.28
%difference to target value:	98.6	102
in-house leave standard (n= 10)		
Average:	2.27	48.5
RSD [%]:	5.40	4.31

Table S3.3. *Overview of analytical details for major and trace elements analyzed by ICP-OES after acid pressure digestion. Methodological detection limits (mdl) calculated based on extraction blind solutions (3-times standard deviation, n= 68) and a sample targeted weight of 0.05 g. Element concentrations in litter samples were corrected to the certified standard material BCR®-129 (hay powder, Institute for Reference Materials and Measurements). RSD= relative standard deviation.*

element:	K	P
wavelength [nm] measuring mode	766.490 axial	213.617 axial
mdl [mg kg^{-1}]:	8.56	2.21
n	20	20
average concentration [mg kg^{-1}]:	27584	1965
RSD [%]:	11	6
certified value [mg kg^{-1}]:	33800	2360
average recovery rate [%]:	82	83
applied correction factor:	1.23	1.20

Figure S3.1. *Location of the study sites in Chile. AR = Arid; SA = Semi-Arid; ME = Mediterranean; TE = Temperate.*

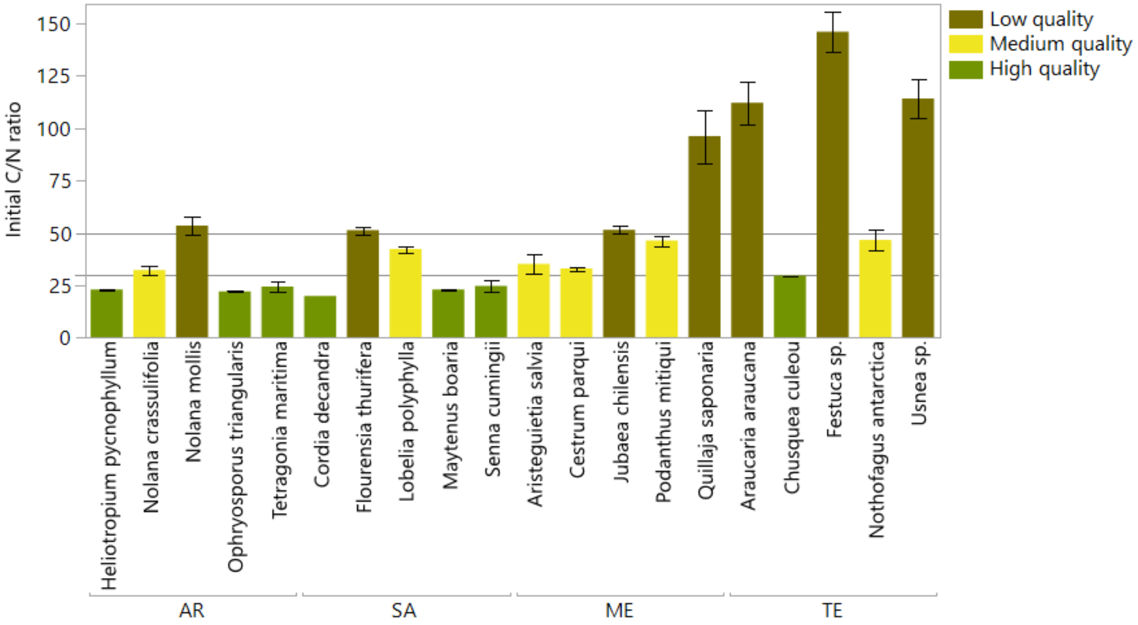

Figure S3.2. *Litter carbon to nitrogen ratio (C/N) from 20 species used in a reciprocal litter transplant experiment at four sites along the coastal cordillera of Chile. Species are ordered per origin (AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate), and classified in three litter quality categories (colors): high (C/N ratio < 30), medium (C/N ratio 30-50) and low quality (C/N ratio > 50). Error bars represent standard error.*

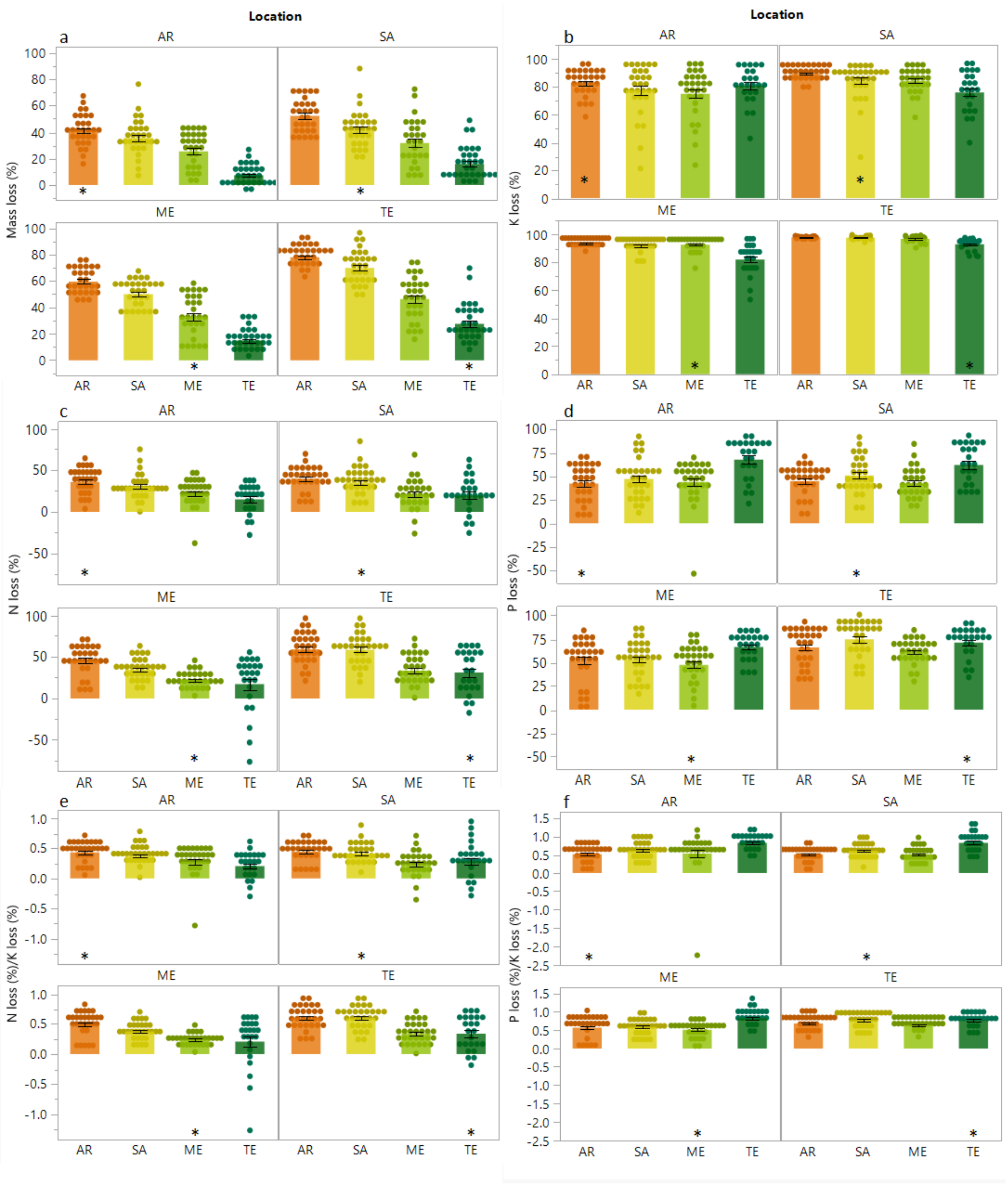

Figure S3.3. *Mass loss (%) (a), K loss (%) (b), N loss (%) (c), P loss (%) (d), N loss (%)/K loss (%) (e) and P loss (%)/K loss (%) (f) after 12 months of decomposition for litter from 19 plant species from different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile* ***(****AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate). Error bars represent the standard error. Significance is expressed per site with different letters. * = litter decomposing "at home".*

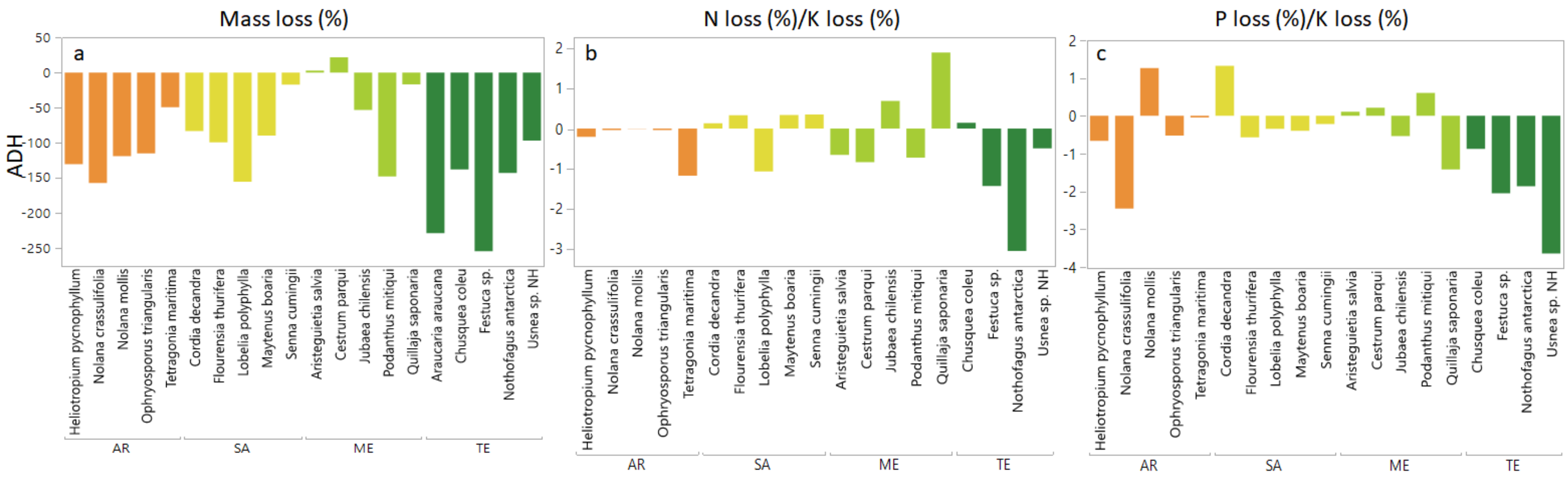

Figure S3.4. *ADH of litter mass loss (%) (a) N loss (%)/K loss (%) (b) and P loss (%)/K loss (%) (c) after 12 months of decomposition for litter from 20 plant species with different origin (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile (AR = arid, SA = semi-arid, ME = mediterranean, TE = temperate humid).*

Appendix chapter 4 – Space cannot substitute for time – an integrated experimental assessment of climate-change effects on litter decomposition

Table S4.1. *Site information, including climatic and in situ microclimatic data, averaged at site level, for the study period May 2017-May 2018). For temperature min and max and solar radiation max are the lowest and highest monthly averages. For precipitation max is the highest daily amount. Soil moisture depict means ± SD along the gradient. Solar radiation and precipitation* were measured in climate stations nearby (Übernickel et al., 2020); Soil temperature and soil moisture were measured in situ with TMS-3 loggers (TOMST, Czech Republic).*

	Soil temperature (˚C) Mean (min-max)	Solar radiation (W m^{-2}) Mean (max)	Annual precipitation* (mm y^{-1}) Total (max)	Soil moisture (m^3 m^{-3}) Mean (±SD)	Elevation (m asl)
Arid (AR)	17.6 (13.5-23.6)	235 (1124)	22 (5.2)	0.12 (±0.05)	523-529
Semi-arid (SA)	17.8 (12.4-22.9)	237 (1091)	75 (31)	0.17 (±0.09)	624-690
Mediterranean (ME)	13.7 (7.4-20.2)	211 (1096)	136 (44.4)	0.17 (±0.12)	493-778
Temperate (TE)	7.1 (0.7-14.0)	169 (1177)	2158 (136)	0.31 (±0.11)	1195-1290

* Precipitation data: Uebernickel et al. (2020) for AR, SA and TE; INIA (2020) for ME (La Cruz climate station).

Table S4.2. *Volumetric soil moisture per slope in each site and effect of drought treatment per slope in each site on volumetric soil moisture for each recollection period (3, 6 and 12 months).*

Site	Exposure	Treatment	Volumetric soil moisture (m^3/m^3)		
			3 months	6 months	12 months
Arid (AR)	Dry		0.17	0.14	0.12
Arid (AR)	Wet		0.17	0.14	0.12
Semi-Arid (SA)	Dry		0.32	0.24	0.19
Semi-Arid (SA)	Wet		0.27	0.21	0.15
Mediterranean (ME)	Dry		0.29	0.25	0.15
Mediterranean (ME)	Wet		0.32	0.28	0.19
Temperate (TE)	Dry		0.38	0.36	0.29
Temperate (TE)	Wet		0.40	0.39	0.32
Semi-arid (SA)	Dry	Control	0.32	0.24	0.19
Semi-arid (SA)	Dry	Drought	0.21	0.16	0.13
Semi-arid (SA)	Wet	Control	0.27	0.21	0.15
Semi-arid (SA)	Wet	Drought	0.22	0.17	0.12
Mediterranean (ME)	Dry	Control	0.34	0.28	0.20
Mediterranean (ME)	Dry	Drought	0.24	0.19	0.15
Mediterranean (ME)	Wet	Control	0.33	0.29	0.19
Mediterranean (ME)	Wet	Drought	0.31	0.25	0.18

Table S4.3. *Litter species and litterbag mesh used.*

Origin	Species	Litterbag
Arid (AR)	*Heliotropium pycnophyllum* Phil.	Double mesh
	Nolana crassulifolia Poepp.	Double mesh
	Nolana mollis I.M. Johnst.	Double mesh
	Ophryosporus triangularis Meyen	Double mesh
	Tetragonia maritima Barnéoud	Simple mesh
Semi-arid (SA)	*Cordia decandra* Hook. & Arn.	Simple mesh
	Flourensia thurifera (Molina) DC	Simple mesh
	Lobelia polyphylla Hook. & Arn.	Simple mesh
	Maytenus boaria Molina	Double mesh
	Senna cumingii (Hook. & Arn.) H.S. Irwin	Simple mesh
Mediterranean (ME)	*Aristeguietia salvia* (Colla) R.M. King & H. Rob.	Simple mesh
	Cestrum parqui (Lam.) L`Hér.	Double mesh
	Jubaea chilensis (Molina) Baill.	Simple mesh
	Podanthus mitiqui Lind.	Simple mesh
	Quillaja saponaria Molina	Simple mesh
Temperate humid (TE)	*Araucaria araucana* (Molina) K. Koch	Double mesh
	Chusquea culeou É. Desv.	Double mesh
	Festuca sp.	Double mesh
	Nothofagus antarctica (G. Forst.) Oerst.	Double mesh
	Usnea sp.	Double mesh
Standard litter	Lipton Green tea (EAN 87 10908 90359 5)	Teabag

Table S4.4. *Results of linear mixed model on the influence of litterbag material on mass loss of C. parqui, L. tupa and T. maritima. Species, plot and their interaction are used as random factors.*

Response	Months	Factor	DF	F Ratio	Prob>F
Decomposition	3	Material_Litterbag	3, 3	0.98	0.5684
Decomposition	6	Material_Litterbag	3, 3	0.97	0.5828
Decomposition	9	Material_Litterbag	3, 3	0.69	0.7548
Decomposition	12	Material_Litterbag	4, 6	0.36	0.6662

Table S4.5. *Detection limits and quality control (Certified Standard IVA 33802150, sediment (high organic), lot: 155656, 144137) for CN measurements. idl= instrumental detection limit (for a sample weight of 0.04 g), wt%= weight percentage, RSD= relative standard deviation.*

element	N [wt%]	C [wt%]
idl [wt%]	0.03	0.1
IVA 33802150 (n= 196)		
Average:	0.65	8.03
RSD [%]:	4.57	3.28
%difference to target value:	98.6	102
in-house leave standard (n= 10)		
Average:	2.27	48.5
RSD [%]:	5.40	4.31

Table S4.6. *Results of linear mixed models (Least Squares) on mass loss of local litter decomposing at home (space-for-time) for the effect origin, and for litter translocated to all sited (experiment-for-time, native litter, 20 species per site and standard litter (green tea)) after 3. 6 and 9 months for the effects of origin, location, exposure and all their interactions, including species, plot and their interaction as random factors. Significant results are in bold.*

	3 months			6 months			9 months		
Space-for-time									
Litter (at home)	**DF**	**F-ratio**	**p**	**DF**	**F-ratio**	**p**	**DF**	**F-ratio**	**p**
Origin (O)	2, 16	0.86	0.373	3, 21	2.63	**0.018**	NA	NA	NA
		Wald Z	**p**		**Wald Z**	**p**		**Wald Z**	**p**
Species (S)		2.38	**0.018**		1.74	**0.007**		7.68	0.197
Plot (P)		0.58	**0.021**		0.49	**0.011**		-0.54	0.112
S*P		0.18	0.078		0.23	**0.014**		4.00	**0.004**
Experiment-for-time									
Litter (translocation)	**DF**	**F-ratio**	**p**	**DF**	**F-ratio**	**p**	**DF**	**F-ratio**	**p**
Origin (O)	3, 16	20.90	**<0.001**	3, 16	22.39	**<0.001**	3, 16	18.95	**<0.001**
Location (L)	2, 12	101.38	**<0.001**	3, 16	67.54	**<0.001**	NA	NA	NA
Exposure (E)	1, 12	20.99	**0.001**	1, 16	14.90	**0.001**	1, 4	0.15	0.715
O * L	6, 313	10.46	**<0.001**	9, 423	10.57	**<0.001**	NA	NA	NA
O * E	3, 313	2.76	**0.042**	3, 423	5.24	**0.002**	3, 91	3.13	**0.030**
L * E	2, 12	12.87	**0.001**	3, 16	3.01	0.061	NA	NA	NA
		Wald Z	**p**		**Wald Z**	**p**		**Wald Z**	**p**
Species (S)		2.67	**0.006**		2.67	**0.006**		12.59	**0.006**
Plot (P)		0.06	0.236		0.22	**0.028**		0.06	0.547
S*P		0.96	**<0.001**		0.92	**<0.001**		1.18	**<0.001**
Tea									
Location (L)	2, 12	50.73	**<0.001**	3, 16	61.32	**<0.001**	NA	NA	NA
Exposure (E)	1, 12	0.89	0.365	1, 16	3.01	0.102	1, 4	0.63	0.4707
L * E	2, 12	1.51	0.261	3, 16	0.50	0.688	NA	NA	NA
		Wald Z	**p**		**Wald Z**	**p**		**Wald Z**	**p**
Plot (P)		2.37	**0.045**		0.86	0.087		0.82	0.401

Table S4.7. *Results of linear mixed models on decomposition fraction of local litter (5 species) and standard litter (green tea) after 3 and 6 months for the effects of treatment (drought vs. control), location (semi-arid vs. mediterranean), exposure (dry vs. wet) and all their interactions, including species, plot and their interaction as random factors. Significant results are in bold.*

		3 months			**6 months**	
Litter	**DF**	**F-ratio**	**P**	**DF**	**F-ratio**	**P**
Treatment (T)	1, 18	26.18	**<.001**	1, 18	23.63	**<.001**
Location (L)	1, 8	1.20	0.304	1,9	0.09	0.773
Exposure (E)	1, 18	29.83	**<.001**	1, 18	15.89	**0.001**
T * E	1, 18	0.58	0.456	1, 18	1.12	0.304
L * E	1, 18	16.26	**<.001**	1, 18	3.41	0.081
		Wald Z	**p**		**Wald Z**	**p**
Species (S)		3.72	0.050		3.16	0.052
Plot (P)		0.16	0.174		0.39	0.059
S*P		0.05	**<0.001**		0.74	**<0.001**
Tea	**DF**	**F-ratio**	**P**	**DF**	**F-ratio**	**P**
Treatment (T)	1, 18	11.80	**0.003**	1, 18	18.80	**<.001**
Location (L)	1, 18	163.13	**<.001**	1, 18	61.54	**<.001**
Exposure (E)	1, 18	10.17	**0.005**	1, 18	8.08	**0.011**
T * E	1, 18	10.29	**0.005**	1, 18	6.21	**0.023**
L * E	1, 18	6.31	**0.022**	1, 18	4.43	**0.050**
		Wald Z	**p**		**Wald Z**	**p**
Plot (P)		-0.05	0.826		0.96	0.058

Table S4.8. *Tukey post-hoc results for mass loss of species from Figure R3 and R4. Nm = Nolana mollis, Tm = Tetragonia maritima, Nc = Nolana crassulifolia, Sc = Senna cumingii, Ft = Flourensia thurifera, Ot = Ophryosporus triangularis, Lt = Lobelia tupa, Hp = Heliotropium pycnophyllum, Cp = Cestrum parqui, Cd = Cordia decandra, Pm = Podanthus mitiqui, Mb = Maytenus boaria, As = Aristeguietia salvia, Qs = Quillaja saponaria, Cc = Chusquea coleu, Fsp. = Festuca sp., Jc = Jubaea chilensis, Usp. = Usnea sp., Na = Notofagus antarctica, Aa = Araucaria araucana.*

Months	Location		Nm	Tm	Nc	Sc	Ft	Ot	Lt	Hp	Cp	Cd	Pm	Mb	As	Qs	Cc	Fsp.	Jc	Usp.	Na	Aa
3	AR		A	A	AB	BC	CD	CDE	CDE	DEF	DEF	EFG	FG	FG	GH	HI	IJ	IJK	IJK	IJK	JK	K
	SA		AB	A	BC	AB	D	D	CD	CD	D	D	E	D	D	E	EF	G	G	FG	G	G
	ME		A	B	B	B	DE	CD	C	C	CDE	F	GH	CD	E	FG	H	I	I	I	I	I
6	AR		AB	A	ABC	EF	CDE	DEF	BCD	F	FG	F	F	H	GH	I	IJ	JK	JK	K	JK	K
	SA		A	AB	BCD	ABC	EFG	EFG	CDE	DEF	FGH	GH	I	EFG	EFG	HI	I	J	J	J	J	J
	ME		A	AB	BC	CD	E	E	CD	E	DE	F	FG	CDE	E	FG	G	H	H	H	H	H
	TE		A	AB	A	BC	F	E	DE	CD	E	F	G	DE	F	F	GH	IJ	I	H	I	J
9	TE		A	AB	A	BC	FG	FG	DE	CD	EF	H	I	DE	G	H	I	KL	KL	J	K	L
12	AR		A	A	AB	CD	BC	CD	A	CDE	CDE	DE	BCD	E	CDE	F	F	FG	FGH	GH	FGH	H
	SA		A	A	ABC	AB	FG	BCDE	DEF	BCD	DEF	DEF	EF	DEF	CDEF	GH	HI	HI	IJ	HI	IJ	J
	ME		A	A	A	AB	E	DE	BC	CDE	CDE	F	G	CD	DE	G	G	H	HI	H	H	I
	TE		A	A	A	AB	E	CD	CD	BC	CD	DE	G	ABC	E	F	G	HI	H	G	H	I
3	SA	drought				AB	BC		B			C		BC								
		control				A	BC		BC			BC		BC								
6	SA	drought				ABC	BCD		BCD			D		BCD								
		control				A	BCD		AB			CD		BCD								
12	SA	drought				BC	BC		BC			BC		BC								
		control				A	C		B			BC		BC								
3	ME	drought									AB		E		BC	DE			F			
		control									A		CDE		A	CD			F			
6	ME	drought									B		C		B	C			D			
		control									A		BC		A	BC			D			
12	ME	drought									DE		E		CD	F			G			
		control									B		BC		A	E			G			

Table S4.9. *Carbon, Nitrogen and C/N of the initial litter. Species marked in grey are supposed to have low litter quality (C/N > 50).*

Species	Origin	Mean C [%]	Mean N [%]	Mean C:N ± SD	
Ophryosporus triangularis	Arid	41.53	1.89	22.02	± 0.84
Heliotropium pycnophyllum	Arid	25.21	1.10	22.91	± 0.89
Tetragonia maritima	Arid	26.21	1.12	24.26	± 5.08
Nolana crassulifolia	Arid	28.35	0.90	32.10	± 4.69
Nolana mollis	Arid	20.69	0.40	53.41	± 9.54
Cordia decandra	Semi-arid	38.87	1.96	19.86	
Maytenus boaria	Semi-arid	40.69	1.77	22.96	± 0.66
Senna cumingii	Semi-arid	41.44	1.84	24.66	± 6.55
Lobelia polyphylla	Semi-arid	43.45	1.03	42.14	± 2.54
Flourensia thurifera	Semi-arid	44.44	0.87	51.11	± 4.13
Cestrum parqui	Mediterranean	41.97	1.28	32.86	± 2.04
Aristeguietia salvia	Mediterranean	42.61	1.33	35.08	± 10.30
Podanthus mitiqui	Mediterranean	43.38	0.95	46.18	± 5.53
Jubaea chilensis	Mediterranean	49.21	0.96	51.30	± 4.13
Quillaja saponaria	Mediterranean	44.05	0.49	95.96	± 28.47
Chusquea coleu	Temperate	42.90	1.45	29.49	± 0.06
Nothofagus antarctica	Temperate	48.24	1.08	46.57	± 11.51
Araucaria araucana	Temperate	47.25	0.44	111.86	± 22.62
Usnea sp.	Temperate	43.83	0.40	114.02	± 21.05
Festuca sp.	Temperate	44.72	0.31	145.73	± 21.63

Table S4.10. *Mean percentage of carbon, nitrogen and C/N ratio ± SD of the initial litter per origin. See supplementary data table R4 for values per species.*

Origin	Mean C [%]	Mean N [%]	Mean C/N ± SD	
Arid (AR)	28.40	1.08	30.94	± 12.97
Semi-arid (SA)	42.39	1.41	34.94	± 13.47
Mediterranean (ME)	44.24	1.00	52.27	± 26.59
Temperate (TE)	45.73	0.64	97.72	± 44.97

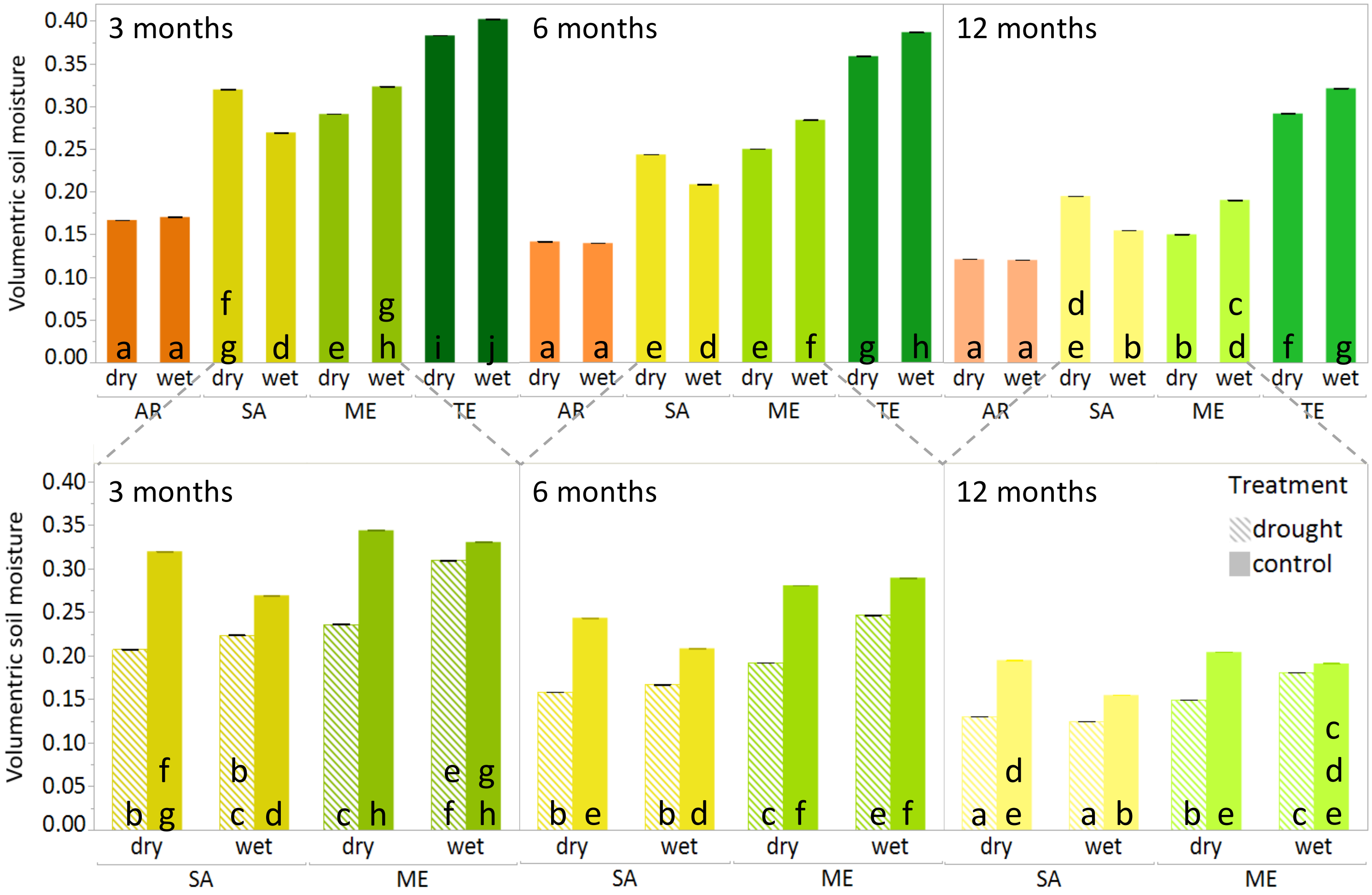

Figure S4.1. *Mean volumetric soil moisture (m³/m³) per site (above) and in the drought treatment (below) after 3, 6 and 12 months in two sites (semi-arid and mediterranean) on dry (north facing) and wet (south facing) slopes. Drought treatment in the 2 central sites is depicted with striped bars, the control with full bars. Error bars represent standard error. Results from least squares means, and Tukey HDS post-hocs, analyzing volumetric soil moisture, with site, exposure (and treatment) and their interaction(s) are used as fixed factors.*

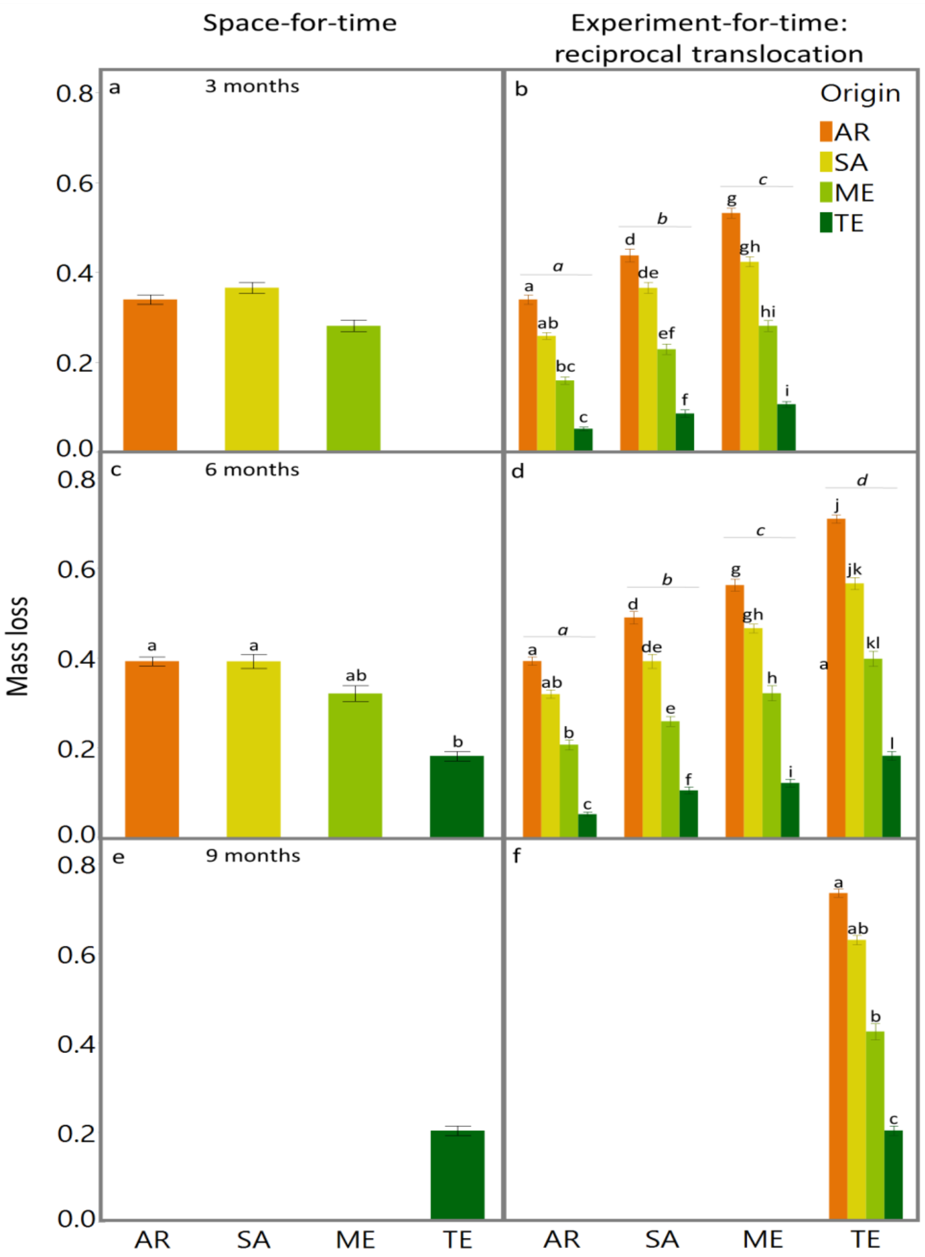

Figure S4.2. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight, in proportion) of 20 species from 4 climates (Origin) along a climate gradient in Chile after 3 (a and b), 6 (c and d) and 9 (e and f) months shown in each climate (Location of decomposition, AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate) with increasing precipitation from left to right. Left panels (a, c, and e) represent litter mass loss of local litter at the home site (i.e. space-for-time). Significant differences (p<0.05) of litter decomposing at home are indicated in above the bars (n=3). Right panels represent litter mass loss of reciprocally translocated litter (i.e. experiment-for-time), significant differences in mass loss (p<0.05) between climates are indicated above the bars in underlined italic letters (n=3), significant differences between origins of litter are indicated directly above the bars (n=3) (NOTE: letters of significance can only be compared within climates, not between). See Table 4.1 for statistics.*

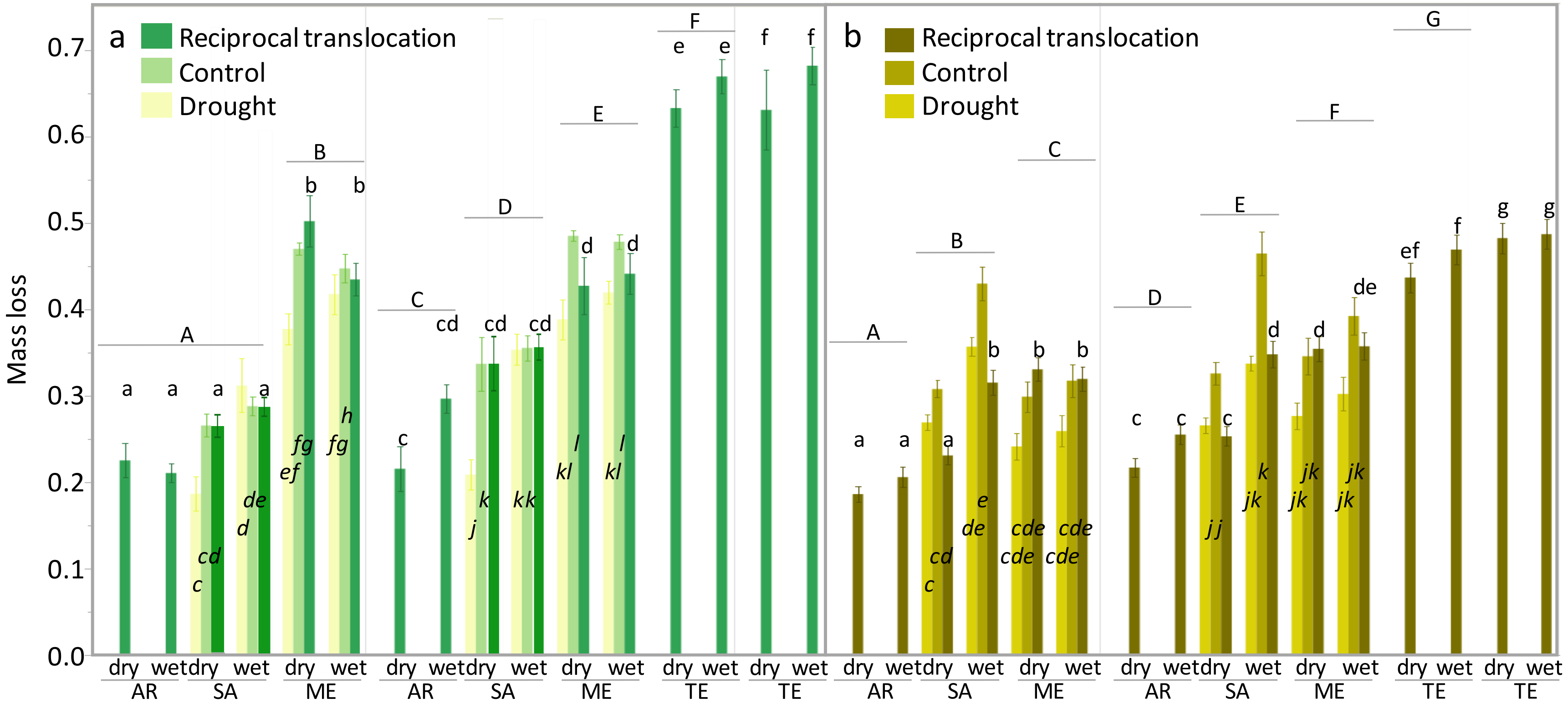

Figure S4.3. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight) along a climate gradient in Chile after 3 and 6 months shown in each climate (Location of decomposition, AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing precipitation from left to right for a) all native litter combined and b) standard litter (Lipton green tea). Dark bars show the mass loss from the reciprocal transplant of 20 species (n=3), or tea (n=2) along the climate gradient (significant differences in uppercase) at both expositions (dry vs wet: significant differences, $p<0.05$, in lowercase). Lighter bars in the SA and ME climate show the mass loss of the 5 local species (n=3) and tea (n=2) in the drought experiment (significant differences between drought and control plots, $p<0.05$, in italic. NOTE: letters of significance can only be compared within climates, not between). See Table 4.2.for corresponding statistics.*

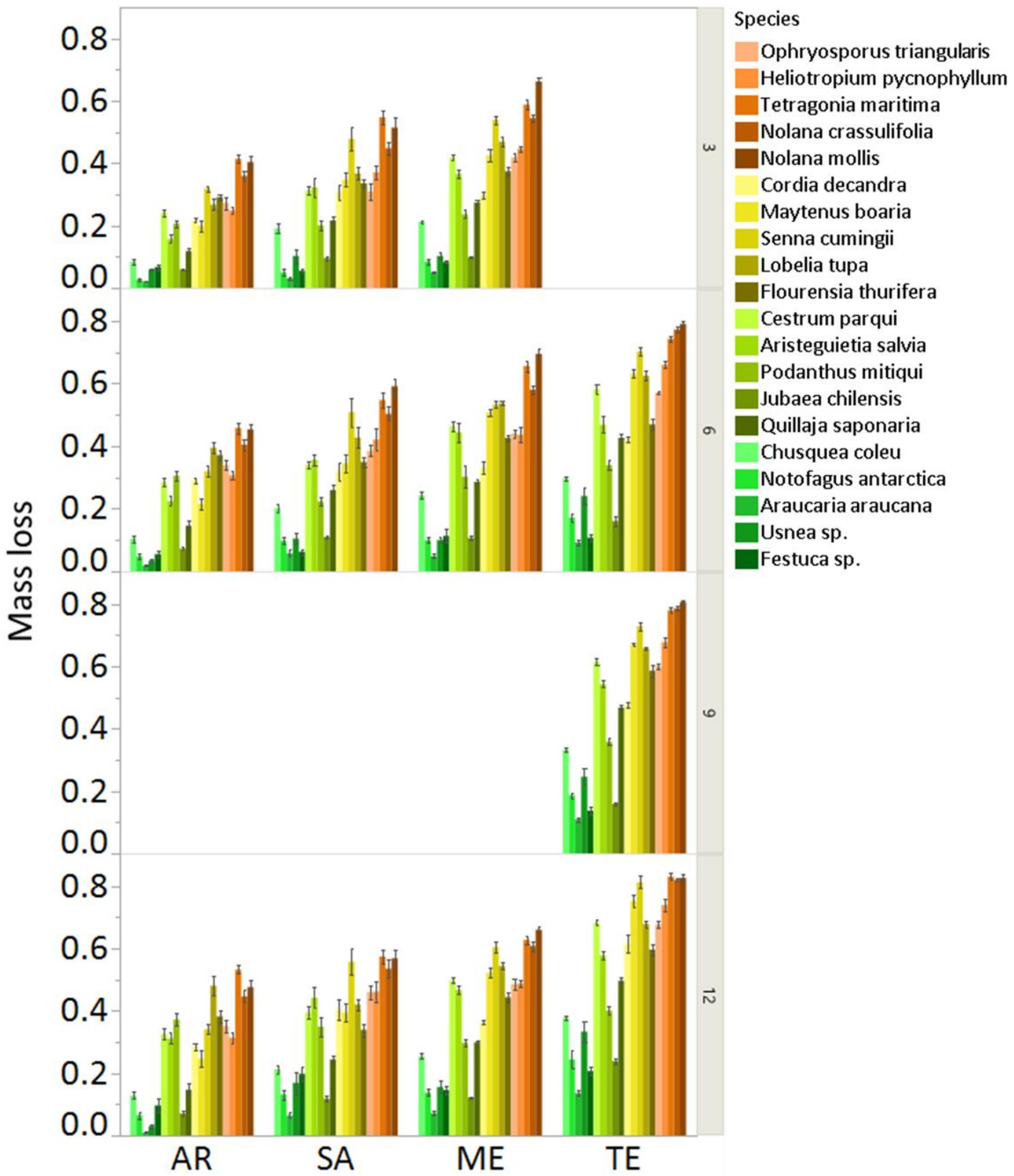

Figure S4.4. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight, in proportion) per species (Orange = Arid (AR) species, yellow = semi-arid (SA) species, yellow green = mediterranean (ME) species, green = temperate (TE) species), along a climate gradient in Chile after 3, 6, 9 and 12 months (top to bottom), shown in each climate (Location of decomposition, AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing precipitation from left to right. See Table R3 for Tukey post-hoc results*.

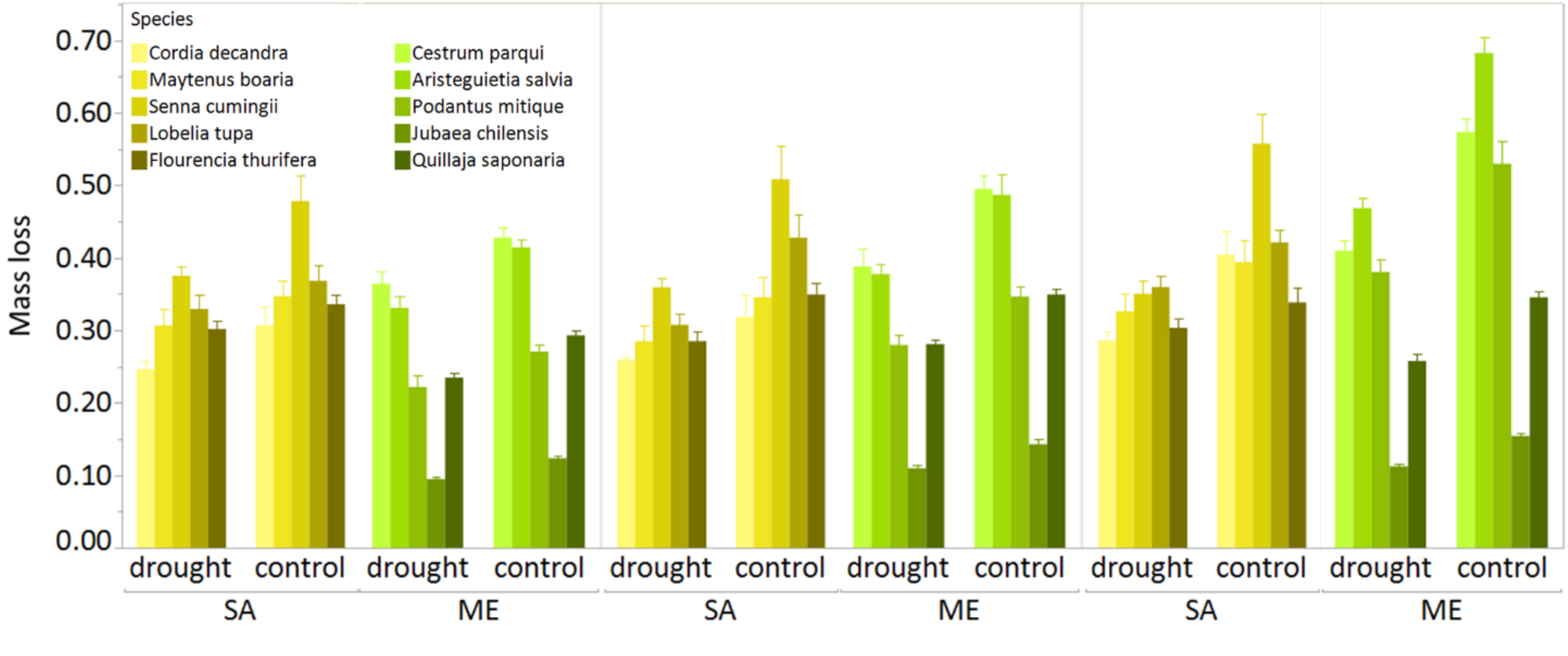

Figure S4.5. *Mean ± SE mass loss (i.e. ratio between mass loss and initial weight, in proportion) per species (yellow = semi-arid (SA) species, green = mediterranean (ME) species) in the drought experiment in the two central sites (Location of decomposition, SA=semi-arid, ME=mediterranean), with increasing precipitation from left to right for 3 (left), 6 (middle), and 12 months (right). See Table R3 for Tukey post-hoc result.*