Interactive plant-trait and climate effects on litter decomposition along the Chilean coastal range

Dissertation

zur Erlangung des Doktorgrades

der Naturwissenschaften (Dr. rer. nat.)

dem Fachbereich Geographie

der Philipps-Universität Marburg

vorgelegt von

Rafaella Canessa Mesías

aus Santiago, Chile

1. Gutachterin: Prof. Dr. Maaike Bader
2. Gutachter: Dr. Paul Kardol

Einreichungstermin: 13. Januar 2021

Prüfungstermin: 10. März 2021

Marburg/Lahn, 2021

1180

Vom Fachbereich Geographie

der Philipps-Universität Marburg als Dissertation

Gutachterinnen und Gutachter:

Prof. Dr. Maaike Bader (Faculty of Geography, University of Marburg, Marburg, Germany)

Dr. Paul Kardol (Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden)

To my grandparents

who joined me in this journey

overcoming all physical distance

[…]
One breathes
the change
of borders,
from moisture to wind
from the wind to the roots.
Something muffled, profound,
works beneath the earth
storing dreams.
[...]

Pablo Neruda, *"Oda al Otoño"* [Ode to autumn].
Odas Elementales, 1954.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

ANCOVA = Analysis of covariance

ANOVA = Analysis of variance

AD = Arid Dry (dry desert)

AF = Arid Fog (fog influenced desert)

AIC = Akaike information criterion

Al = Aluminium

AP = Annual precipitation

AR = Arid

C = Carbon

Ca = Calcium

CO_2 = Carbon dioxide

CONAF = Corporación Nacional Forestal (Chilean National Forest Corporation)

DF = Degrees of freedom

DFG = Deutsche Forschungsgemeinschaft (German Research Foundation)

Fe = Iron

FDis = Functional dispersion

Fp = Force to punch

HFA = Home-field advantage

K = Potassium

LAI = Leaf area index

LM = Linear model

LMM = Linear mixed model

MAT = Mean annual temperature

ME = Mediterranean

Mg = Magnesium

Mo = Observed mass loss of a mixture

Mp = Predicted mass loss of a mixture

Mn = Manganese

MS = Mean of squares

MSM = Mean soil moisture

MST = Mean soil temperature

N = Nitrogen (chemical element) or Newton (force unit)

Na = Sodium

P = Phosphorus

Pg = Petragram = 10^{15} g

Relative N/K loss = N loss (%) / K loss (%)

Relative P/K loss = P loss (%) / K loss (%)

SA = Semi-Arid

SD = Standard deviation

SLA = Specific leaf area

SS = Sum of squares

TE = Temperate

TL = Temperate Lowland

TU = Temperate Upland

UV = Ultraviolet

Veg. cover = Vegetation cover

Preface

This study is part of the EarthShape project, a transdisciplinary Chilean-German research initiative that aims to understand how microorganisms, plants and animals influence the shape and development of the Earth's surface over time scales from the present-day to the distant geologic past. All different projects were (and are being) developed along a large climatic gradient along the Chilean coastal range, ranging from the arid Atacama Desert to humid temperate forests. Thus, the gradient allows a variation in climate and vegetation, while keeping bedrock type, glacial and volcanic influences controlled.

This study represents a link between climate, vegetation and nutrient cycles. In particular, I studied the ecological aspects of an important ecosystem function, litter decomposition, by analyzing the effects of climate, plant and litter functional traits and functional diversity on litter mass loss and nutrient loss.

My project worked in very close collaboration with the Plant Ecology Group of the University of Tübingen, Germany. Within this collaboration, several other manuscripts in preparation will complete this story of litter decomposition along the Chilean costal range.

I hope that this thesis will contribute to a better understanding of this important ecological process, its influences on the carbon and nutrient cycles and thus, its relevance for the Earth's surface and life.

January 2021 Rafaella Canessa Mesías

Summary

Litter decomposition is the breakdown of dead organic matter along with the transformation and liberation of its components as inorganic forms. This process is of high importance in ecosystem ecology, as it determines the available resources to below and aboveground communities, as well as nutrient and carbon dynamics and soil formation.

Climate, vegetation (via litter traits) and decomposers are the main drivers of litter decomposition. However, these factors interact with each other, which makes the evaluation of their relative importance for decomposition a difficult task. For example, climate controls have both direct (e.g. via moisture and temperature) and indirect (via changes in species abundance, composition and litter traits) influences. Studies along natural gradients and litter transplant experiments can help to disentangle these effects. In this doctoral research, I particularly studied the role of climate and litter traits in litter decomposition across a large climatic gradient in the Chilean coastal range, by using different litterbag experiments and litter from species with a high variation of functional traits (i.e. litter quality).

In the first study, I tested whether soil decomposers are "adapted" to local litter types and thus, these decompose faster compared to the decomposition of non-local litter with similar quality. Under the assumptions of this so-called "home-field advantage" (HFA) hypothesis, I tested whether this adaptation occurs and differs across a wide range of ecosystems, where litter input and microbial specialization may vary. I used a reciprocal litter translocation experiment with 20 species of different litter quality among four different study sites distributed along the Chilean costal range. In addition to mass loss, I used the loss ratios of decomposable and leachable fractions of litter (relative N/K and P/K loss) to understand the specific contribution of decomposers to decomposition and to avoid confounding climatic effects. The results showed no support for the HFA hypothesis in any ecosystem, since the mass and nutrient loss ranking of litter species was consistent along the climatic gradient, i.e. in every site, litter from the arid sites always decomposed the fastest, and litter from the mediterranean and temperate sites decomposed the slowest. These results supports the hypothesis that, in the studied ecosystems, litter quality drives decomposer activity independently of litter origin, and that the decomposer community can probably quickly adjust when foreign litter enters their ecosystem.

In the second study, I unraveled the relative importance of litter quality and microclimate (soil moisture and temperature) for litter decomposition, and identified how their effects varied along the decomposition process. By using a reciprocal litter translocation experiment along the climatic gradient in Chile, I followed the decomposition of 30 species with a wide spectrum of functional traits for two years. Litter traits had a strong impact on litter decomposition across the gradient, while an increase in decomposition with soil moisture was observed only in the wettest climates. Overall, litter traits drove decomposition in the first year of decomposition after which soil moisture increased considerably in importance. Moreover, statistical analyses of subsets of the 30 species showed that litter trait effects on litter decomposition gain in importance when the variation in trait values was larger. Thus, the relative effects of litter traits and climate on decomposition depend on the ranges in climate and litter traits considered in the study, and also change with time.

In the last study, I evaluated the role of diversity (species number and functional dispersion, FDis) on litter mixture decomposition across ecosystems. I used FDis values based on litter traits related to nutrient transfer among litters or litter recalcitrance, two mechanisms that could explain litter mixture effects. I found only a small number of significant mixture effects on decomposition (both positive and negative) along the climatic gradient, which occurred more often in the most arid sites. These mixture effects were independent of the number of species in the litter mixtures at all sites, but were stronger with increasing FDis at the two most arid sites. At these sites, FDis based on litter traits related to nutrient content correlated with positive mixture effects on decomposition, whereas traits related to inhibitory secondary compounds correlated with negative mixture effects. Overall, this study indicates that mixture effects on decomposition are rather rare across the climatic gradient. However, it suggests that a mechanistic approach to functional diversity metrics could help to further understand under which conditions and in which direction diversity influences decomposition.

Altogether, this thesis highlights the importance of litter traits in litter decomposition: this factor not only drives the affinity of decomposers and determines species rankings in decomposability, but can also exert additional controls via functional diversity. I demonstrated that the study of a broad range of litter traits and litter species is decisive to correctly predict the relative importance of litter quality on decomposition, and likely controls the occurrence of litter mixture effects. Similarly, the use of a large climatic range allows to detect critical differences among ecosystems. These results are of particular importance to correctly predict litter decomposition feedbacks on climate and highlight the importance of studies including representative ranges in climate and vegetation. Of particular interest are the underrepresented ecosystems, such as arid and semi-arid areas. In these ecosystems, I showed that litter quality can strongly drive decomposition and litter mixture effects, in contrast to the results from mediterranean and temperate forests. The importance of litter quality, highlighted in all three studies, opens a frame for new research focusing in the understanding of human-driven changes in the functional composition of vegetation for decomposition and thus, for carbon and nutrient cycling.

Zusammenfassung

Im Verlauf des Prozesses der Streuzersetzung zerfällt tote, organische Materie, wird transformiert und ihre Bestandteile werden dann in anorganischer Form freigesetzt. Dieser Prozess ist von hoher Bedeutung in der Ökosystemökologie, da er für überirdische und unterirdische Lebensgemeinschaften die Menge der vorhandenen Ressourcen bestimmt sowie sowohl den Nährstoff- und Kohlenstoffhaushalt als auch die Bodenbildung beeinflusst.

Klima, Vegetation (über funktionelle Merkmale) und Zersetzer sind die wichtigsten Einflussfaktoren der Streuzersetzung. Trotzdem interagieren diese Faktoren miteinander, was die Einschätzung ihrer relativen Bedeutung für den Prozess erschwert. So nehmen zum Beispiel Klimafaktoren sowohl direkten (e.g. über Feuchtigkeit, Temperatur) als auch indirekten (über Veränderung der Artenvielfalt, Artenzusammensetzung und Merkmale des Streus) Einfluss. Studien entlang von natürlichen Gradienten und Experimente mit der Translokation von Streu können helfen, diese Effekte zu entwirren. Im Rahmen der vorliegenden Doktorarbeit wurde über den hohen Klimagradienten der Küstenregion Chiles die Bedeutung von Klima- und Streumerkmalen für die Streuzersetzung erforscht. Es wurden Streubeutelexperimente ausgeführt und Streu von Pflanzenarten mit einer hohen Variation funktioneller Merkmale (i.e. Streubeschaffenheit) verwendet.

Das Ziel der ersten Studie bestand darin, zu testen, ob sich Destruenten im Erdboden an lokale Streu „anpassen“ und diese somit schneller zersetzen als nicht heimische Streu von ähnlicher Qualität. Unter Annahme dieser so genannten „Heimvorteil- Hypothese“ (home-field advantage hypothesis, HFA) wurde untersucht, ob die Anpassung auftritt und inwiefern dabei verschiedene Ökosysteme unterschieden werden, in denen Streuvorkommen und mikrobiologische Spezialisierung variieren können. Um die HFA zu überprüfen, wurde ein reziprokes Streutranslokationsexperiment zwischen vier Orten entlang der Chilenischen Küste, mit 20 Pflanzenarten verschiedener Streuqualität durchgeführt. Zusätzlich zum Gewichtsverlust sollte der Verlustanteil von zersetzbarem und auslaugbarem Material (relativer N/K und P/K Verlust) herangezogen werden, um den spezifischen Beitrag der Destruenten zur Zersetzung zu verstehen, und weiterhin eine Verwechslung der klimatischen Effekte zu vermeiden. Die Ergebnisse widerlegen für jedes Ökosystem die HFA Hypothese, da die Gewichts- und Nährstoffverluste der verschiedenen Streuarten auf einer Rangliste konstant bleiben. Bei jedem Standort wurde Streu aus den ariden Zonen am schnellsten zersetzt, während Streu aus den mediterranen und gemäßigten Zonen den langsamsten Gewichts- bzw. Nährstoffverlust erfuhr. Die Resultate unterstützen somit die These, dass in den untersuchten Ökosystemen die Beschaffenheit des Streus die Aktivität der Destruenten steuert und diese unabhängig von der Herkunft des Materials variiert. Zudem kann postuliert werden, dass die Destruentengemeinschaft sich wahrscheinlich schnell anpassen kann, wenn auswärtige Streu in das Ökosystem gelangt.

Im zweiten Experiment konnte die relative Bedeutung des Einflusses der Streuqualität und des Mikroklimas (Bodenfeuchtigkeit und Temperatur) auf die Streuzersetzung näher bestimmt und weiterhin identifiziert werden, wie die Effekte der beiden Faktoren während des Zersetzungsprozesses variieren. Durch die Nutzung eines reziproken Streutranslokationsexperiments entlang des Klimagradienten in Chile war es möglich, der Zersetzung von 30 Pflanzenarten mit hoher Variation funktioneller Merkmale über zwei Jahre

hinweg zu folgen. Die Merkmale hatten einen starken Einfluss auf die Streuzersetzung im Gradienten, während eine Erhöhung der Zersetzung mit steigender Bodenfeuchtigkeit nur in den feuchtesten Klimazonen beobachtet werden konnte. Insgesamt bestimmten im ersten Jahr des Experiments die funktionellen Merkmale über das Maß der Zersetzung. Danach gewann der Faktor der Bodenfeuchtigkeit merklich an Bedeutung. Darüber hinaus zeigten statistische Analysen von Untergruppen der 30 Pflanzenarten, dass der Effekt funktioneller Merkmale auf die Streuzersetzung an Bedeutung gewinnt, wenn die Variation von Merkmalsausprägungen höher ist. Folglich hängen die relativen Effekte der funktionellen Merkmale und des Klimas auf die Zersetzung von der Variation des Klimas und der funktionellen Merkmale ab, ändern sich aber auch mit der Zeit.

In der dritten Untersuchung wurde die Rolle der Diversität (Artenvielfalt und funktionelle Dispersion, FDis) auf die Zersetzung von Streumischungen über Ökosysteme hinweg beurteilt. Hier wurden FDis Werte genutzt, basierend auf den funktionellen Merkmalen, in Beziehung stehend zum Nährstofftransfer innerhalb der Streu oder Widerständigkeit der Streu, zwei Mechanismen, welche die Streumischungseffekte erklären könnten. Es konnte nur eine kleine Anzahl von signifikanten Mischungseffekten auf die Zersetzung (sowohl positiv als negativ) entlang des Klimagradienten gefunden werden, was am meisten an den aridesten Standorten passierte. Diese Mischungseffekte waren an allen Standorten unabhängig von der Anzahl der Arten in der Streumischung, waren aber stärker mit steigender FDis an den zwei aridesten Standorten. An diesen Standorten stand die FDis basierend auf funktionellen Merkmalen in Beziehung zum Nährstoffgehalt, korrelierend mit positiven Mischungseffekten, während Merkmale in Beziehung zu hemmenden sekundären Zusammensetzungen mit negativen Mischungseffekten korrelierten. Insgesamt weist diese Studie darauf hin, dass Mischungseffekte auf Zersetzung eher selten entlang des klimatischen Gradienten auftreten. Allerdings lässt dies erkennen, dass eine mechanische Herangehensweise an die Messung funktioneller Diversität zu einem tieferen Verständnis führen könnte, unter welchen Bedingungen und in welche Richtung Diversität Zersetzung beeinflusst.

Insgesamt unterstreicht diese Doktorabeit die Wichtigkeit von funktionellen Merkmalen in der Streuzersetzung: dieser Faktor bestimmt nicht nur die Affinität der Destruenten und legt Artenrankings in Bezug auf Unzersetzbarkeit fest, kann aber auch über funktionelle Diversität erweiterte Kontrolle ausüben. Es wurde demonstriert, dass die Studie einer breiten Vielfalt funktioneller Merkmale und Streuarten entscheidend dafür ist, die relative Wichtigkeit der Streumerkmale auf die Zersetzung korrekt vorherzusagen und wahrscheinlich das Auftreten von Streumischungseffekten kontrolliert. Ebenso erlaubt die Nutzung eines großen klimatischen Bereichs kritische Unterschiede zwischen Ökosystemen zu erkennen. Diese Ergebnisse sind von besonderer Wichtigkeit, um Streuzersetzungsfeedbacks auf das Klima korrekt vorherzusagen und die Wichtigkeit von Studien zu unterstreichen, die einen repräsentativen Umfang in Klima und Vegetation beinhalten. Von besonderem Interesse sind unterrepräsentierte Ökosysteme, wie zum Beispiel aride und semiaride Klimazonen. In diesen Ökosystemen konnte gezeigt werden, dass Streumerkmale die Zersetzung und Streumischungseffekte stark bestimmen können, im Kontrast zu den Resultaten von mediterranen und gemäßigten Wäldern. Alle drei der durchgeführten Experimente verdeutlichen die Wichtigkeit der funktonellen Merkmale und schaffen zusätzlich einen Rahmen für neue Forschung zum Verständnis von menschengemachten Veränderungen in der

funktionellen Komposition von Vegetation für die Zersetzung und somit für Kohlenstoff- und Nährstoffkreisläufe.

Chapter 1

General Introduction

1.1 State of the art

1.1.1 Organic matter decomposition and the cycling of nutrients

In the majority of ecosystems on Earth, most of the annual net primary production falls to the ground (McNaughton et al., 1989, Cebrian et al., 1999), providing both resources and habitat to decomposer communities of microbes and detritivores (Bardgett & Wardle 2010). This litter layer is mainly composed by leaves (which in forests can account for more than 70% of litterfall) but also contains stems, twigs and reproductive structures (Robertson and Paul 1999). Here, the dead organic residues enter a decomposition process where organic matter is broken down into smaller particles, soluble compounds and gases. At a molecular scale, this implies the transformation of complex organic molecules (e.g. carbohydrates and proteins) to simpler forms such as sugars, amino acids, and inorganic compounds such as carbon dioxide (Weathers et al. 2013). At the ecosystem level, this process is responsible for the mineralization and recycling of nutrients and carbon and strongly regulates plant nutrient supply (Swift et al. 1979). Furthermore, litter decomposition rates control the nutrient holding capacity and pH of the soil, as well as the diversity and functioning of food webs (Weathers et al. 2013).

The litter decomposition process is strongly linked to the carbon cycle: it determines the immobilization of carbon in soils (Scholes, Powlson, & Tian, 1997) as well as the release of an important flux of carbon dioxide (CO_2) to the atmosphere via the respiration of microorganisms (De Deyn, Cornelissen, & Bardgett, 2008). In a certain way, the release of CO_2 is the reverse process of carbon fixation, as the bonds formed during primary production are broken. It has been estimated that 50-70% of the soil respiration across ecosystems (a total of 68 Pg of carbon per year) is due to organic decomposition, whereas the remaining portion is associated to mycorrhizae and roots respiration (Raich & Schlessinger 1992). The balance between a complete mineralization of the organic matter (producing CO2 and inorganic nutrients) and a partial process that sequesters elements in stable organic compounds is key to global atmospheric carbon budgets (Berg & McClaugherty 2008, Schlesinger & Andrews 2000). Moreover, it also influences the structure and formation of soil (humification) and weathering. For example, when part of the litter is stored as humus, it can act as a carbon source for microorganisms that subsequently produce acids and contribute to mineral weathering (Berg & McClaugherty 2008).

Over the last decades, this balance between release and immobilization of nutrients in soils has become of particular importance in the context of global change. Anthropogenic activities have resulted in increasing fossil fuel burning, deforestation and a global rise in CO_2 emissions (IPCC 2007). In this context, to understand the drivers of decomposition has become a central objective in ecology and biogeochemistry. In the following sections, I will provide an overview of the current knowledge about the drivers of this important ecosystem process (Fig. 1-1), as well as the gaps that were investigated within this project.

1.1.2 Climate and plant traits, the main drivers

The same type of litter decomposes differently under different environmental conditions, while different litter types decompose differently under the same environmental conditions. These observations in early decomposition studies led to identify the most important drivers of litter mass loss: the substrate composition (i.e. litter quality), the environmental conditions (i.e. temperature, moisture, soil properties) and the microorganisms involved (identity and

abundance) (Fig. 1-1; Tenney & Wacksman 1929; Meentenmeyer 1978, Swift et al., 1979). Moreover, these factors affect and are affected by each other (Aerts 1997; Suseela & Tharayil 2018; García-Palacios et al. 2013), which has made the study of their relative importance a difficult task. Understanding these interactions is yet highly relevant for the parameterization of global biogeochemical and carbon models.

It has been widely established that litter decomposition increases with increasing temperature and precipitation (Cornwell et al., 2008; Zhang et al., 2008), as moist and warm conditions stimulate the activity of decomposers (Bardgett & Wardle, 2012). Another climatic parameter that strongly and positively correlates with decomposition is evapotranspiration (AET; Meetenmeyer 1978; Coûteaux et al., 1995). Nonetheless, because decomposition occurs in and at the near-surface of soils, soil temperature and moisture can be even more relevant than classic macroclimatic parameters (Bradford et al., 2016, 2017; Gotschall et al., 2019).

Despite the strong effects of these climatic parameters, Zhang et al. (2008) demonstrated that none of them alone can explain the global variability of litter mass decay and that the addition of litter quality increased significantly the explained variation of decomposition models. The correlation between chemical and physical properties of the litter with decomposition implies that litter quality has a strong influence on nutrient cycling and carbon sequestration in soils. High-quality litter (i.e. low C/N ratio, lignin concentration, lignin/N ratio, leaf toughness and high nutrient content) is associated with high decomposition rates, whereas the low litter quality (recalcitrant litter with opposite traits) is associated with low decomposition rates (Zhang et al. 2008; Makkonen et al., 2012) and thus, with nutrient and carbon sequestration.

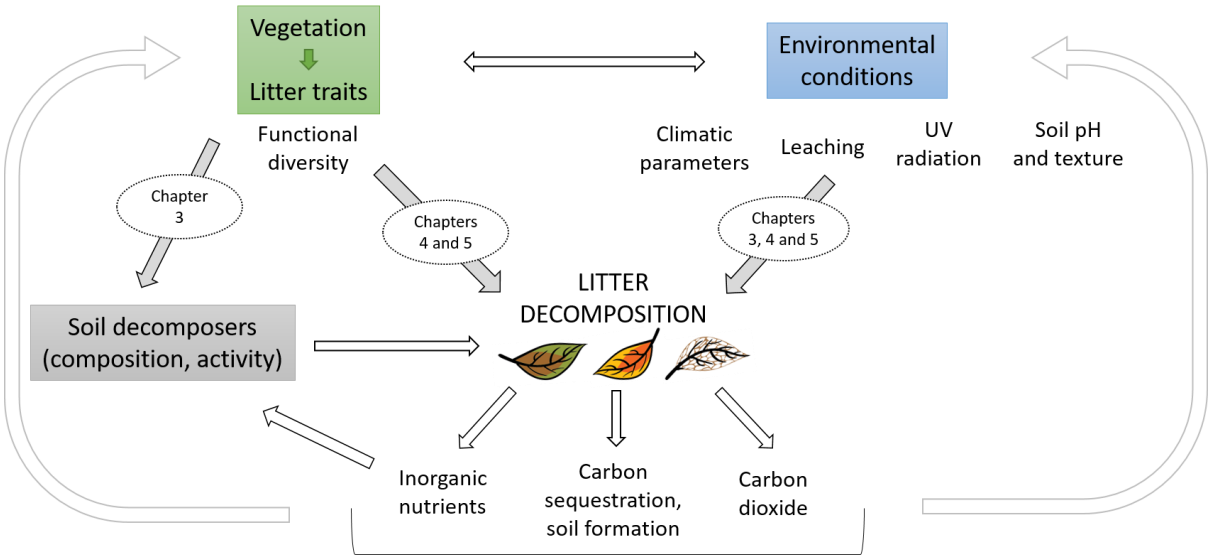

Figure 1-1. Schematic representation of factors driving litter decomposition and how its products determine feedbacks to the process. Circles show in which chapters of this thesis each of these factors and their effects on decomposition are addressed.

The relative importance of litter quality, compared to the importance of climate is, however, not well understood. To disentangle the effects of climate and litter quality, studies have made use of natural climatic gradients and litterbag experiments. By translocating different litter types among climate zones, it is possible to study the decomposition of similar litter types under

differing climate conditions as well as the decomposition of different litter types under one common environment. Although several decomposition experiments across sites have been performed (e.g. Trofymow et al., 2002; Zhou et al., 2008; Currie et al., 2010), the use of large and strong gradients in combination with a wide range of litter types are rare (Makkonen et al., 2012). Studies differ in the number and identity of species evaluated (therefore in the trait spectrum included), ecosystems and the experimental decomposition time. However, the variable ranges of climate, litter types and decomposition period included likely determine the importance of these drivers and thus, their effects are still incompletely understood. In Chapter 4, I will address these inconsistencies, by using a litterbag translocation experiment including a wide range of litter quality and climates and a relatively large decomposition period.

While the role of decomposers on litter decomposition has been traditionally highlighted, recent studies suggest that they are indirect drivers of decomposition, as litter quality and climate strongly modulate their effects (Hättenschwiler et al., 2005; García-Palacios et al., 2013; Bradford et al., 2016). For instance, increasing precipitation increases the effect of soil on decomposition (García-Palacios et al., 2013). On the other hand, macrofauna can change their feeding preferences for particular litter species depending on the total litter composition (Hättenschwiler & Bretscher, 2001). An important interaction between litter types and soil organisms is the so-called home-field advantage (HFA). This hypothesis predicts that soil microorganisms are adapted to local litter (i.e. from plant growing in the same site or area) and that local litter will decompose faster than non-local litter. This implies that litter quality effects are not only related to its physical and chemical traits, but also to the specialization and previous exposure of the decomposer community to certain litter types (Strickland et al., 2009; Austin et al., 2014). This hypothesis is, however, still controversial, with several studies offering evidence which support and contradict it. In Chapter 3, I will test the HFA in different ecosystems, to understand to which extend litter origin is relevant for decomposers.

1.1.3 The pathways of litter decomposition

Although litter decomposition is typically addressed as the biological mineralization process carried out by microorganisms and detritivores, the overall process is the result of different pathways of mass loss, including also photodegradation and leaching (abiotic agents; Swift et al., 1979). Photodegradation is the photochemical mineralization of organic carbon compounds that occurs by the exposure of litter to ultraviolet (UV) or full solar radiation (Austin et al., 2015). This mechanism of litter breakdown is considered highly relevant in arid and semi-arid ecosystems (Austin & Vivanco, 2006). Alternatively, leaching represents the loss of nutrients and incompletely decomposed organic compounds transported out by water from the organic litter (Berg and McClaugherty, 2008). During the initial stages of decomposition, soluble organic materials and nutrients such as potassium (K), tannins and some sugars can be quickly lost from the litter through dissolution and leaching (McClaugherty 1983; Kuiters & Sarink 1986). Differentiating these mechanisms, important for understanding the controls of carbon and nutrient sequestration in ecosystems, is difficult in typical litter mass loss experiments.

Because lignin is difficult to break down by microorganisms but is a preferential target of photodegradation (Austin & Ballaré, 2010), an alternative to evaluate photodegradation in arid systems is the comparison of litter mass loss of species with low and high lignin content along the latitudinal gradient. This approach is mentioned in Chapter 4, in the context of a decomposition experiment aiming at understanding the main drivers of litter mass loss.

To assess biotic vs. leaching processes, it is possible to contrast the loss of leachable elements of litter (e.g. K; Schreeg et al. 2013) from the loss of elements that require a major biological breakdown (e.g. phosphorus and nitrogen; Laskowski et al 1995). In Chapter 3, I used this approach to disentangle the relative importance of climatic (i.e. precipitation) and decomposers effects, in the context of understanding the litter affinities of decomposers across sites.

1.1.4 Diversity and decomposition

While a big part of the research on litter decomposition drivers has been done using monospecific litter material, most natural ecosystems are composed of several species and produce a mixed litter layer. To accurately estimate the effects of litter quality in decomposition models, it is thus necessary to understand the role of litter identity and diversity (Hättenschwiler, 2005). On the other hand, global change, including human-induced climate and land use change, are leading to alterations in species distribution and an overall loss of biological biodiversity (May, 2011). These consequences are expected to impact ecosystem functions and the services they provide (Hooper et al., 2012; Naeem et al., 2012). Consequently, the study of the effects of diversity (e.g. species richness and functional diversity) on litter decomposition has become a relevant area of research.

Some studies have suggested that litter diversity can alter decomposition rates through changes in the microhabitat where litter decomposes (i.e. pH and temperature; Hobbie et al., 1999), which in turn can modulate the diversity and activity of decomposers. Other authors suggest that the translocation of nutrients or certain compounds among litters can also alter decomposition (e.g. nitrogen, phenolic acids; Schimel et al., 1998; Handa et al., 2014). The underlying mechanisms of mixture effects are, however, poorly understood, and identifying which litter functional traits can stimulate or inhibit the decomposition of litter mixtures could provide evidence for better conclusions (Hättenschwiler, 2005).

To test diversity effects, researchers have developed experimental studies that use artificial litter mixtures of varying number, identity and/or functional characteristics and explored the deviation in decomposition of these mixtures from expected values based on single-species decomposition (i.e. litter mixture effect). Litter decomposition has proved to be sensitive to changes in litter diversity in some ecosystems, showing both higher (e.g. Scherer-Lorenzen, 2008) and lower (e.g. Leppert et al., 2017) decomposition rates than single-species litter. In other cases, however, litter mixture does not have an effect on decomposition (e.g. Wardle et al. 1997).

All in all, the consequences of mixing different litter species are not yet clear and likely differ among ecosystems. In Chapter 5, I will address some of these knowledge gaps to explore the relevance of litter quality, in terms of functional diversity, for decomposition.

1.2 Objectives and hypothesis

With this background in mind, in the following chapters I present three different litterbag experiments that aimed to investigate the interactive effects of climate and plant traits (i.e. litter quality) on litter decomposition along the Chilean costal range. Three main research questions were established:

1) *Chapter 3*: Is there an affinity of decomposers for local litter qualities (home-field advantage, HFA) and does this affinity vary along a climatic gradient?
2) *Chapter 4:* What is the relative contribution of litter traits and climate effects on litter decomposition across different decomposition stages?
3) *Chapter 5:* How does litter diversity affect litter decomposition, and how do these effects vary along the climatic gradient and across decomposition stages?

In Chapter 3, I evaluated the potential affinity of decomposers for local litter species (i.e. the HFA hypothesis) in contrasting ecosystems along the Chilean gradient. To do this, however, it is necessary to disentangle the effects of decomposers from confounding factors such as leaching. By using a reciprocal translocation litterbag experiment among sites, I employed ratios of relative N/K and P/K loss in addition to mass loss, to unravel the role of biotic vs. abiotic processes along the climate gradient, as N and P are (mainly) structural elements released during decomposition, while K is leached with precipitation. In particular, I tested the hypothesis that litter mass loss, N loss/K loss and P loss/K loss are higher for local than for non-local litters at each site. Additionally, I expected this effect to be stronger on the arid end of the gradient, were a higher specialization of decomposers occurs.

Furthermore, in Chapter 4 I aimed to understand how climate, plant functional traits and time interact in their effects on litter decomposition. I especially aimed to understand to what extent the variation in trait values as well as the range of climate zones included in the research determine the conclusions about the relative importance of these factors for decomposition. By using a reciprocal litter translocation experiment along the large climatic gradient in Chile, I followed decomposition for two years and used 30 plant species with a wide spectrum of functional-trait values. I tested the hypotheses that i) plant functional traits are more important relative to climate when climate conditions are favorable for decomposition (e.g. high soil moisture), ii) litter-trait control decreases compared to climate control along the decomposition process, and that iii) the importance of litter traits for decomposition increases with increasing trait variation.

In Chapter 5, I evaluated the importance of litter quality in terms of diversity for decomposition. I evaluated litter mixture effects on litter decomposition by varying two aspects of diversity, species number and functional trait dispersion (FDis), along the climatic gradient in Chile. In particular, I used two FDis values based on traits that define nutrient transfer among litter types and litter recalcitrance. I aimed to test whether diversity in these types of traits can explain litter mixture effects, thereby hinting at the underlying mechanisms. Specifically, I hypothesized that litter mixture effects (1) occur less often in arid and semi-arid sites, which are climatically less favourable for decomposition, than in mediterranean and temperate forests; (2) are better explained by FDis than by species richness; and (3) are positively correlated to an increasing trait diversity in transferable nutrients and negatively to an increasing trait diversity of inhibitory compounds.

Chapter 2

General Methods

2.1 The Chilean coastal range for the study of earth-shaping processes

Natural climatic gradients are excellent laboratories to study the role of climate effects on organisms and ecological processes. Although several climatic factors can co-vary across space, strong gradients shape ecosystems and help us to understand their functioning (Koch et al., 1995). The Chilean costal range features a spectacular latitudinal gradient that exhibits strong climate and vegetation changes from north to south while keeping a common geologic origin (Moreno & Gibbons, 2007). This factor, together with the lack of volcanic material inputs on this cordillera (Oeser et al., 2018) and the important amount of natural protected areas, make it the perfect spot for studying the effects of climate and vegetation on soil processes. For this reason, the EarthShape project "Earth Surface Shaping by Biota" (DFG SPP-1803) chose several study sites along this gradient to investigate how microorganisms, animals, and plants influence the shape and development of the Earth's surface. The four primary study sites of the EarthShape project are located from the Atacama Desert in the north (~26° S) to humid temperate forests in the south (38° S; Fig. 2-1). The dry-arid site (AR) is located in Pan de Azúcar National Park, a coastal desert formation where vegetation is dominated by succulent shrubs and cacti, as well as annual herbs (Fig. 2-2; Bernhard et al., 2018). The semi-arid site (SA), located in Santa Gracia Private Reserve, corresponds to a scrubland dominated by perennial shrubs, together with perennial and annual herbs and grasses. The mediterranean site (ME) in La Campana National Park corresponds to a mediterranean sclerophyllous forest, and its diverse vegetation comprises sclerophyllous trees, shrubs and herbs, including an endemic palm. Finally, the temperate site (TE or TU), located in Nahuelbuta National Park, corresponds to an upland mixed forest, where the dominant vegetation consists of evergreen and deciduous trees and one conifer (Fig. 2-2; Bernhard et al., 2018). All national parks belong to the Chilean national system of protected areas (SNASPE), however, the private reserve in the SA exhibited an important grazing disturbance by goats and horses. For this reason, in this thesis I decided to use a different SA protected area, the Sendero Quebrada de Talca, belonging to a local community who in 2011 decided to exclude livestock for the conservation of this territory. This study site is located 30 km southern Santa Gracia Private Reserve and at the same distance to the coast. Furthermore, it belongs to the same vegetation formation (Luebert & Pliscoff, 2006), shares similar bedrock and climatic conditions.

In Chapters 4 and 5, I additionally included two more study sites to enlarge this gradient: one arid site with direct coastal fog influence (AF for Arid-Fog), located in the same Pan de Azúcar National Park but in the so-called "Las Lomitas" sector; and one second temperate site located in the lowlands (TL) in the Contulmo National Monument, which exhibits higher soil moisture and temperature than the upland temperate site (Fig. 2-2).

At each study site, we characterized plant communities in three independent 10 x 10 m plots on representative mid-slopes and estimated the percentage cover per species at each plot. Data were then averaged at the site level and plant species were selected for the different experiments based on their relative abundance and litter availability. Examples of these species are shown in Fig. 2-2.

Climate stations located in the four EarthShape study cites provided air temperature and precipitation data (Uebernickel et al., 2020). For other sites, close climate stations of INIA (Institute of Agricultural Research; INIA, 2020) provided similar data. Additionally, I installed

three soil sensors at each site to measure soil temperature and moisture directly under the experiments. Additionally, at each plot we measured soil temperature and moisture. Overall, the studied gradient increases in annual precipitation from 13 in the AD to ca. 1600 mm in the TU, and decreases in mean annual temperature from 15.5 to 7.3 °C in the same sites. Nonetheless, it is important to mention that, during the study period of this project, an important drought affected central Chile (Garreaud et al., 2019), including the SA and ME sites, which resulted in very similar climatic conditions between these two sites. More details on climatic data are given within each chapter.

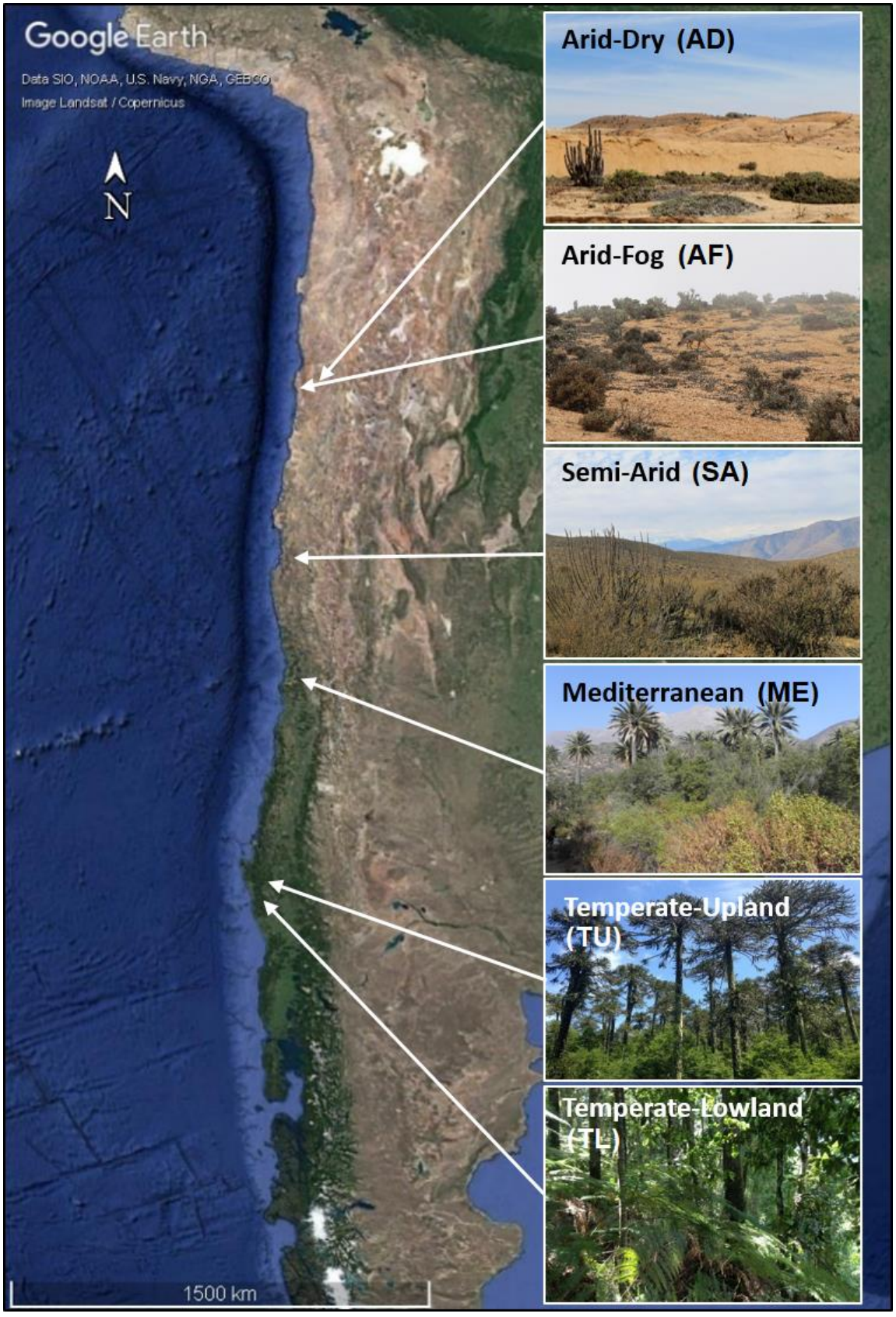

Figure 2-1. Overview of the climate and vegetation gradient where the study sites included in this thesis are located.

Figure 2-2. Example of plant species (and one lichen) chosen for a study of litter decomposition across a large climatic range in Chile. Species 1-6, 7-12, 13-18, 19-24, 25-29, 30-35 belong to the Arid-Dry, Arid-Fog, Semi-Arid, Mediterranean, Temperate-Upland and Temperate-Lowland, respectively. Species names can be found in the Appendix S2-1.

2.2. Litterbag decomposition experiments

In experimental ecological studies, litter decomposition is typically approached as the decrease in litter biomass in a certain amount of time (i.e. mass loss), which allows the calculation of decomposition rates. Methodologically, the most standardized method is the use of litterbags, which implies the addition of a known amount of dry senescent litter into a meshed bag (Fig. 2-3a) and its exposure to decomposition in either laboratory microcosms or natural soils. After a certain amount of time (varying from days to several years), the litterbag is harvested and the litter dried and weighed again to calculate the mass loss compared to the initial weight (Fig. 2-3b). Litterbags mesh sizes can vary (commonly between 1 and 2 mm), hence varying the type of organisms that have access to the litter and that are responsible for its decomposition. Despite this variability in the methodology, it has been shown that the effect of soil fauna on decomposition is robust to different mesh sizes (García-Palacios et al., 2013). Also, while this method excludes macroarthropods (which can affect decomposition by the ingestion of litter), much larger amounts of the mass loss occur due to the activity of microorganisms (e.g. 95% in boreal and temperate ecosystems, Berg & McClaugherty 2008) and henceforth, litterbags are one of the most straightforward methods to study litter decomposition.

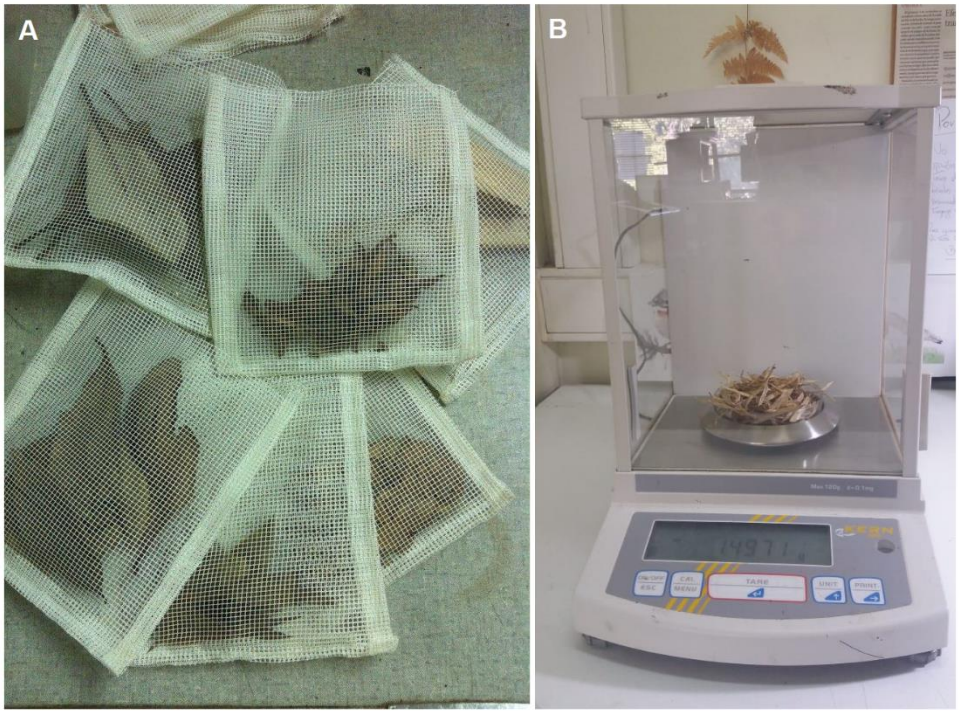

Figure. 2-3. (a) Examples of litterbags containing dry litter of different species before being closed and placed in the field. (b) Litter being weighed in the laboratory during a litterbag experiment.

Because the decomposition process exhibits different phases (Zukswert & Prescott, 2017), the duration of a litterbag study must be chosen considering this aspect: during a first phase, defined normally within the first year, high decomposition rates occur as a consequence of the dissolution, leaching and degradation of labile and soluble compounds (e.g. sugars and some

micronutrients; Melillo et al., 1989). In a second phase, large macromolecules (e.g. cellulose, lignin) are degraded at slower rates (Berg & McClaugherty, 2008).

In this doctoral work, I developed three litterbag decomposition experiments of different duration (from 12 to 24 months of decomposition) between 2016 and 2018. Two of them included several harvests to account for potential differences between the two decomposition phases. For each litterbag, I used 2 g of freshly senescent litter of local abundant species (e.g. Fig. 2-2), collected at each one of the mentioned study sites. Fresh litter of these species was collected in summer and early autumn before the start of each experiment, either manually, with litter traps or by shaking trees. In chapters 3 and 4, five species per site were chosen and each litterbag contained litter from only one species. In chapter 5, between seven and ten species per site were selected, and litters of different species were mixed. Further details on the methodology of the experiments are found in each chapter.

Chapter 3

No home-field advantage for litter decomposition: an integrated assessment along a climatic gradient in Chile

Submitted to *Ecography*

Rafaella Canessa[*,+,1], Liesbeth van den Brink[+,2], Harald Neidhardt[3], Timo Knüver[3,4], Rodrigo S. Rios[5,6], Alfredo Saldaña[7], Lohengrin A. Cavieres[7,8], Yvonne Oelmann[‡,3], Maaike Y. Bader[‡,1], Katja Tielbörger[‡,2]

[1]Ecological Plant Geography, Faculty of Geography, University of Marburg, Deutschhausstrasse 10, 35032 Marburg, Germany
[2]Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany
[3]Geoecology, Department of Geosciences, University Tübingen, Germany
[4]Ecophysiology, Department of Botany, University of Innsbruck, Austria
[5]Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile
[6]Instituto Multidisciplinario de Investigación en Ciencia y Tecnología, Universidad de La Serena, La Serena, Chile
[7]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile
[8]Institute of Ecology and Biodiversity (IEB), Santiago, Chile.

* corresponding author

+ contributed equally as first-author

‡ share senior-author position

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 faster 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 climate) along the climate gradient. Thus, at each site, we tested whether litter mass loss, N/K loss and P/K loss were higher than expected for local than for non-local litter. Despite the different approaches we used, across a wide range of environments and 20 different litter types, our findings unequivocally contradicted the HFA. Neither mass loss nor nutrient loss ratios were higher than expected for local litter. Instead, our study indicates an overriding effect of litter quality on decomposer activity. Our study questions the generality of the HFA and suggests that for litter decomposition, probably due to the fast adjustment of microbial communities to changing conditions, it is not a valid concept.

Keywords: climate gradient; dryland ecosystem; litter quality; nutrient leaching; nutrient loss; reciprocal translocation

3.1 Introduction

Litter decomposition, the breakdown of organic matter and the release of its elements, is an important process in carbon and element cycles and determines the speed at which carbon and nutrients are transferred to soils, groundwater and/or the atmosphere (Cornelissen et al. 2007, Cornwell et al. 2008, Suding et al. 2008). Litter decomposition accounts for about half of the global soil respiration (Raich & Schlesinger 1992, Couteaux et al. 1995) and decomposition rates are therefore an important input for climate-change models (Berg & 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 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 conditions and climate determine the plant and decomposer community compositions (Prentice et al. 1992, García-Palacios et al. 2013, Suseela & 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 so-called home-field advantage (HFA; Gholz et al. 2000, Ayres 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 et al. 2006). This "adaptation" should be manifested in faster decomposition when litter and decomposer communities come from the same site, compared to the decomposition of non-local litter with similar quality. The HFA may be one of the factors explaining litter decomposition variability across studies within similar climates (Ayres et al. 2009b). However, empirical tests of the HFA hypothesis are highly inconsistent (Austin et al. 2014), with some studies confirming (Ayres et al. 2009b, Veen et al. 2014) and others contradicting (Gießelman et al. 2011, St. John et al. 2011) or remaining inconclusive (Sun and Zhao 2016, Lu et al. 2017) about the occurrence of a HFA in litter decomposition. These contradictions could either indicate that the HFA does not apply, that it does not apply in all types of ecosystems and/or for all plant species and functional types, or that the methods used were not suitable or comparable among studies. Studies on HFA usually translocate litter between different study sites within similar ecosystems or climates (e.g., Wallenstein et al. 2013, Yuan et al. 2019). Studies contrasting different climates with fully reciprocal transplant studies to test for the HFA are rare, yet needed to determine under which conditions it 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 (Wallenstein et al. 2013, Wang et al. 2013, Veen et al. 2014). 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 correctly (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 et al. 1999, Wright et al. 2004, Griffiths and Males 2017). This low diversity of litter types (Schlesinger & Pilmanis 1998, Carrera & Bertiller 2013), along with harsh environmental conditions (e.g., low moisture availability and high radiation), could function as environmental filters that favor a specialized soil microbial community, capable of efficiently decomposing local litter. In contrast, wet and diverse ecosystems (e.g., rainforests) with more dynamic climates produce a more variable litter, which together with fewer environmental filters, can lead to relatively less specialized microbial communities (Gießelman et al. 2011, Moskwa et al. 2020).

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 & Fischer 2008). Nevertheless, the use of this approach to test the HFA in litter decomposition is less common because comparing local and non-local species decomposing within the same site needs to be interpreted with caution. 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. 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 et al. 2012a, Makkonen et al. 2012, He et al. 2016). Namely, decomposition is faster for litter of high quality (with low C:N ratios) than for litter of low quality (Zhou et al. 2018a). Since decomposition also varies according to abiotic factors, this creates confounding factors, making the detection of HFA very difficult. Therefore, differences between litter decomposition at "home" and "away" are likely to be dominated by climatic or general site conditions, especially when conditions differ substantially. Thus, we need 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.

Here, we propose a novel approach to overcome the above-mentioned problems of detecting a HFA 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 et al. 2006, Schreeg et al. 2013). On the other hand, structural elements such as nitrogen (N) and phosphorus (P) are lost by physical leaching (a proportion is present as dissolved ions) combined with biological decomposition, driven by the local decomposer community (Laskowski et al. 2013, Berg 2014). We suggest that a "local advantage" for species placed within their home site (HFA) could be detectable by an overproportional release of the decomposer-dependent elements relative to leachable cations compared to non-local litter.

To address the general applicability of the 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. 2014). In this study, we conducted a fully reciprocal litterbag translocation experiment, with litter of 20 different plant species, along a very steep 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 litter mass loss, we discriminated among 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, under the HFA hypothesis, we expected at each site 1) local litter to have a relatively higher mass loss and relatively higher N/K loss and P/K loss ratios as compared to foreign litter, and 2) this effect to be 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, Supporting information Fig. S3-1). The study sites share a homogeneous granitoid parent material but contrast in micro and macro-climatic conditions (Table 3-1, (Oeser et al. 2018). Namely, along the gradient, mean annual temperatures (MAT) decreased slightly from the (semi-)arid (18 °C) to the mediterranean site (14 °C) and then more sharply towards the temperate site (7 °C) (i.e., from north to south), whereas annual precipitation (AP) increased in the same direction (from 22 to 2158 mm, Table 3-1). Rainfall occurs during the austral winter, between May and August. The arid site ("AR", Parque Nacional Pan de Azúcar) has a sparse cover (<5%) of desert vegetation (cacti and small succulent shrubs), the semi-arid site ("SA", Reserva Privada Quebrada de Talca) presents shrubby vegetation with 30-40% cover, the mediterranean site ("ME", Parque Nacional La Campana) exhibits a sclerophyllous forest with almost full cover, and the temperate site ("TE", Parque Nacional Nahuelbuta) presents a fully covered mixed evergreen and deciduous Nothofagus-dominated forest. Further information on vegetation and geomorphology can be found in Bernhard et al. (2018) and Oeser et al. (2018). At each site, six independent plots were randomly selected for the experiments, assuring a distance of 100 m or a separation by ravines and vegetation patches.

3.2.2 Plant species and litterbag experiment

Five abundant and representative plant species per site were selected for the experiment (Table 3-2). At the TE site, one lichen species was chosen, as it was highly abundant on trees and present in the litter layer. Freshly senesced leaves were collected from plants during the dry season preceding the experiment (December 2016-January 2017). Litter was oven-dried at 45°C for 48h 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 (data not shown).

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 (M0-Mt)/M0*100, where M0 is the initial dry mass of a sample and Mt 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 the element 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 and average (min-max)	Annual Precipitation (mm) [1]	Mean Soil Moisture at 0-15 cm depth (m^3/m^3)	Elevation (masl)
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 AR, SA and TE; INIA (2020) for ME (La Cruz weather station).

Table 3-2. Plant species (including one lichen species) selected for this study.

Origin	Species	Growth form
Arid	*Heliotropium pycnophyllum* Phil.	Perennial succulent shrub
	Nolana crassulifolia Poepp.	Perennial succulent shrub
	Nolana mollis I.M. Johnst.	Perennial succulent shrub
	Ophryosporus triangularis Meyen	Perennial succulent shrub
	Tetragonia maritima Barnéoud	Perennial succulent shrub
Semi-arid	*Cordia decandra* Hook. & Arn.	Deciduous shrub
	Flourensia thurifera (Molina) DC	Deciduous shrub
	Lobelia polyphylla Hook. & Arn.	Deciduous shrub
	Maytenus boaria Molina	Evergreen tree
	Senna cumingii (Hook. & Arn.) H.S. Irwin	Evergreen or deciduous shrub
Mediterranean	*Aristeguietia salvia* (Colla) R.M. King & H. Rob.	Deciduous shrub
	Cestrum parqui (Lam.) L`Hér.	Deciduous shrub
	Jubaea chilensis (Molina) Baill.	Palm
	Podanthus mitiqui Lind.	Deciduous shrub
	Quillaja saponaria Molina	Evergreen tree
Temperate	*Araucaria araucana* (Molina) K.Koch	Evergreen conifer
	Chusquea culeou É. Desv.	Perennial grass
	Festuca sp.	Perennial grass
	Nothofagus antarctica (G. Forst.) Oerst.	Deciduous tree
	Usnea sp.	Lichen

3.2.3 Elemental analyses

Five subsamples per species were separated from the initial litter and analysed to determine initial element contents per species (Supporting information, 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 Analysesysteme GmbH, Langenselbold, Germany), and were used to calculate C/N mass ratios. For details regarding detection limits and quality controls, see Supporting information 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 HNO3 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; Supporting information 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 x (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 ratios therefore give an estimate of biological decomposition, as they standardize N and P losses for leaching effects. This means that within a site, an increase in the relative loss ratios represents an increase in biological decomposition, as leaching is expected to be the same for all litters. Additionally, across sites (i.e., across the precipitation gradient), an increase in the ratios also 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 et al. 2018b) we additionally analysed 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, according to Zhou et al. 2018a, Supporting information Fig. S3-2).

3.2.4 Statistical analyses

To analyze the home-field advantage hypothesis along the gradient, we used linear mixed effect models with least-square means, testing the response of litter mass loss (%), K loss (%) 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. Based on the common approach of testing for local adaptation, a significant site*origin interaction with a home-site advantage would be indicative for local adaptation. *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 Litter mass loss

Overall, litter mass loss (%) increased from the arid (AR) to the temperate (TE) site, i.e., along the precipitation gradient (Fig. 3-1), although a significant interaction site*origin and site*litter quality was observed (Table 3-3). This interaction, however, showed no evidence for a HFA (Fig. 3-1), as litter mass loss of local litter was not higher than of non-local litter (Fig. 3-1). The differences among litter origins within each site showed the same pattern across sites, except in the TE, the only site where decomposition of litter from the mediterranean site (ME) was significantly slower than that of litter from the semi-arid (SA). However, this difference did not involve the home litter and does not indicate a HFA (Fig. 3-1). Thus, litter at home decomposed at the rate expected according to the climate gradient and the decomposition ranking of that same litter at the other sites. At each site, species with AR origin decomposed significantly quicker than species from the ME and the TE, whereas species from the semi-arid (SA) decomposed quicker than species from TE. Species originating from the ME and TE sites consistently decomposed the slowest (Fig. 3-1).

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 sites (96% at TE; 90% at ME; 83 at SA and 79 at AR). Losses were similar among litter types at the AR and SA sites but at the ME and TE sites the loss of K was lower in litter from the TE site, compared to litter from other origins (Fig. 3-2). As a result, the model contained a significant interaction between site and origin (Table 3-3). Nitrogen (N) and phosphorus (P) loss (32 and 58% on average over species and sites, respectively) also varied among sites and showed an interaction between litter quality and site, but this interaction was not related to a HFA (Supporting information Fig. S3-3, Table S3-4).

For relative N/K loss ratios, the statistical model showed an interaction between site and litter quality, but not between site and origin (Table 3-3). Thus, we found no evidence for a home-field advantage in relative N/K loss (Fig. 3-3a). Relative N/K loss ratios were higher at the TE compared to the other climates, indicating that microbial decomposition increased with increasing precipitation, as expected. 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 litters from the wetter site (Fig. 3-3a).

Similar to the results observed for relative N/K loss, we did not find an interaction between site and origin for relative P/K loss (Fig. 3-3b), again indicating that a HFA is not prevalent. The relative P/K loss was higher at the TE compared to the other sites, but there was no consistent pattern according to litter origin (Fig. 3-3b).

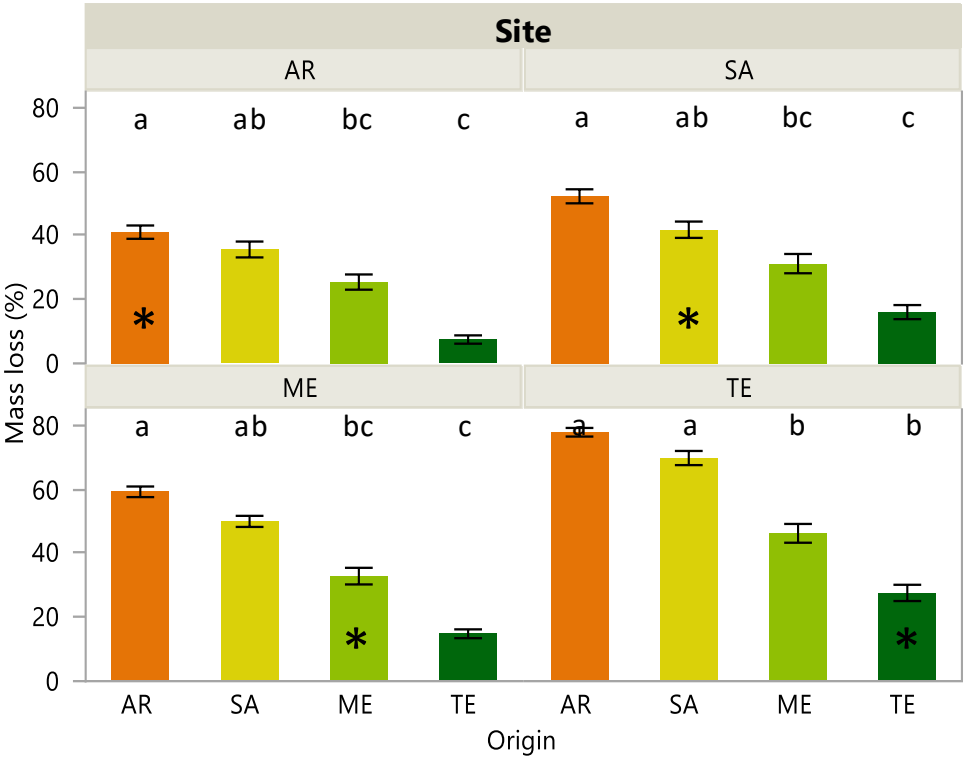

Figure 3-1. Mass loss (%) for litter from 20 plant species with different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile after 12 months of decomposition. AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate. Error bars represent the standard error. Significance is expressed per site with different letters according to Tukey HSD tests. * = litter decomposing at their "home site".

Table 3-3. Linear mixed models for Mass loss, relative N/K loss and relative P/K loss of reciprocally translocated litter decomposing at four sites along a steep climatic gradient in Chile. DF = degrees of freedom, F = F statistic, p = statistical significance.

Response	Source	DF	F	p
Mass loss (%)	Site	3	175.63	<.001 ***
	Origin	3	16.16	<.001 ***
	Site*Origin	9	2.50	0.003 **
	Litter quality	2	2.09	0.112
	Site*Litter quality	6	2.07	0.033 *
K loss (%)	Site	3	93.17	<.001 ***
	Origin	3	1.77	0.202
	Site*Origin	9	4.41	<.001 ***
	Litter quality	2	0.03	0.973
	Site*Litter quality	6	2.69	0.014 *
Relative N/K loss	Site	3	27.37	<.001 ***
	Origin	3	1.72	0.211
	Site*Origin	9	1.11	0.355
	Litter quality	2	1.29	0.310
	Site*Litter quality	6	2.63	0.016 *
Relative P/K loss	Site	3	7.99	<.001 ***
	Origin	3	1.97	0.169
	Site*Origin	9	1.80	0.067
	Litter quality	2	0.24	0.791
	Site*Litter quality	6	4.00	0.001 ***

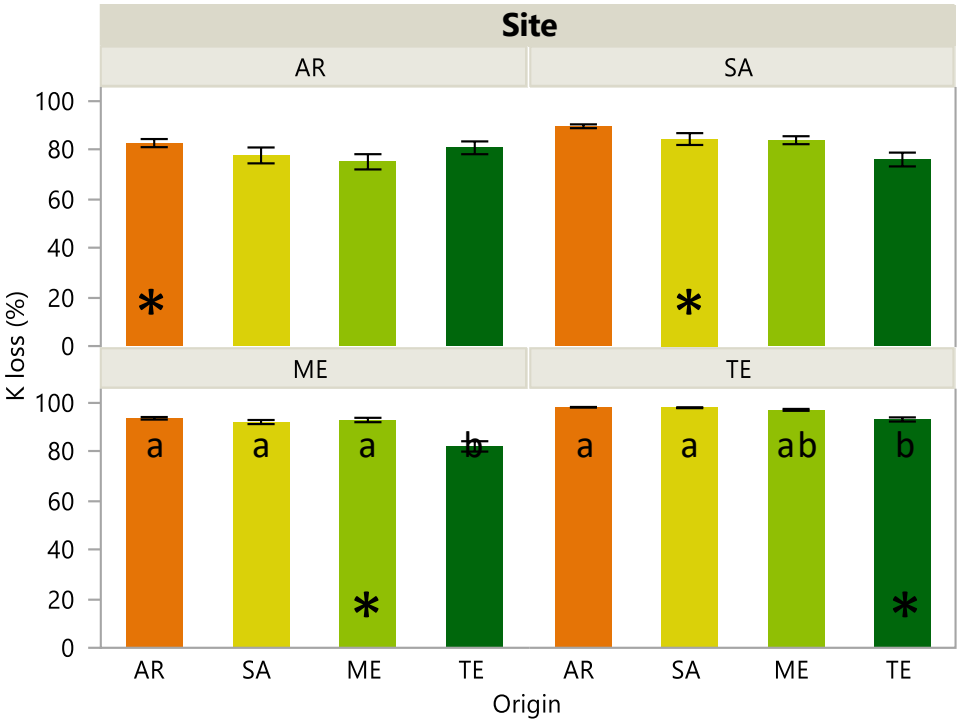

Figure 3-2. K loss (%) for litter from 19 plant species with different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile after 12 months of decomposition. AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate. Error bars represent the standard error. Significance is expressed per site with different letters after Tukey HSD tests (the absence of letters indicates that no significant differences were observed within a site). * = litter decomposing at their "home" site.

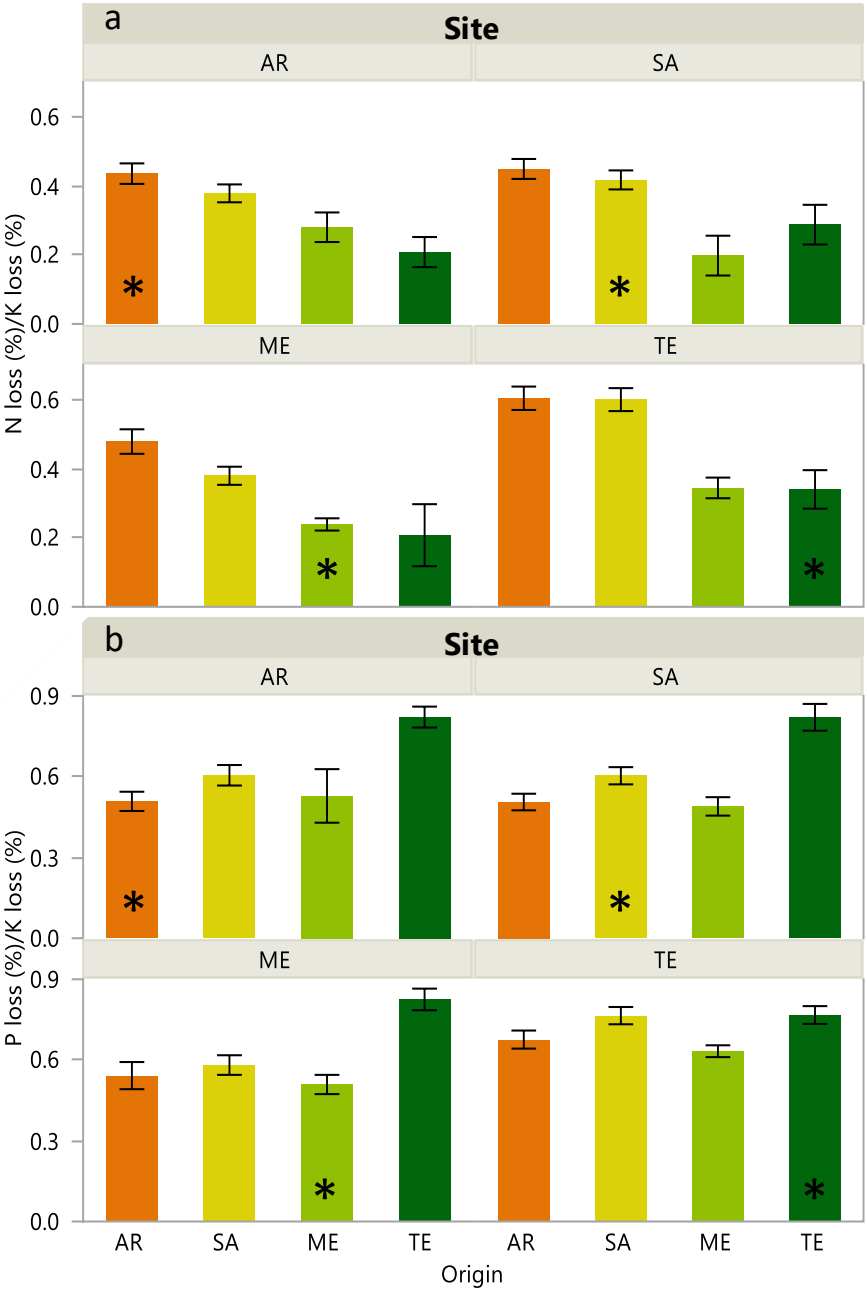

Figure 3-3. (a) Relative N/K loss and (b) relative P/K loss after 12 months of decomposition for litter from 19 plant species with different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile. AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate. Error bars represent the standard error. No significant effects within sites were observed (Tukey HSD tests). * = litter decomposing at their "home site".

3.4 Discussion

We found no support for the home-field advantage (HFA) hypothesis for litter decomposition. Neither changes in litter mass loss nor the contrast between biological decomposition and physical leaching showed that local litter decomposed faster than expected across sites. Instead,

the ranking and relative differences between decomposition speeds were strikingly consistent among species across sites.

3.4.1 The HFA across ecosystems

Due to the large range of environmental conditions and number of species studied, we consider the lack of a HFA a highly robust result. If decomposer communities differ, they should be more likely to do so between biomes (i.e. our study) than between sites within a single biome. Previous studies have mainly tested this hypothesis using translocations of litter within similar climates (e.g., Gholz et al. 2000, Ayres et al. 2006, 2009b, St. John et al. 2011, Wallenstein et al. 2013, Veen et al. 2014, Sun & Zhao 2016, Lu et al. 2017, but see Makkonen et al. 2012 and Fujii et al. 2018). While this design has the advantage that there is no confounding between climate and home-site effects, it comes at the cost of a low power, i.e., the generality of a "home advantage" cannot be assessed with this setup. Our study addressed this aspect, as it included 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, showing that the HFA, although it may occur in specific situations, is not a prevalent phenomenon across ecosystems. A HFA has been found specifically in mono-dominant stands (Ayres et al. 2009a, b). However, in most ecosystems litter is provided by a mix of plant species, so that decomposer communities likely contain decomposers for all litter types and are therefore more generalistic (Gießelman et al. 2011, Moskwa et al. 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.

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 truly evaluate the HFA hypothesis, it is necessary to disentangle the effects of climate and decomposers on litter decomposition. We did this by contrasting the leachable fraction (here: K) against the biological decomposition fraction (here: N and P), an approach that, to our knowledge, is implemented for the first time here. The increasing loss of potassium (K) along the precipitation gradient was constant among species within sites and nicely depicts that this element was mainly lost by physical leaching (Xu et al. 2006, Schreeg et al. 2013) and is 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. However, this was not the case, which provides another strong point of evidence against the generality of the HFA hypothesis for decomposition.

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) suggest 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 & 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 Litter quality effects on decomposition

Our results failed to support a HFA for litter decomposition, in accordance with several previous studies (e.g., Gholz et al. 2000, Ayres et al. 2006, 2009b, St. John et al. 2011, Makkonen et al. 2012, Wallenstein et al. 2013, Veen et al. 2014, Sun & Zhao 2016, Fujii et al. 2018). 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 et al. 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 & Bouvier 2006). Our findings support this hypothesis and indicate that microorganism communities can quickly re-adjust when alternative resources are available.

As an alternative to the HFA hypothesis, Freschet et al. (2012b) proposed that the affinity of decomposers for litter increases when fresh litter input is more similar to the organic layer. Hence, non-local litter with similar litter quality to the local litter layer could be preferentially degraded in comparison to litter with a very different quality. The authors, however, showed that, although this interaction is relevant for litter decomposition, the direct effects of litter quality are still stronger than those of quality differences between the fresh litter and the soil organic layer when predicting decomposition rates. Makkonen et al. (2012), in their reciprocal translocation experiment, found that the ranking of plant species, based on their mass loss, remained the same in all climates. Our results support those findings, as the species rankings based on mass loss, relative N/K loss and relative P/K loss were also highly consistent along our climate gradient, highlighting the importance of species-specific litter quality for decomposition (see also Supporting information Fig. S3-4, S3-5, S3-6). 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 communities can clearly differ among ecosystems (in terms of species and functional group composition and in abundance; (Evans et al. 2014, Moskwa et al. 2020), this does not imply a local adaptation to local litter, as litter quality exhibits a larger control of litter breakdown by decomposers, than the origin of the litter.

Our novel approach to disentangle biotic and abiotic effects on HFA in decomposition shows that even if we account for climate effects (by standardizing to K loss), litter mass loss does not show any HFA. Thus, local litter was not favored by local decomposer communities and 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. We suggest that the hypothesis of a HFA in litter decomposition should be critically revised, and we advocate to distinguish between biological and leaching processes in future studies of litter decomposition to understand 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 CO2 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 HFA.

3.5 Declarations

Authors contributions

KT, MYB and YO: Conceptualization (lead), funding acquisition, methodology, project administration, resources, supervision, writing-review and editing. RC and LB: Data curation, formal analysis, investigation, project administration, validation, visualization, writing-original draft, writing-review & editing. HN: Conceptualization (lead), formal analysis, funding acquisition, methodology, resources, project administration, visualization, writing-review and editing. LC, AS and RSR: Conceptualization (supporting), resources, writing-review and editing; TK: Formal analysis, writing - review and editing.

Acknowledgements

The authors thank all their park rangers from P.N. Pan de Azúcar, P.N. La Campana and P.N. Nahuelbuta for their on-site support of our research. We are deeply grateful to all the students and technical assistants who helped with the field and laboratory work.

Funding

This study was funded by the German Research Foundation (DFG) Priority Program SPP-1803 “EarthShape: Earth Surface Shaping by Biota” (BA 3843/6-1, OE 516/7-1 and -2, and TI 338/14-1 and -2) and additional support from CONICYT PIA CCTE AFB-17008 funding the Institute of Ecology and Biodiversity.

Conflicts of interest

The authors declare that there is no conflict of interest.

Permits

Permission to work in the national protected areas was given by CONAF (Corporación Nacional Forestal, Chile), authorization n° 033/2015. Permission to work in Sendero Quebrada de Talca was kindly given by Comunidad Agrícola Quebrada de Talca (2016).

Chapter 4

Relative effects of climate and litter traits on decomposition change with time, climate and trait variability

Published in 2021 in *Journal of Ecology*, 109:447–458.

https://doi.org/10.1111/1365-2745.13516

Rafaella Canessa*[1], Liesbeth van den Brink[2], Alfredo Saldaña[3], Rodrigo S. Rios[4,5] Stephan Hättenschwiler[6], Carsten W. Mueller[7,8] Isabel Prater[7], Katja Tielbörger[2], Maaike Y. Bader[1]

[1]Ecological Plant Geography, Faculty of Geography, University of Marburg, Deutschhausstr. 10, 35032 Marburg, Germany
[2]Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany
[3]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile
[4]Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile
[5]Instituto Multidisciplinario de Investigación en Ciencia y Tecnología, Universidad de La Serena, La Serena, Chile
[6]CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France
[7]Chair of Soil Science, Technical University of Munich, Emil-Ramann-Str. 2, 85354 Freising, Germany
[8]Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

*Corresponding author

Abstract

1. Climate and litter quality drive litter decomposition, but there is currently little consensus on their relative importance, likely because studies differ in the duration, the climatic gradients, and variability in litter-trait values. Understanding these drivers is important because they determine the direct and indirect (via vegetation composition) effects of climate change on decomposition and thereby on carbon and nutrient cycling.

2. We studied how microclimate (soil moisture and temperature) and litter traits interactively affect litter mass loss, by using a reciprocal litter translocation experiment along a large climatic gradient in Chile. We followed decomposition for two years and used 30 plant species with a wide spectrum of functional-trait values.

3. Litter traits had a strong impact on litter decomposition across the gradient, while an increase in decomposition with soil moisture was observed only in the wettest climates. Overall, soil moisture increased considerably in importance, relative to trait effects, at later decomposition stages, from ca. 15% of the importance of traits after 3 and 6 months to ca. 110% after 24 months. Moreover, analyzing subsets of the 30 species showed that trait effects on litter decomposition gained in importance when including a greater variation in trait values.

Synthesis. The relative effects of litter traits and climate on decomposition depend on the ranges in climate and litter traits considered and change with time. Our study emphasizes the critical role of representative ranges in climate and functional trait values for understanding the drivers of litter decomposition and for improving predictions of climate-change effects on this important ecosystem process.

Keywords

Arid ecosystem, climate gradient, ecosystem function and services, litter decomposition, litter quality, litter mass loss, plant functional traits, soil moisture

4.1 Introduction

Unravelling the drivers of litter decomposition is crucial for understanding important ecosystem processes such as soil carbon storage and productivity, and for understanding emissions of major greenhouse gases (Raich & Potter, 1995; Berg & McClaugherty, 2003; Knorr, Prentice, House, & Holland, 2005; Canadell et al., 2007). Litter decomposition is responsible for the mineralization and transformation of nutrients and carbon from organic residues, providing a major flux of carbon dioxide to the atmosphere (De Deyn, Cornelissen, & Bardgett, 2008) while fostering soil functionality by releasing nutrients that are used by plants and regulating soil organic carbon formation (Scholes, Powlson, & Tian, 1997).

Environmental factors, including climate, soil conditions and decomposer activity, are important drivers of litter decomposition (Meentemeyer, 1978; Aerts, 1997, Cornwell et al., 2008; Zhang, Hui, Luo, & Zhou, 2008; García-Palacios, Maestre, Kattge, & Wall, 2013). Decomposition tends to increase with temperature and precipitation because warm and moist conditions stimulate decomposer activity (Zhang et al., 2008). In addition to the external abiotic conditions, litter quality is another important control of decomposition (Cornwell et al., 2008). Leaf litter quality is determined by a suite of leaf functional traits (Freschet, Aerts, & Cornelissen, 2012a; Dias, Cornelissen, & Berg, 2017), i.e., leaf structural and chemical properties related to the acquisition and conservation of resources (Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). Strategies for carbon gain and nutrient economy differ widely among species and climates, ranging from high resource conservation (i.e., dense, well-defended, resistant and nutrient-poor structures) to fast resource acquisition (with opposite traits, Wright et al., 2004). Structural traits (e.g., leaf toughness and lignin content), nutrient traits (e.g., N and major cations), and defence traits (e.g., phenolic compounds) collectively control litter decomposability, modulating chemical recalcitrance and nutrient availability for decomposers (Freschet et al., 2012a). For instance, litter with a high C/N ratio and a high concentration of particular phenolic compounds, such as tannin, decomposes slowly (Aerts, 1997; Zhang et al., 2008; Makkonen et al., 2012). Instead, high concentrations of nutrients such as P, K, Ca and Mg often increase decomposition rates (Zhang et al., 2008; Makkonen et al., 2012). Even though it has become clear that both litter traits and climate play a central role in controlling litter decomposition rates, the relative importance of these two main drivers is still under debate (Cornwell et al., 2008; Bradford, Berg, Maynard, Wieder, & Wood, 2016).

The relationships between climate, plant traits and litter decomposition have been studied in several ecosystems (Aerts, 1997; Makkonen et al., 2012) and are the basis for model parameterizations up to the global scale (Cornwell et al., 2008; Zhang et al., 2008). Different experiments and meta-analyses show contrasting results: some refer to climate as the most relevant factor (Aerts, 1997; Dyer, Meentemeyer, & Berg, 1990), while recent results called for more attention to litter-quality-driven effects (Cornwell et al., 2008; Zhang et al., 2008; Makkonen et al., 2012). Such apparent inconsistencies may be due to differences in the decomposition stage studied (Currie et al., 2010; Zukswert & Prescott, 2017) and the width and position of the climatic gradients considered (e.g., climatic variables better predicted litter decomposition in cold ranges; Bradford et al., 2016) combined with differences in the species and the trait variation included. It is intuitive that studying a limited number of species or

species with low trait variation can underestimate the effect of litter quality on decomposition (Makkonen et al., 2012). Likewise, climate gradients that fail to include sufficiently large and sensitive ranges for decomposition are unlikely to yield strong climate effects (Bradford et al., 2016). It is unclear, however, how the ranges of trait variation and climate can modify their relative importance for litter decomposition. To train models predicting direct and indirect climate-change effects on carbon cycling, experiments that simultaneously encompass wide ranges of climates and traits are therefore urgently needed.

Climate and litter quality interact in their effects on litter decomposition, although this interaction is not well understood. Meentemeyer (1978) and later Currie et al. (2010) observed that, in the early stage of decomposition, the slope of the negative relationship between litter decomposition rate and initial lignin concentration decreased with decreasing actual evapotranspiration, suggesting that in drier and cooler climates, litter traits had weaker effects on decomposition rates. In order to understand climate and litter traits interactions, various studies used reciprocal translocation experiments of litter across climate zones. Most of these experimental studies were done at relatively small spatial scales (Powers et al., 2009; Zukswert & Prescott, 2017), included few litter types (Berg et al., 1993; Trofymow et al., 2002; Currie et al., 2010; Bradford et al., 2017), or focused on a particular plant functional group (Cornelissen & Thompson, 1997; Makkonen et al., 2012), thus reducing the analysed trait spectrum below that of natural communities and limiting the conclusions regarding trait effects. To disentangle climate and trait effects, however, it is essential to include sufficient variability in trait values as well as in climate (Currie et al., 2010; Bradford et al., 2016). Using a reciprocal translocation experiment of litter from 16 woody species across four climate zones ranging from subarctic to tropical forests, Makkonen et al. (2012) showed the critical importance of litter traits for decomposition, with a consistent ranking of the species decomposition rates across climate zones. Although the climate range they assessed was large, it encompassed only four points, varying mainly in temperature regimes while all sites except one (a mediterranean site) were rather moist year-round. The validity of their findings for extrapolation to other, more distinct climate types with different vegetation than forests therefore remains uncertain. Most importantly, the potential effect of including different climate ranges or trait variability, and the changes in the relative importance of climate and traits during the decomposition process has not been assessed.

Melillo et al. (1989) and Coûteaux, Bottner, and Berg (1995) proposed to distinguish two phases in the decomposition process. During the first phase (normally less than a year) a rapid mass loss occurs, resulting from the degradation of labile and soluble compounds, which attenuates the initial quality differences among different litter types (see also Parsons, Congdon, & Lawler, 2014; Preston, Nault, Trofymow, Smyth, & CIDET Working Group, 2009). These authors suggested that both litter traits and environmental conditions determine the rate of decomposition during the first phase, while environmental conditions dominate after that. This prediction received support from a study in North and Central America (Curie et al., 2010), where litter chemistry was observed to be a better predictor of decomposition than climate only in the early phase (first year). In contrast, Trofymow et al. (2002) showed that, in upland Canadian forests, litter quality control increased in importance over time. Thus, no consistent patterns for changes in the controls of litter decomposition with time have yet

emerged and predictions may vary among ecosystems (Currie et al., 2010; Bradford et al., 2016) and litter types considered.

In this study, we assess the relative contribution of plant litter traits and climatic conditions on litter decomposition along a wide climate and vegetation gradient in the Chilean coastal range (26 to 38°S). The gradient is characterized by a 120-fold increase in precipitation and a decrease in temperature from north to south. This large climatic variation is ideal for disentangling the effects of climate and litter quality, evaluated through a wide range of morphological and chemical traits. Along this gradient, we used a fully reciprocal litterbag translocation experiment with 30 plant species, and followed decomposition for two years. We aimed to understand how climate, plant functional traits and time interact in their effects on litter decomposition, and to what extent the variation in trait values and the range of climate zones included in the experiment determine the conclusions about the relative importance of traits and climate for decomposition. We predicted that i) plant functional traits are more important relative to climate when climate conditions are favourable for decomposition, ii) litter-trait control decreases compared to climate control along the decomposition process, and that iii) the importance of litter traits for decomposition increases with increasing trait variation.

4.2 Materials and methods

4.2.1 Study sites

We conducted our study along the coastal range of Chile (26°S to 38°S), along a gradient with homogenous granitoid parent material (Oeser et al., 2018). We selected six sites with contrasting macroclimatic conditions (Fig. 4-1, Table 4-1): arid desert (Pampa Blanca - Pan de Azúcar National Park, henceforth, "AD" for Arid Dry), arid desert with fog influence (Las Lomitas - Pan de Azúcar National Park, "AF" for Arid Fog), semi-arid shrubland (Quebrada de Talca Private Reserve, "SA" for Semi-Arid), mediterranean forest (La Campana National Park, "ME" for Mediterranean), upland temperate rainforest (Nahuelbuta National Park, "TU" for Temperate Upland) and lowland temperate rainforest (Contulmo Natural Monument, "TL" for Temperate Lowland). The study sites are ranked along a climatic gradient with decreasing mean annual temperature from 15.5°C in AD to 7.3°C in TL, and increasing mean annual precipitation from 13 mm yr^{-1} in AD to 1642 mm yr^{-1} in TU (Table 4-1). During the study period, the climate was drier than usual in Central Chile (Garreaud et al., 2020), which was especially notable at the ME site, so that precipitation differed little and mean soil moisture did not differ at all between the ME and SA sites. The rainfall seasonality is similar at all sites, with rainfall occurring mainly during the austral winter (from May to August). AD and AF are located in the Atacama Desert, almost without rainfall. The coastal fog, however, is a relevant source of water at AF (Lehnert et al., 2018). Some fog-water input may also occur at AD on an irregular basis, but at much lower frequency and overall quantity compared to AF. More detailed information about the study sites is available in Bernhard et al. (2018) and Oeser et al. (2018). At each study site, three independent 10x10 m plots were selected.

Figure 4-1. Geographic location of sites included in our litter transplant experiment in Chile. AD = Arid-Dry, AF = Arid-Fog, SA =Semi-Arid, ME = Mediterranean, TU = Temperate upland, TL = Temperate Lowland.

3.2.2 Microclimatic data

Because conditions at the microsites in which decomposition takes place are poorly represented by macroclimatic parameters (Bradford et al., 2016; 2017), we measured local soil moisture and temperature directly next to the litterbags (see next section) in each of the three plots per site for the duration of the experiment. We measured soil temperature at a depth of 2 cm using HOBO Micro Station dataloggers (H21-002) with two sensors (S-TMB-M002) and volumetric soil moisture at a depth from 0 to 14 cm using TMS-3 dataloggers (TOMST, Czech Republic). Based on the clay and sand content of our study sites (Bernhard et al., 2018), calibrations for sandy loam (AD and AF), loamy sand (SA and ME) and loamy soils (TH and TL) were used for the soil moisture measurements, as suggested by the provider (Wild et al. 2019). Sensors recorded data every 30 (temperature) or 15 minutes (moisture). We calculated mean soil temperature (MST) and soil volumetric water content (henceforth, mean soil moisture, MSM) for each decomposition period (0-3, 0-6, 0-9, 0-12 and 0-24 months, from June 2016 to June 2018). MST and MSM data were aggregated at the level of the plot (mean of two sensors) and site (mean of three plots, Table 4-1). Additionally, to characterize the radiation environment in the plots, canopy cover and leaf area index (LAI) were estimated. LAI was measured with a Licor LAI-2200C Plant Canopy Analyzer and is given as the average of three measurements per plot (Table 4-1).

Table 4-1. Description of study sites across the climatic gradient considered in this study, including dominant vegetation, selected species for the litter transplant experiment, latitude, meteorological and soil microclimatic data. Meteorological and microclimatic data represent the average for the experimental period (2016-2018). AD = Arid-Dry, AF = Arid-Fog, SA =Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland, Veg. cover = vegetation cover, LAI = Leaf area index, MAT = mean air temperature, AP = annual precipitation, MST = mean soil temperature, MSM = mean soil moisture.

Site (climate)	Dominant vegetation type and selected species	Veg. cover (%) / LAI	Latitude / Longitude	Elevation (m)	MAT (C°)	AP (mm)	MST (C°)	MSM (m^3/m^3)
AD	Very open desert scrub: *Cistanthe grandiflora* (Lindl.) Schltdl., *Cristaria integerrima* Phil., *Frankenia chilensis* C.Presl ex Schult. & Schult.f., *Nolana mollis* I.M. Johnst., *Tetragonia maritima* Barnéoud	3 / 0.11	-25.95 / -70.61	538	15.5*	13§	20.6	0.11
AF	Open coastal desert scrub: *Eulychnia breviflora* Phil., *Euphorbia lactiflua* Phil., *Nolana crassulifolia* Poepp., *Nolana paradoxa* Lindl., *Usnea* sp.	5 / 0.15	-26.01 / -70.61	798	11.3†	13§	17.8	0.13
SA	Mediterranean scrub: *Cordia decandra* Hook. & Arn., *Flourensia thurifera* (Molina) DC., *Gutierrezia resinosa* (Hook. & Arn.) S.F.Blake, *Haplopappus decurrens* J.Rémy, *Porlieria chilensis* I.M. Johnst.	45 / 0.26	-30.05 / -71.1	798	14.3‡	132‡	19.1	0.18
ME	Mediterranean sclerophyll forest: *Acacia caven* (Molina) Molina, *Aristeguietia salvia* (Colla) R.M.King	91 / 2.90	-32.95 / -71.06	719	16.1‡	211‡	14.1	0.18

	& H.Rob., *Colliguaja odorifera* Molina, *Jubaea chilensis* (Molina) Baill., *Lithraea caustica* (Molina) Hook. & Arn.							
TU	Temperate upland rainforest: *Araucaria araucana* (Molina) K.Koch, *Gaultheria mucronata* (L.f.) Hook. & Arn., *Nothofagus dombeyi* (Mirb.) Oerst., *Nothofagus obliqua* (Mirb.) Oerst., *Festuca* sp.	100 / 2.77	-37.81 / -73.01	1206	7.3*	1642*	7.9	0.31
TL	Temperate lowland rainforest: *Drimys winteri* J.R.Forst. & G.Forst., *Greigia sphacelata* (Ruiz & Pav.) Regel, *Laureliopsis philippiana* (Looser) Schodde, *Lophosoria quadripinnata* (J.F. Gmel.) C. Chr., *Nothofagus obliqua* (Mirb.) Oerst.	100 / 5.14	-38.01 / -73.18	426	11.6‡	783‡	10.3	0.36

*Ehlers, Blanckenburg, & Übernickel, 2019; data represent the experimental period of June 2016- May 2018.

† Laboratory for Climatology and Remote Sensing, University of Marburg, Germany, personal communication, April 2019.

‡ INIA 2019. Stations Gabriela Mistral, La Cruz and La Isla were used for SA, ME and TL, respectively.

§ Thompson, Palma, Knowles, & Holbrook, 2003 (AP for AF is assumed to be the same as for AD).

4.2.3 Plant species and functional trait measurements

From the dominant plant species at each site, we selected five species per site (Table 4-1; at the AD site one lichen species was included) covering a wide spectrum of leaf traits expected to affect litter decomposition (Dias et al., 2017). For each species, we selected five individuals and measured specific leaf area (SLA, $cm^2 g^{-1}$) and force to punch (Fp, N cm^{-1}) on 10 randomly-selected green leaves. For three to five subsamples of leaf litter per species, obtained from leaf mixtures collected from at least 10 individuals (senescent litter used in the litter translocation experiment, see next section), we determined concentrations of lignin, carbohydrates, proteins, lipids, total phenolic compounds, tannins and the elements C, N, Al, Ca, Fe, Mg, Mn, Na and P. Finally, we calculated the ratios C/N and Lignin/N. A description of specific measurements and methods of chemical analyses can be found in Appendix S2-1. For all analyses, traits were averaged at the species level per site.

4.3.4 Litter translocation experiment

We performed a full reciprocal litterbag translocation experiment, where litter from each species and site was incubated at each site (i.e., each climate zone). We harvested fresh senescent litter from a minimum of 10 individuals per species near the study plots during the late summer of 2016, either manually or with litter traps, depending on the height and deciduousness of the species. When used, litter traps were installed only under trees that allowed to obtain leaf litter of a single species to avoid potential contamination. For succulent species, green leaves were used. Litter was not washed to avoid the loss of leachable elements, and was oven-dried at 60° C for 72 h (or 96 h for succulent species) until constant weight. Subsamples of this litter material were used to determine nutrient contents (Appendix S1). We prepared 10x10 cm bags with a polyester mesh (1 mm). Bags were filled with 2 g of oven-dry single-species litter, recording the dry weight of each sample. For a few species with small leaf sizes, we used a second layer (same mesh size) to prevent losses. Litterbags were transported in individual paper bags and the initial weights corrected for any material left in these bags during transportation. One sample per incubation period, species and site was placed in each of the three plots per site. Considering 5 incubation periods, 30 species and 6 sites (climates), this triple replication added up to a total of 2700 litterbags.

The experiment was installed in early June 2016 (late autumn in the southern hemisphere). At each site, we carefully removed local soil litter and organic material, if present, and placed litterbags on top of the mineral soil. In study sites with a patchy vegetation cover, litterbags were placed between patches, but close (0.5 to 1 m) to shrubs. The experiment was protected against animals with poultry-wire mesh. In spite of this safeguard, some litterbags were damaged and could not be analyzed.

Groups of litterbags were harvested at five decomposition stages: 3, 6, 9, 12 and 24 months after installation, to observe both fast short-term changes and slower middle- and long-term changes (Zukswert & Prescott, 2017). At harvesting, litterbags were placed in individual paper bags, oven-dried at 60° C for 48 h and then litter samples were weighed. For each sample, the percentage of litter mass loss was calculated as M_0-Mt/M_0*100, where Mt is the final dry mass at decomposition stage t, M_0 is the initial dry mass of a sample.

4.2.5 Data analysis

Mass-loss data were logit transformed given that they were proportions, whereas trait data (except for proteins, lipids, lignin and P content) were log transformed to achieve normality. As a first data exploration, we calculated the single-factor Pearson correlations of mass loss across all five harvests with the microclimatic variables (using the corresponding MST and MSM for each decomposition period). Because the autocorrelation between MST and MSM was high (r=-0.88, p<0.0001, n=18), we used the variable that best correlated to litter mass loss, MSM (p<0.0001 and r=0.32 for site-level data, n=2556), for subsequent statistical analyses. Likewise, we further explored our data by calculating the Pearson correlations between all traits and of all traits with litter mass loss.

We analysed how litter mass loss changed among sites (as a proxy for climate) and through time, by performing a two-way ANOVA with mass loss as a function of site and time, both as factors, followed by Tukey pairwise-comparisons as post-hoc analyses.

To determine how the relative importance of climate and traits for litter mass loss and their interaction changed with decomposition stage, we used linear mixed models (LMMs) to explain mass loss for each decomposition stage separately, comparing the models to detect changes in the driving factors through time. We tested MSM, functional traits and their interaction terms as predictor variables, with study sites as a random factor, using the *lmer* function from the *lme4* package (Bates, Maechler, Bolker, & Walker, 2014) in R. For each decomposition stage, model selection was performed using forward selection, selecting the most parsimonious model following the Akaike information criterion (AIC). At each step, we quantified the variance inflation of the added variable, using the *check_collinearity* function (vif threshold = 10) from the *performance* package in R (Lüdecke, Makowski, Waggoner & Patil, 2020) to restrict multicollinearity in the model. For each selected decomposition model (i.e., for each decomposition stage), the explained variance per predictor was approached using dominance analysis (Azen & Budescu, 2006; Luo & Azen, 2013) and calculated using the S&B R^2 metric at level 1 (Snijders & Bosker, 1994) with the *dominanceanalysis* package in R (Bustos & Soares 2020). For each decomposition model, we calculated the relative importance of traits to MSM (RI Traits) as the total variance explained by traits (traits R^2) divided by the variance explained by MSM (MSM R^2).

To evaluate the effect of trait variation (expressed as the standard deviation) on the importance of traits for litter decomposition, we used randomization-based statistical procedures. For each decomposition stage, we created models with 1000 replicates each of 6-, 8- and 10-random-species selections out of our 30 species. Because this randomization uses smaller sample sizes, mixed models could not be developed (models did not converge). Therefore, we used linear models (LM) with the same predictors contained in the selected LMM for each decomposition stage. Similarly to LMMs, the explained variance per predictor was approached using dominance analysis (Azen & Budescu, 2006). A comparison between these LMs and the selected LMMs shows that differences in the relative importance of their predictors are minimal (Tables S4-1 and S4-2). For each randomization, we obtained the variance explained by each trait retained in the models (trait R^2). For each retained trait at each decomposition stage, we

determined the Pearson correlation between the R^2 of the trait and its standard deviation (SD) in the respective randomized set of species.

As an *a posteriori* analysis, we explored a possible effect of photodegradation at the arid and semi-arid sites. For this, we tested for an interaction between lignin content and soil moisture in explaining litter mass loss using a LMM with site as a random factor.

All statistical analyses were implemented using the R statistical environment v.3.6.0 (R Core Team, 2019).

4.3 Results

4.3.1 Climate and functional traits effects through time

After 12 months, the site-average litter mass loss ranged from 27% at the semi-arid (SA) to 63% at the temperate lowland site (TL). At all sites, the variation among species was very high (SD between 26 and 27%, Table S4-3). The smallest mass loss was 3% (the lichen *Usnea sp.* when decomposing at the SA), the largest 97% (the succulent *Frankenia chilensis* when decomposing at the TL). After 24 months of decomposition, the site-average litter mass loss ranged from 41% (SD=26%) at the dry arid site (AD) to 85% (SD=27%) at TL (Table S4-3). The smallest mass loss was 6% (the tree fern *Lophosoria quadripinnata*) at the mediterranean site (ME). At TL, some species (e.g., the soft-leaved species *Cristaria integerrima, Nolana crassulifolia*, *Euphorbia lactiflua*) were completely decomposed.

Across all species and decomposition stages, litter mass loss was strongly positively related to soil moisture (MSM, r=0.30, p<0.0001) and negatively to soil temperature (MST, r=-0.21, p<0.0001). Litter mass loss differed significantly among climates at all decomposition stages (3 months: $F_{(5,494)}$=15.9, p<0.0001; 6 months: $F_{(5,507)}$=16.7, p<0.0001; 9 months: $F_{(5,507)}$=36.1, p<0.0001; 12 months: $F_{(5,504)}$=35.6, p<0.0001; 24 months: $F_{(5,514)}$=55.5, p<0.0001, Fig. 4-2). In general, differences were small among the four driest sites (AD, AF, SA and ME) and high between these and the two wettest sites (TU and TL), as well as between the two wet sites in later decomposition stages. After three months of decomposition, the four driest sites already had significantly lower mass loss than the two wettest sites (Fig. 4-2). In the following stages, differences increased between the two wet sites, with the lowland temperate site (TL) having the highest mass losses (TL, Fig. 4-2). The four driest sites did not differ in mass loss at any stage.

In almost all decomposition stages, soil moisture, proteins, sodium (Na) and magnesium (Mg) content and specific leaf area (SLA) correlated positively with decomposition, while force to punch (Fp) correlated negatively (Fig. 4-3, Tables S4-1 and S4-4). Among traits, Na was consistently the strongest predictor, followed by the protein and Mg content (Fig 4-3). Small but significant interactions between MSM and Na, and between MSM and protein content were included in the models at several decomposition stages (Fig. 4-4, Table S4-1), suggesting that the effect of these litter traits on decomposition changed along the climatic gradient and that the effect of climate differed in dependence of the trait values. In the driest range of the gradient (<0.25 m^3/m^3), litter mass loss differed between species with medium and high Na content and

between medium and low protein content, but did not change with soil moisture (Fig. 4-4). In contrast, in the wettest range, the mean and the variation in litter mass loss increased and were driven by both traits and climate (Fig. 4-4). Interactions of MSM with some other traits were also significant, but less frequent across decomposition stages (Table S3-1). An interaction between climate and lignin was hypothesized because of the contrasting roles of lignin for photodegradation vs. biological decomposition (Fig. 4-5a, and see discussion), but this interaction was not observed (Tables S4-1 and S4-5, Fig 4-5b). In all species, independently of their lignin content, decomposition decreased with decreasing moisture in the wetter sites and remained stable in the drier site (Fig. 4-5b). Some traits usually correlating well with decomposition speed, such as C/N, were not included in the models because they were strongly correlated to other factors included (e.g., C/N to protein content) and were thus removed by the variance inflation criterion (vif). This does not imply of course, that they are not related to decomposition (see Table S4-4), but that e.g. protein content (which is rarely measured in decomposition studies as this is more elaborate than C/N) was a better predictor.

The importance of traits for litter mass loss (traits R^2) decreased and the importance of MSM increased with time (Fig. 4-3, Table S4-1). Thus, during the first year of decomposition, traits exhibited higher relative importance than MSM (with traits about 6x more important than MSM after 3 and 6 months and 2.5x after 9 and 12 months), while MSM became more important than traits (with traits 0.8x the importance of MSM) after 24 months of decomposition.

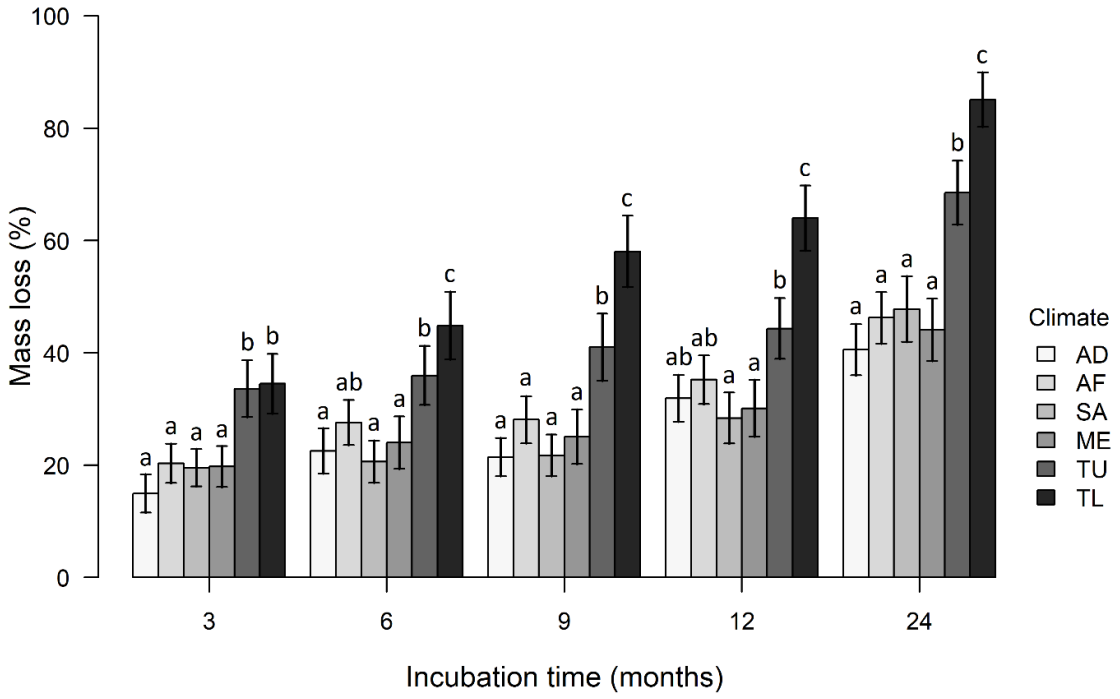

Figure 4-2. Mean litter mass loss (%) after 3, 6, 9, 12 and 24 months of decomposition under different climates. Error bars represent ± 1 SE. Different letters indicate significant differences ($p<0.05$) among climates for each incubation period after post-hoc analyses, where mass loss was logit transformed. Refer to Table 4-1 for climate names.

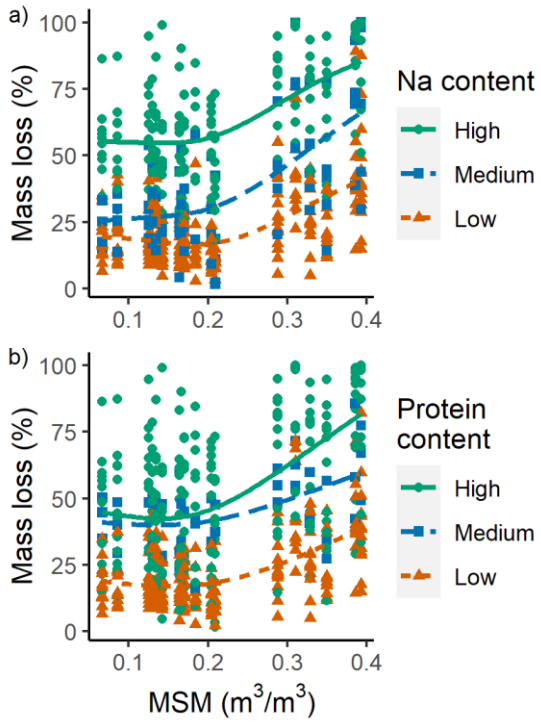

Figure 4-3. Explained variance of mean soil moisture (MSM), functional traits and their interaction in models of litter mass loss across different decomposition stages, for 30 plant species used in a reciprocal litter transplant experiment along the coastal cordillera of Chile. Explained variance of the predictors was approached as the S&B R^2 contribution at level 1 (Snijders & Bosker, 1994) using dominance analysis (Azen & Bodescu, 2006).

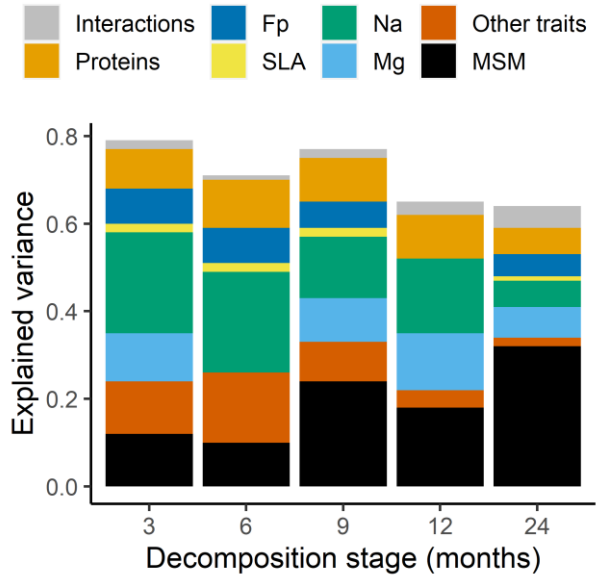

Figure 4-4. Mass loss (%) after 12 months of leaf litter decomposition for 30 species translocated along the coastal cordillera in Chile showing the significant interactive effects of soil moisture (MSM, x-axis) with two plant functional traits: a) sodium (Na) and b) protein content). The interaction is visualised using three categories for each trait (green, high; blue, medium; orange, low; with cuts at median ± 0.25*SD). Lines shown are smoothed fits through the data, for illustration only, and do not represent the final models. Each point represents observed data for one species decomposing in one plot. Similar results were observed for other decomposition stages; therefore, those results are not shown.

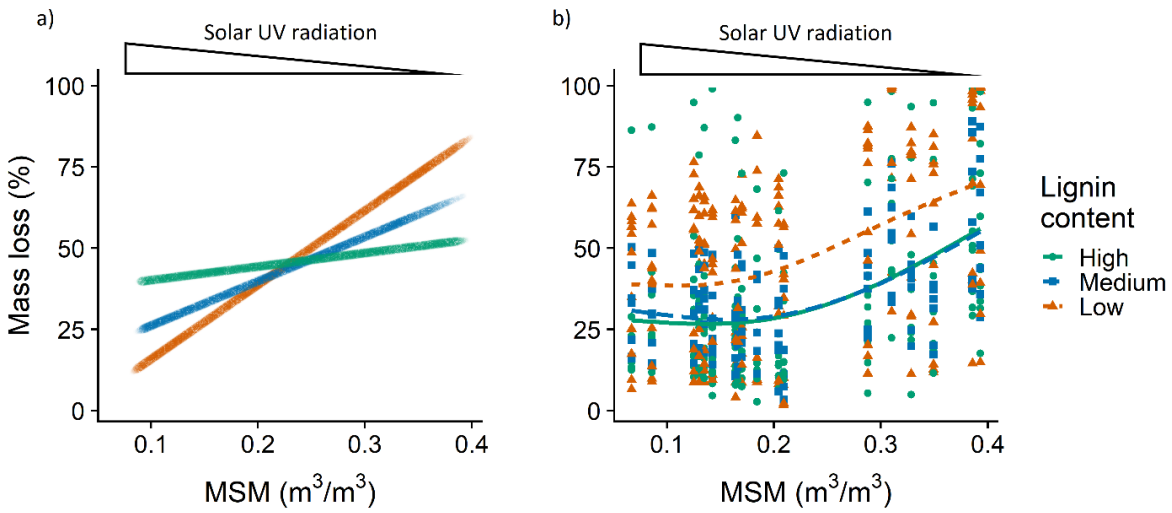

Figure 4-5. a) Hypothesized and b) observed response of litter mass loss (%) to mean soil moisture (MSM) and solar UV radiation (increasing from right to left) gradients after 12 months of decomposition for species with different lignin content (green, high; blue, medium; orange, low). Lignin-content groups were divided at the median ± 0.25*SD. Lines shown are smoothed fits through the data, for illustration only, not related to the linear model, which showed no interaction between the effects of lignin content and MSM.

4.3.2 Effects of trait variation on the importance of traits for decomposition

Litter varied strongly in Fp, tannins, Ca, Na and P content (>100-fold variation), considerably in SLA, C/N, Lignin/N, protein, lignin, Al, Mg content (≥10-fold variation) and to a less degree in carbohydrate and Fe content (<10-fold variation, Table S4-6). For most traits, an increase in trait variation (higher SD), for the same number of species (6 or 8 or 10), led to an increase in the average importance of traits (trait R^2) in explaining differences in decomposition (Table 4-2). Correlations between trait SD and trait explanatory power (R^2) were generally weak, even when significant, with a maximum R^2 of 0.36, but consistently positive. Of all traits retained in the models, the variation of proteins and carbohydrates presented the strongest correlation with the R^2 of these traits (Table 4-2).

Table 4-2. Pearson correlation coefficients of the importance of different traits with the range of trait-values considered in the selected linear models of litter mass loss at different decomposition stages. The importance of each trait was approached as the R^2 using dominance analysis (Azen & Bodescu, 2006). The range of a trait was expressed as its standard deviation (SD). Data represent 1000 randomizations of a 10-species-selection out of the 30 species studied, for each model of litter mass loss. Randomizations with 6 and 8 species yielded similar results and thus results are not shown. Bold values represent correlations with $p<0.05$.

	Decomposition stages (months)				
Trait	3	6	9	12	24
Na	**0.14**	**0.19**	**0.14**	**0.17**	**0.15**
Mg	**0.24**		**0.33**	**0.14**	**0.16**
K	**0.19**	**0.31**	**0.18**		
Fp	**0.25**	0.03	**0.22**		**0.13**
SLA	0.03	0.02	**0.14**		**0.13**
Protein	**0.26**	**0.27**	**0.36**	**0.28**	**0.22**
Lignin/N	**0.10**	**0.07**	0.03		
Tannins	**0.08**		0.02		
Carbohydrates		**0.26**		**0.27**	
Lignin		**0.26**			
Lipids				**0.10**	
Fe	**0.19**				**0.07**
Mn	0.01		0.08		

4.4 Discussion

Our results show that both climate (represented by mean soil moisture, MSM) and litter traits are key factors for litter decomposition, with traits being most important in early and climate in later decomposition stages. Moreover, the importance of traits relative to climate increased with the range of trait values included and the importance of climate was dependent on the particular section of the climate gradient considered. Therefore, it is clear that the relative importance of litter traits and climate in controlling litter decomposition depends not only on the decomposition stage, but also on the variability in both factors.

4.4.1 Effects of climate and plant functional traits

We observed higher mass loss in climate zones with higher precipitation and soil moisture, in line with global patterns (Bradford et al., 2017). While a lower mass loss in climates with higher soil temperature appears to contradict the prevalent positive relationship with decomposition (Cornwell et al., 2008; Zhang et al., 2008), this was likely due to the negative correlation of temperature and moisture within our gradient. Differences in decomposition between the two wet sites (upland and lowland temperate sites) show that higher temperatures indeed result in higher decomposition when moisture is not limiting decomposer activity.

Litter mass loss varied among climates in all decomposition stages, but not among the four driest sites. This is remarkable, given the considerable difference in rainfall among these

climate zones, at least between the two arid sites and the semi-arid and mediterranean sites – these last two differed less in precipitation than usual due to a very dry period in Central Chile (rainfall deficits between 20 and 40%, Garreaud et al., 2020). We had expected lower decomposition rates at the arid end of the gradient than at the semi-arid and particularly the mediterranean areas, because of low humidity and very shallow soils, which together with the patchy plant distribution create unfavourable conditions for decomposers (Coûteaux et al., 1995; Bernhard et al., 2018). On the other hand, litter decomposition studies from arid and semi-arid areas have shown that solar radiation can cause photodegradation of plant material and thereby increase litter decomposition (Austin & Vivanco, 2006; Gallo, Sinsabaugh, & Cabaniss, 2006) irrespective of biotic drivers. This process could provide an additional factor for decomposition at our three driest sites (AD, AF and SA), where radiation loads are high and litter was not shaded under vegetation. Although we did not explicitly assess the effects of solar radiation in our study, we evaluated its potential impact by comparing litter mass loss of species with low and high lignin content along the latitudinal gradient. Lignin is difficult to break down by microorganisms but is a preferential target of photodegradation (Austin & Ballaré, 2010). We therefore predicted that if photodegradation would be compensating for the lack of biological decomposition in the arid areas, the litter mass loss of species with high lignin contents should decrease less towards the driest, sun-exposed sites compared to species with low lignin contents. If photodegradation (in arid areas) were stronger than biological decomposition (in wetter areas) in these high-lignin species, they could even show a reversed response, with the highest decomposition at the driest end of the gradient. However, we found no interaction in the effects of lignin content and soil moisture on litter mass loss, and no difference in the shape of the response between species with low or high lignin contents along the gradient. High-lignin species showed lower decomposition than low-lignin species in all climate zones, as expected if biological decomposition dominated everywhere. Based on this result, it seems unlikely that photodegradation explains the lack of a climate effect among the driest four sites. This does not mean that photodegradation does not occur, but it probably could not compensate for a decrease in biological decomposition completely.

Apart from photodegradation, regular input of fog water to the soil surface at one of the arid sites (AF; Lehnert et al., 2018) could also stimulate decomposition of surface litter without any measurable effects on soil humidity. This process might explain why decomposition was not much lower at this arid site compared to semi-arid and mediterranean sites, in spite of the higher rainfall in the latter two, though it does not explain why in the low-fog site decomposition was also only slightly and non-significantly slower than in the semi-arid and mediterranean sites. Perhaps the most important explanation for the small effect of climate among the four dry sites may lie in the fact that the climate during the experimental period was drier than usual in Central Chile (with rainfall deficits between 20 and 40%; Garreaud et al., 2020), reducing the expected differences among them. The low rainfall frequency observed could particularly have slowed down decomposition, by leading to temporary litter dryness and by severely limiting substrate diffusion and the enzymatic activity of decomposers (Vanlauwe, Vanlangenhove, Merckx, & Vlassak, 1995).

The influences of some litter traits on litter decomposition varied along the latitudinal gradient. As indicated by the interactions between some traits (e.g., Na and Proteins) and MSM, and by

the differences between the sites through time, litter decomposition was mainly associated to litter traits at the less favourable end of the range (i.e., driest sites). At the most favourable end (wet temperate sites), litter decomposition was related to both trait and soil moisture values. Consequently, our results do not support our first hypothesis that traits should have a stronger relative effect in favourable climates (Bradford et al., 2016). It is likely that in the drier climates, where moisture should strongly limit decomposition, a combination of the abovementioned reasons (i.e., some additional decomposition due to photodegradation, additional water input from fog, and the relatively small differences in soil moisture due to the exceptionally dry year) partially decoupled decomposition rates from gradients in soil moisture and temperature or reduced the strength of these gradients, giving more relative weight to litter-trait effects.

4.4.2 Drivers of litter decomposition through time

Traits were clearly important determinants of decomposition rates and together explained between 26 and 66% of the total variation in litter mass loss, with decreasing explanatory power along the decomposition stages. Both nutrient-related traits (Na, proteins and Mg), and morphological traits (Fp, SLA) were found to be good predictors of litter decomposition rates at several stages of decomposition. One of the main controllers of mass loss was Na, an element abundantly available near coastlines due to deposition of oceanic aerosols and critical for consumers but not plants. Previous studies have demonstrated that the addition of Na can promote detritivore activity and decomposition (Kaspari, Clay, Donoso, & Yanoviak, 2014). Clay, Donoso, and Kaspari (2015) reported higher decomposition rates in coastal compared to inland tropical forests, while the addition of Na alleviated these differences. In our study sites, plants with high sodium content were mostly found in the coastal arid and semi-arid sites. In line with previous findings (Clay et al., 2015), our study suggests that Na may stimulate litter decomposition in these coastal ecosystems. However, further experiments (e.g., coastal *vs.* inland experiments) are needed to confirm this geographic pattern.

By following the decomposition process for over two years, we revealed a shift in the relative importance of plant traits and climate for litter decomposition. In the first year, trait effects exceeded climate effects. In the second year, however, climate gained in importance relative to traits, but traits remained influential. Due to the loss of soluble and labile compounds in early decomposition stages, litter materials tend to attain a more similar chemical quality over time (Preston et al., 2009; Parsons et al., 2014; but see Wickings, Grandy, Reed, & Cleveland, 2012), after which abiotic conditions become the main drivers of decomposition. García-Palacios, Shaw, Wall, and Hättenschwiler (2016) found that biotic factors, in particular the decomposer community, are the most important drivers during early-stage decomposition, and that abiotic factors, mostly soil moisture, were increasingly important in the late stages of decomposition. Still, they also observed a marked legacy effect of litter traits in late-stage decomposition, which is also supported by our results. Currie et al. (2010), in a 10-year litter decomposition experiment that included six litter types, found that climate provided superior predictors on both long and short time scales, while, similar to our findings, litter quality declined in its predictive power with time. Currie et al. (2010) also reported that climate-trait interactions occurred during the first-year decomposition, but not afterwards. However, our results suggest

that climate and litter-trait interactions must be interpreted with caution because different interaction terms were retained in different decomposition stage models and overall their relative importance was small.

4.4.3 Importance of the ranges of climate and plant functional traits studied

Our results support our hypothesis that the relative importance of plant functional traits for litter decomposition increases with the variation of the trait values covered by the species included in the evaluation. This is an important finding, given that the conclusion of whether it is climate or traits that are more important in controlling decomposition dynamics may be determined simply by the range of traits considered. In other words, when inter- and intraspecific variation in litter traits of a specific plant community are not well represented, it is difficult to determine the drivers of decomposition correctly, which in the past may have contributed to the prevailing climate-control paradigm (Zhang et al., 2008). Our study included litter from 30 species, with high variation in litter traits among species (e.g., 12-fold in lignin/N, and 13-fold in C/N, which is higher than the variation reported in any previous study, including Harmon et al. (2009), based on nine litter types and ten-fold variation in lignin/N, or Zhang et al. (2008), who used litter types with 2.5-fold variation in C/N). Trait variation resulted in important differences in litter decomposition among species, with the litter of some species almost completely decomposed after one year of incubation, while others remained mostly intact, even after two years. By reciprocally translocating litter from species of very different ecosystem types, we may have inflated the range of trait values compared to local plant communities. High variation in litter traits, however, was also present within each community (e.g., an average of 5-fold variation in C/N and Lignin/N, or 17-fold in Na per community). Moreover, the ranges in trait values reported here are comparable to species-rich plant communities such as tropical rainforests (Hättenschwiler, Aeschlimann, Coûteaux, Roy, & Bonal, 2008). Our study also shows that the range in climatic conditions and the types of climate zones included in decomposition studies affect the relative importance of trait vs. climate in driving decomposition.

4.5 Conclusions

Our study is unique in its very wide range of litter trait values, climatic conditions and the relatively long litter incubation time, including harvests at several decomposition stages. This combination made it possible to identify the major factors that determine the relative importance of climate and litter traits for decomposition dynamics. Soil moisture and plant functional traits both played a key role in driving litter decomposition. Importantly though, their relative contribution and interactions varied through time and with the range of climates and trait variation considered, larger variation leading to larger effect size and relative importance. Experiments in other broad climate ranges, including a similarly large variation in trait values as in our experiment and several litter harvests along the decomposition process, are recommended to further elucidate under what conditions climate dominates as the driver of litter decomposition and when traits become more important. Quantifying these drivers is essential to correctly model decomposition rates and their role in carbon cycling on a global scale. As climate change will additionally induce shifts in the trait distributions of the

vegetation, the outcome of carbon-model scenarios depends strongly on a profound and balanced understanding of both vegetation processes and plant- and climate-based controls on litter decomposition.

4.6 Acknowledgements

RC and LB express their deep gratitude to all students, technical assistants and colleagues who helped during field and laboratory work. Peter Chifflard and Martin Reis are acknowledged for their involvement in the initial project proposal. Glenda Mendieta-Leiva provided valuable comments on the statistical analyses. We also acknowledge the editors and two anonymous reviewers for their constructive comments and suggestions. We are grateful to the Chilean National Forest Corporation (CONAF) and Comunidad Agrícola Quebrada de Talca who provided access to the study sites. This study was funded by the German Science Foundation (DFG) Priority Program SPP-1803 "EarthShape: Earth Surface Shaping by Biota" (grant MB 3843/6-1; MU 3021/6-1; KT 338/14-1 and 338/14-2). All authors declare that there is no conflict of interest.

4.7 Authors' contributions

MB conceived the ideas and designed methodology, in coordination with KT, AS and RR; RC and LB developed the experiment and collected the data; RC, CM, IP and SH provided laboratory results, RC analyzed the data and led the writing of the manuscript, supervised by MB. All authors contributed critically to the drafts and gave final approval for publication.

4.8 Data availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ttdz08kwb (Canessa et al., 2020).

Chapter 5

Trait functional diversity explains mixture effects on litter decomposition in arid but not in humid ecosystems in Chile

submitted by Rafaella Canessa to *Functional Ecology*

Rafaella Canessa*[1], Liesbeth van den Brink[2], Monica B. Berdugo[1], Stephan Hättenschwiler[3], Rodrigo S. Rios[4,5], Alfredo Saldaña[6], Katja Tielbörger[2], Maaike Y. Bader[1]

[1]Ecological Plant Geography, Faculty of Geography, University of Marburg, Deutschhausstr. 10, 35032 Marburg, Germany
[2]Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany
[3]CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France
[4]Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile
[5]Instituto Multidisciplinario de Investigación en Ciencia y Tecnología, Universidad de La Serena, La Serena, Chile
[6]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile.

*Corresponding author

Abstract

1. Litter decomposition, an important ecosystem process, is driven by climate and litter quality. In litter mixtures, the decomposition of each litter type is also influenced by the quality of other litter types in the mixture, which may lead to non-additive effects on overall litter decomposition rates. The strength of these effects seems to depend on the litter functional diversity, rather than on species richness. It is unknown, however, which functional traits explain litter mixture effects and how these depend on the range of trait values and the ecosystem involved, hampering our ability to predict decomposition in mixed plant communities.

2. We aimed at understanding which components of diversity (species number and/or functional dispersion, FDis) influence litter mixture decomposition across different climates in Chile. We calculated FDis based on litter traits related to nutrient transfer among litters or to litter recalcitrance, and tested whether mixture effects correlated to these FDis measures.

3. Some litter mixture effects on decomposition were found across sites, but the direction was inconsistent and most mixtures showed just additive effects, except in the most arid sites. Interestingly, non-additive mixture effects were negative in one and positive in the other arid site. Both were amplified by FDis, as defined by diversity in recalcitrance and in nutrient transfer traits, respectively. The other ecosystems showed no correlation between mixture effects and FDis, and no effects of species richness were found at any site.

4. Overall, litter diversity does not appear to have strong effects on decomposition rates in the studied Chilean ecosystems, and the direction and intensity of the mixture effects are context-dependent, with stronger effects in the dryest ecosystems. Where effects are found, the diversity of functional traits related to nutrient transfer and litter recalcitrance can predict mixture effects, especially when the range of trait diversities included is large, though much of the variation remains unexplained. Functional diversity metrics based on relevant litter traits applied to diverse site-specific litter mixtures in different climates could help to further understand under which conditions and in which direction diversity affects decomposition.

Keywords

Arid ecosystem, climate gradient, functional dispersion, litter decomposition, litter mixture, litter recalcitrance, nutrient transfer, plant functional traits

5.1 Introduction

Litter decomposition, i.e. the breakdown of organic matter and the release of its components in mineral form (e.g. CO_2) or as organic molecules, is a fundamental process in biogeochemical cycles and plays a central role in ecosystem functioning (Berg & McClaugherty, 2003). Litter inputs to ecosystems vary tremendously as a function of the identity and diversity of plant species, as species differ widely in their litter phenology, chemistry and morphology (Cornwell et al., 2008). Some studies suggest that litter diversity can have significant effects on decomposition (Hättenschwiler et al., 2005; Kou et al., 2020; Liu et al., 2020). However, the responses to litter diversity vary strongly among studies, along with environmental conditions, the species contributing to litter mixtures, decomposer community composition, decomposition stage and the approaches in the assessment of diversity (Handa et al., 2014; Kou et al., 2020; Liu et al., 2020). Reliable predictions on how litter diversity affects decomposition are critically needed in order to assess how carbon and nutrient cycling may change in the context of species loss and global change (Balvanera et al., 2006; Gessner et al., 2010).

The significance of plant diversity for litter decomposition is commonly tested by manipulating the diversity of litter types (i.e. mixing a variable number of species and/or functional groups) and evaluating litter mixture effects on decomposition. Mixture effects are defined as the deviation in decomposition rates of litter mixtures ("observed decomposition") from those expected from single-species litter ("predicted decomposition" *sensu* Hättenschwiler et al., 2005). Recent meta-analyses suggest that several species together decompose either faster (positive effect) or slower (negative effect) than predicted by single species decomposition, i.e. non-additive effects prevail (Gartner & Cardon, 2004; Kou et al., 2020; Liu et al., 2020). Previous studies have shown no clear trends in litter mixture effects with increasing species richness (e.g. Wardle et al., 1997; Barantal et al., 2014). Yet, larger differences in initial litter quality (i.e. higher functional diversity) likely correlate to stronger litter mixture effects (Gessner et al., 2010), because the mechanisms behind these effects are driven by specific litter traits (Liu et al., 2020).

While several traits have been described to drive litter decomposition (Zhang et al., 2008; Makkonen et al., 2012; Canessa et al., 2021), only a few of them may be particularly important in determining litter mixture effects. For example, nutrients such as nitrogen, potassium, calcium or magnesium can be transferred from high-quality to low-quality litters within mixtures (Briones & Ineson, 1996; Schimel & Hättenschwiler, 2007; Bonanomi et al., 2014). As a result, low-quality litter types may decompose faster in litter mixtures, while mixing does not affect decomposition rates of high-quality litter (Liu et al., 2020). Nutrient transfer in litter mixtures could optimize the nutrient acquisition of decomposers and produce an overall positive effect, i.e. faster decomposition than predicted (Hättenschwiler et al., 2005; Lummer et al., 2012). Apart from transferable nutrients, other relevant litter traits are secondary compounds that may inhibit microbial activity and litter decay (e.g. polyphenols; Hättenschwiler et al., 2005) and can thus produce negative mixture effects (i.e. slower decomposition than predicted). Therefore, any expected correlation between functional diversity and litter-mixture effects (Gessner et al., 2010) may be related to transferable nutrients and/or secondary compounds. Because these trait-related mixture effects can be positive or

negative, the net mixture effect may be zero. It is therefore important to characterize traits of both types in the studied litter to disentangle their relative role in litter mixture effects (Hoorens, 2003). Unfortunately, such a combination of litter traits was rarely explicit in previous studies on diversity controls of decomposition.

Litter mixture effects seem to differ among ecosystems: while positive effects of litter mixtures on decomposition have been reported in grasslands (Scherer-Lorenzen, 2008) and tree plantations (Alberti et al., 2017), they are more variable in natural forests, with either positive, negative or null mixture effects reported (Gartner & Cardon, 2004; Barantal et al., 2014, Leppert et al., 2017; Gripp et al., 2018), but overall positive (Liu et al., 2020; Kou et al., 2020). Duan et al. (2013) suggested that positive effects should occur in extreme-cold climates because in these ecosystems nutrient leaching is lower, and active microbial transfer can occur among litter and thus increase overall decomposition. However, one may also argue that if soil decomposer activity is highly restricted by climatic conditions (e.g. in cold or dry ecosystems), positive effects could also be hindered, turning into null or negative effects (Liu et al. 2020). In fact, for boreal forests and alpine shrublands mainly null and negative effects have been reported (Kou et al., 2020; Zhou et al., 2020). The same responses may be expected in other extreme climates such as arid and semi-arid areas, where decomposer communities are strongly restricted by low moisture availability (Moskwa et al., 2020).

In order to understand how and why litter mixture effects on decomposition differ among ecosystems, studies that concurrently investigate mixture effects across large climatic gradients including contrasting ecosystems are urgently needed. However, such experimental studies are rare (but see Zhou et al., 2020) and large meta-analyses are biased towards temperate forests (Kou et al., 2020). The comparison of litter-mixture effects across different climates is challenging, not only because of practical reasons but also because litter decomposition rates vary with temperature and precipitation (Cornwell et al., 2008; Zhang et al., 2008). Thus, comparing the effects of litter mixtures in different climates needs particular caution, because of different stages of decomposition possibly associated with variable mixture effects (Santonja et al. 2019). To control for climate differences, multiple decomposition stages should be considered as mixture effects tend to decrease with time (Wu et al., 2013; Butenshoen et al., 2014), probably due to converging litter quality during decomposition, and thus, a weaker potential for mixture effects in late decomposition stages (Currie et al., 2010; Canessa et al., 2021).

Here, we conducted a field experiment that ran for almost two years to unravel the effects of two aspects of litter diversity, species richness and functional dispersion (FDis, a measure of functional richness and divergence), on litter decomposition along a pronounced climate and vegetation gradient ranging from the Atacama Desert (26°S) to humid temperate forests (38°S) in Chile. Using different sets of functional traits to calculate FDis, we studied which traits reflect the mechanisms that are more important for functional diversity effects: transferable nutrients that can boost decomposition in nutrient-poor litter fractions, or those complex molecules known to inhibit decomposition. We hypothesized that non-additive litter mixture effects (1) occur less often in arid and semi-arid sites, which are climatically less favourable for decomposition, than in mediterranean and temperate forests; (2) are better explained by FDis than by species richness; and (3) are

positively correlated to an increasing trait diversity in transferable nutrients and negatively to an increasing trait diversity of inhibitory compounds.

5.2. Materials and Methods

5.2.1 Study sites

We conducted our study along the coastal cordillera of Chile, from 26°S to 38°S, including six sites with contrasting climates (Fig. 5-1, Table S5-1) but homogenous granitoid parent material (Oeser et al., 2018): arid desert (Pampa Blanca - Pan de Azúcar National Park, henceforth, "AD" for Arid Dry), coastal arid desert with fog influence (Las Lomitas - Pan de Azúcar National Park, "AF" for Arid Fog), semi-arid shrubland (Quebrada de Talca Private Reserve, "SA" for Semi-Arid), mediterranean forest (La Campana National Park, "ME" for Mediterranean), highland temperate rainforest (Nahuelbuta National Park, "TU" for Temperate Upland) and lowland temperate rainforest (Contulmo Natural Monument, "TL" for Temperate Lowland). The study sites are arranged along a climatic gradient that decreases in mean annual temperature from 14.4°C in AD to 6.7°C in TU, and increases in annual precipitation from 13 mm yr^{-1} to 2167 mm yr^{-1} (Table S5-1). The monthly rainfall distribution pattern is similar at all sites, where most of the rainfall occurs during the austral winter months, from May to August. AD and AF are located in the Atacama Desert with almost no rainfall but, at AF, the coastal fog is a relevant source of water (Lehnert et al., 2018). At AD some fog-water input may also occur, but with a much lower frequency than at AF. Further information on the study sites can be found in Bernhard et al. (2018) and Oeser et al. (2018).

5.2.2 Plant species and functional traits

At each study site, we characterized plant communities in three independent 10 x 10 m plots on representative mid-slopes and estimated the percentage cover per species at each plot. Data were then averaged at the site level and plant species were selected for the experiment based on their relative abundance (cover >5%, except for AD and AF where the threshold was 3%) and litter availability, with the aim to cover a large range of functional traits while including the most abundant species at each site. This led to a selection of between seven and ten species per site, with a total of 50 species (see Table S5-2). Among these, two species occurred at two different study sites (*Nolana crassulifolia* in AD and AF, *Nothofagus obliqua* in TU and TL), but were considered as two different litter types and used only in their site of origin. For each selected species, we measured the force to punch (Fp), C/N, Ca, Mg, Na, lignin, tannins and total phenolics in 5 individuals per species and 10 leaves per individual. For 30 species, the mentioned functional traits were retrieved from Canessa et al. (2020). For other species not present in that database, data of Fp, C/N, tannins and total phenolics were measured, following the same methodology used in Canessa et al. (2020). All traits were averaged at the species level.

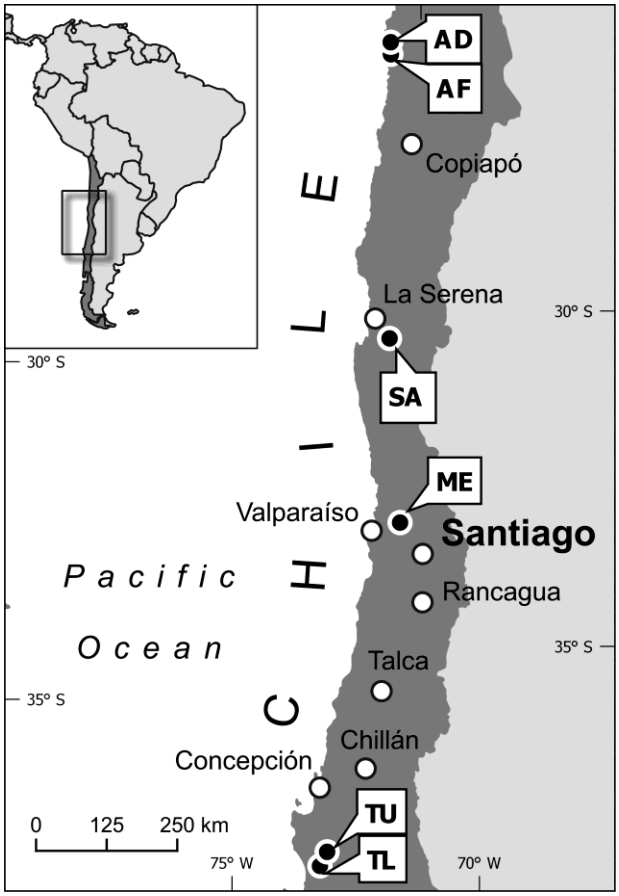

Figure 5-1. Geographic location of study sites included in the litter decomposition experiment conducted in Chile. AD = Arid-Dry, AF = Arid-Fog, SA =Semi-Arid, ME = Mediterranean, TU = Temperate upland, TL = Temperate Lowland.

5.2.3 Decomposition experiment

We performed a litterbag decomposition experiment, where single litter from each species, as well as species mixtures, were incubated at their home site. For each site, we prepared between seven and ten different mixtures containing two species (depending on the species richness of each site), two mixtures with four species and one mixture with six species (Table S5-2). To prepare the litterbags, we harvested fresh senescent litter during the late summer period of 2017, either manually, with litter traps, or by shaking trees. For five succulent species, green leaves were used. Litter was oven-dried at 60°C for 72 h (or 96 h for succulent species). Subsamples of this litter material were used to measure the chemical traits mentioned above.

We prepared 10 x 10 cm bags with a 1 mm mesh size. Bags were labelled and filled with 2 g of oven-dry litter, either with one single species or with treatment-specific mixtures with each species contributing an equal amount. For species with small leaves, we lined a second layer of mesh (same size) to prevent losses. Litterbags were placed into individual paper bags and the initial weight was corrected for any material left in these bags during transportation. To account for temporal

dynamics in decomposition, we prepared nine litter bags per litter treatment, with three bags placed in each of the three independent plots (three per plot) to be harvested after three decomposition periods. Considering a total of 52 single-species litterbags, 68 mixtures, three decomposition periods and three replicates, this added up to a total of 1080 litterbags.

The installation of the experiment took place in early June 2017 (late autumn in the southern hemisphere). At each site, local soil litter and organic material, if present, were carefully removed, and litterbags placed on top of the soil. The experiment was protected against damage from small herbivores with poultry-wire. In spite of this safeguard, a few litterbags were damaged and could not be analysed.

Groups of litterbags were harvested 6, 12 and 20 months after installation. At each harvest, litterbags were placed in individual paper bags, oven-dried at 60°C for 48h and then litter samples were weighed. For each litterbag, the percentage of litter mass loss was calculated as $(M_f - M_i) / M_i * 100$, where M_f is the final dry mass after decomposition and M_i is the initial dry mass. Unfortunately, some litterbags recovered after 20 months of decomposition were accidentally lost (for one plot at the AD and TU sites, and two plots at the TL site). Therefore, the TL site was not included in the analyses of the latest decomposition stage.

5.2.4 Mixture effects

Litter mass loss of each species decomposing alone was calculated at the plot level (single-species mass loss). For each mixture at each plot, we averaged the single-species mass loss of all the species contained in a mixture to calculate the predicted mass loss (M_p). The litter mixture effect (%), i.e. the percent variation in the observed mass loss of a mixture (M_o) relative to M_p, was calculated as $(M_o – M_p) / M_p *100$ for each mixture and plots. Non-additive mixture effects occurred when the observed mixture mass loss was significantly different from the predicted mixture mass loss. These non-additive effects were positive or negative when the observed mixture mass loss was higher or lower than the predicted mass loss, respectively.

5.2.5 Statistical analyses

To evaluate for significant differences between observed and predicted mass loss for each mixture and decomposition stage we used t-tests. To test for the influence of species richness, climate zones (i.e. sites), as well as their interaction, on litter mixture effects, we used an ANCOVA for each decomposition period. Similarly, an ANCOVA was used to test whether the relation between litter mixture effects and functional diversity varied across climate zones. Thereby, we expressed functional diversity as the functional dispersion index (FDis, *sensu* Laliberté & Legendre, 2010). FDis was calculated using the "*fdisp*" function in the FD package of R (Laliberté et al., 2014) on a species-by-species distance matrix (Gower dissimilarity matrix) computed from the functional traits measured. We calculated and tested the effect of three different FDis values, based on different groups of traits: (1) "FDis all" was calculated based on a distance matrix using all measured traits (i.e. C/N, Mg, K, Ca, tannins, total phenolics, lignin and Fp); (2) "FDis+" based on a distance matrix using only those traits potentially related to nutrient transfer among litter and thus, may cause positive mixture effects (C/N, Mg, K and Ca); and (3) "FDis–" based on a distance matrix using only those traits related to recalcitrance and decomposition inhibition and thus, expected to produce

negative mixture effects (tannins, total phenolics, lignin and Fp; Hättenschwiler et al., 2005). If trait data were missing for some or all of the species in a mixture, FDis was based on the available data, i.e. sometimes the number of traits to calculate the FDis was lower. All trait sets used to calculate FDis values included at least one trait with complete data. A Pearson correlation analysis indicated that FDis+ and FDis– were not strongly correlated ($r(66)= 0.17$, $p=0.17$). Because models showed that litter mixture effects were driven by the interaction between FDis values and site (see Table 5-1), to further understand the context-dependency of litter mixture effects we conducted Pearson correlations between litter mixture effects and FDis for each site and decomposition period independently. All statistical analyses were performed in the R statistical environment ver. 3.6.0 (R Core Team, 2019).

5.3 Results

Litter mixture effects varied among litter mixtures (Fig. 5-2a) and among sites (Fig. 5-2b). Most mixtures showed only additive effects, i.e. mixtures decomposed as predicted based on the decomposition of the individual species (Table S5-2). At the most arid site (AD), 40% of the mixtures showed significant negative mixture effects (Fig. 5-3) of, on average, 17.5% less decomposition than predicted after 12 months (Fig. 5-2b). At the other sites, mixture effects were on average positive (i.e. decomposition was between 1.8 and 7.3% higher than predicted) during the first year (Fig. 5-2b), but these effects were significant in less than 30% of the litter mixtures (Fig. 5-3, Table S5-2). Overall, more mixtures exhibited non-additive effects towards the arid end of the gradient (Fig. 5-3). Because after 20 months of decomposition litter mixture effects continued to occur but seemed to decrease (Table S5-2, Fig. 5-3; in agreement with previous studies, e.g. Wu et al. (2013) and Butenshoen et al. (2014)), we focus in the following sections on the first year of decomposition and show the results after 20 months of decomposition in the supplementary material (Table S5-3, Fig. S5-1).

Litter mixture effects did not depend on the number of species in the mixture (i.e. no main effect of species richness or interaction between richness and site, Tables 5-1 and S5-3). Instead, interactions between functional diversity and site indicated that functional dispersion (calculated as FDis all, FDis+ or FDis–) affected litter mixture effects differentially among sites (Tables 5-1 and S5-3, Fig. 5-4).

A higher functional dispersion “FDis all” (i.e. C/N, Mg, K, Ca, tannins, total phenolics, lignin and Fp) amplified litter mixture effects at the AD and AF sites, with negative and positive correlations, respectively (Fig. 5-4). Higher FDis+ of mixtures (dispersion index based on traits related to nutrient translocation) correlated with more positive litter mixture effects at the AF site (Fig. 5-4). On the contrary, higher FDis– of mixtures (dispersion index based on traits related to decomposition inhibition) correlated with more negative litter mixture effects in the AD site (Fig. 5-4). At all other sites, none of the FDis indices correlated to litter mixture effects (Fig. 5-4).

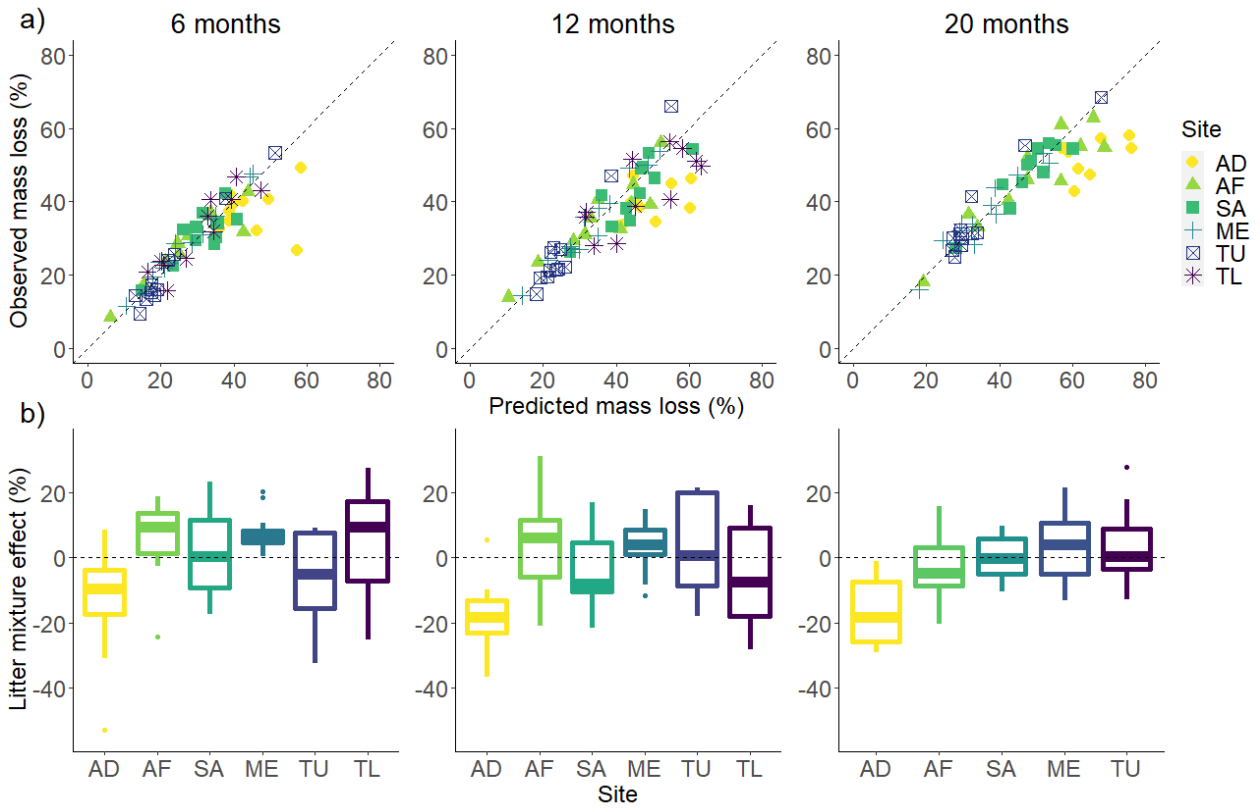

Figure 5-2. Observed mass loss of 68 litter mixtures (%, n=3) against predicted mass loss (a) and litter mixture effects (b) at six different sites across a climatic gradient in Chile (colours) after 6, 12 and 20 months of decomposition (columns). In (a), predicted mass loss results from averaging single species mass loss. Values above and below the dashed lines indicate positive and negative effects, respectively, and in (a) they represent a 1:1 relationship. All mixtures within a site are shown together, as the number of species in the mixtures did not affect the mixture effect. AD = Arid-Dry, AF = Arid-Fog, SA = Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland.

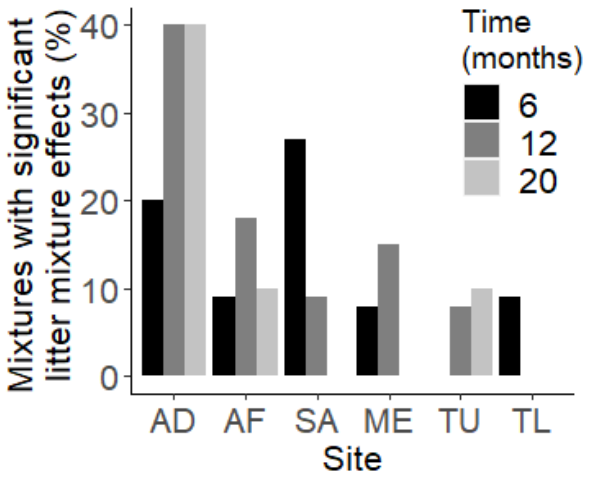

Figure 5-3. Percentage of litter mixtures (i.e. mixture treatments) with significant ($p<0.05$) litter mixture effects according to t-tests at six sites across a climatic gradient in Chile after 6, 12 and 20 months of decomposition (colours). n = 3 for most of the mixtures, except for cases highlighted in Table S5-2 where n = 2.

Table 5-1. Summary of ANCOVAs to predict litter mixture effects from litter diversity (richness or functional dispersion, FDis) of litter mixtures, site, and their interaction at six sites located along an arid-to-temperate-humid gradient in Chile after 6 and 12 months of decomposition. FDis all includes all measured traits, while FDis+ and FDis– include only those traits considered to cause positive and negative diversity effects, respectively. N = 68 litter mixtures; one model was calculated for each decomposition period (6 or 12 months); SS = sum of squares, DF = degrees of freedom, F = F-statistics, p = p-value. Bold values represent $p<0.05$.

	6 Months				12 Months			
Factor	SS	DF	F	p	SS	DF	F	p
Richness	0.04	1	1.19	0.28	<0.01	1	0.09	0.77
Site	1.08	5	6.66	**<0.001**	1.17	5	7.51	**<0.001**
Richness*Site	0.07	5	0.45	0.81	0.26	5	1.67	0.14
FDis all	0.01	1	0.39	0.53	<0.01	1	<0.01	0.94
Site	1.08	5	7.2	**<0.001**	1.12	5	7.52	**<0.001**
FDis all*Site	0.53	5	3.49	**<0.01**	0.52	5	3.46	**<0.01**
FDis+	0.02	1	0.74	0.39	0.1	1	3.27	0.07
Site	1.11	5	6.96	**<0.001**	1.27	5	8.42	**<0.001**
FDis+*Site	0.19	5	1.18	0.32	0.36	5	2.4	**0.04**
FDis–	0.05	1	1.54	0.22	0.02	1	0.72	0.4
Site	1.08	5	7.04	**<0.001**	1.17	5	7.54	**<0.001**
FDis–*Site	0.4	5	2.65	**0.02**	0.31	5	2	0.08

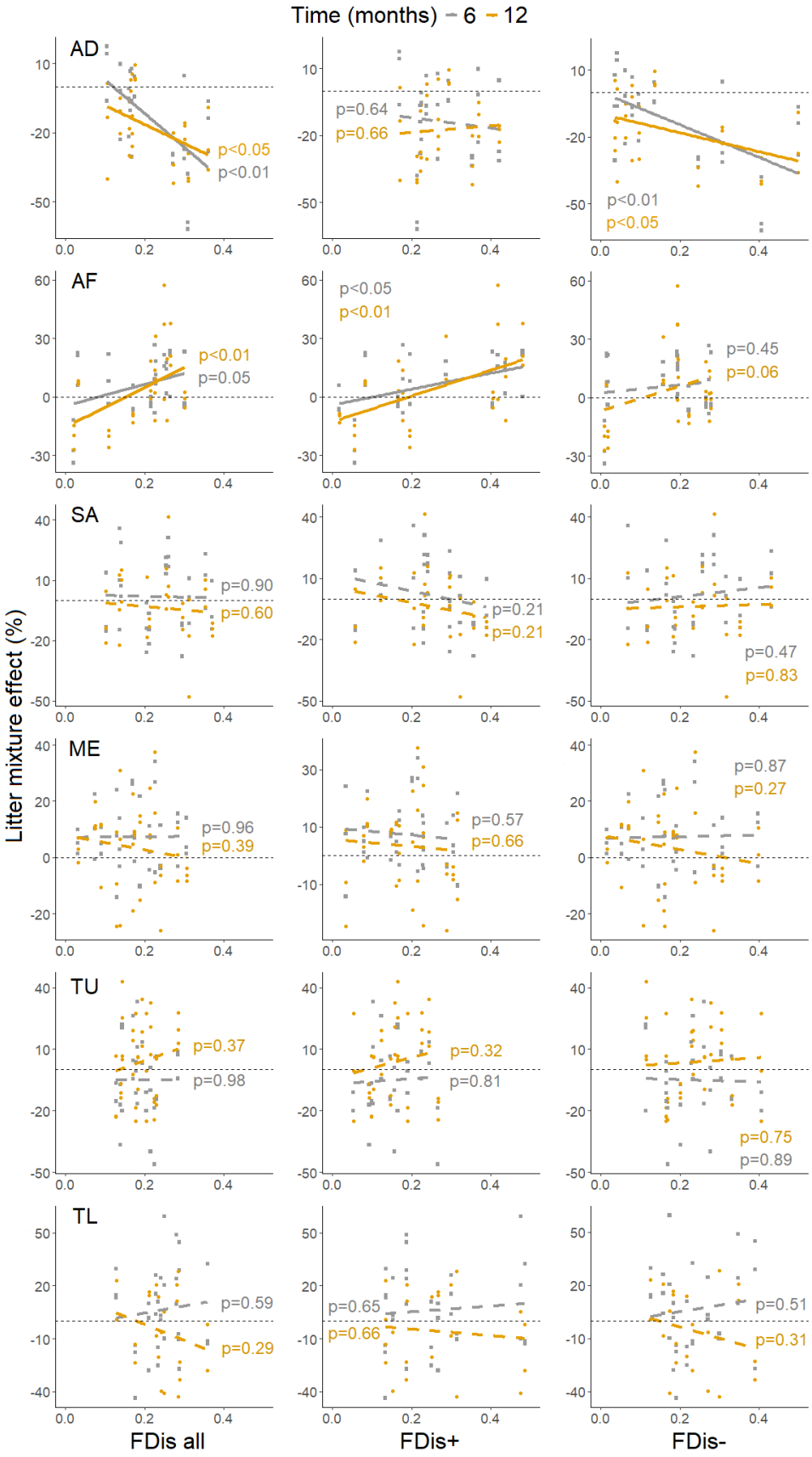
Time (months) 6 12
AD
p<0.05
p<0.01
p=0.64
p=0.66
p<0.01
p<0.05
AF
p<0.01
p=0.05
p<0.05
p<0.01
p=0.45
p=0.06
SA
p=0.90
p=0.60
p=0.21
p=0.21
p=0.47
p=0.83
ME
p=0.96
p=0.39
p=0.57
p=0.66
p=0.87
p=0.27
TU
p=0.37
p=0.98
p=0.32
p=0.81
p=0.75
p=0.89
TL
p=0.59
p=0.29
p=0.65
p=0.66
p=0.51
p=0.31
Litter mixture effect (%)
FDis all
FDis+
FDis-

Figure 5-4. Pearson correlations between functional dispersion (FDis) calculated with different sets of litter traits (columns) and litter mixture effects (%) after 6 and 12 months of decomposition (colours) using different litter mixtures that decomposed along a climatic gradient in Chile (lines, AD = Arid-Dry, AF = Arid-Fog, SA = Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland). FDis all includes all measured traits, while FDis+ and FDis– include only those traits considered to cause positive and negative diversity effects, respectively. Solid lines represent significant correlations ($p<0.05$) and dashed lines represent non-significant correlations.

5.3 Discussion

Our findings revealed a small number of significant litter mixture effects on decomposition (both positive and negative) along a pronounced precipitation gradient, with stronger effects in the most arid than in the humid range of the gradient, opposite to our first hypothesis. These mixture effects were independent of the number of species represented in the litter mixtures at all sites, but were stronger with increasing functional dispersion (FDis) at the two most arid sites, thus partially confirming our second hypothesis. Moreover, according to our third hypothesis, at these sites the FDis based on litter traits related to nutrient content correlated with positive mixture effects on decomposition, whereas traits related to inhibiting secondary compounds correlated with negative mixture effects. Collectively, our study indicates that mixture effects on decomposition are comparatively rare across a wide climatic gradient, but when they occur, they are predictable from litter-trait diversity.

Because litter mass loss could be more advanced at a particular time at the humid temperate sites than in the arid desert sites (Canessa et al., 2021), we evaluated different decomposition stages to compare the effects at different sites. However, even though litter mass loss differed among climate zones, the decomposition at the temperate sites was not more advanced than at the arid sites (Fig. S5-2). Thus, we consider that, at each decomposition stage, a comparison of litter mixture effects among sites is valid, even if mixture effects could decrease with time (Wu et al., 2013; Butenshoen et al., 2014; but see Santoja et al., 2019 for an opposite result). This counter-intuitive result occurred because the litter produced by the plants from arid sites is, on average, of higher quality than the litter from plants in the other sites and thus counteracts the climatic effects.

Our experiment used a large number of litter mixtures comprising a large variety of species combinations from widely different environmental conditions, but still only a relatively small number of mixtures showed significant non-additive effects. The range of the means of these litter mixture effects was similar to that reported in a recent meta-analysis (*ca*. 3-5%; Liu et al., 2020), with the exception of the most arid site, where, after the first year, the decomposition of mixtures was on average 16% lower than predicted. Overall, more species combinations showed significant and larger litter mixture effects in the most arid climates compared to mediterranean and temperate humid climates. This indicates that litter mixture effects vary across climate zones, which has rarely been tested along wide climatic gradients (but see Zhou et al., 2020). While most case studies in temperate and tropical areas showed small positive effects of litter mixtures on decomposition (Gartner & Cardon, 2014; Liu et al., 2020), we observed mainly additive (i.e. null) effects in our semi-arid, mediterranean and temperate sites. Additionally, our results suggest that arid

environments can exhibit both positive and negative mixture effects, similar to studies in other extreme ecosystems such as alpine shrublands and boreal grasslands (Duan et al., 2013; Liu et al., 2020). In our study, the opposing effects between both arid sites (i.e. negative in the AD and more positive in the AF) could be related to the diversity in different groups of functional traits involved in the mixtures.

Species richness had no effect on the decomposition of litter mixtures at any of the sites, but functional diversity, expressed as the dispersion of litter traits (FDis), had very interesting effects, even if only at the two most arid sites. Here, higher FDis values amplified mixture effects, leading to more negative mixture effects at the arid dry (AD) site, and in particular if FDis was defined by decomposition inhibitory traits. At the arid fog (AF) site the effect was positive, and in particular if defined by nutrient traits. Interestingly, the AF site, where FDis+ had a positive effect, also showed the largest range in FDis+ values and the highest absolute FDis+, while the AD site, where FDis– had a negative effect, also showed the largest range in FDis– values and the highest absolute FDis−. That is, there may be a relationship between the variability of nutrient or inhibitory traits involved and the strength of the effect of this variability on litter decomposition. At the AF, a large variance in nutrient traits among species (particularly in C/N and Mg) permitted to have mixtures with very similar (e.g. *Nolana divaricata + N. paradoxa*) and very different (e.g. *Echinopsis deserticola + N. divaricata*) quality. Here, for instance, a nutrient transfer from *N. divaricata* (of high quality litter) to *E. deserticola* (low quality litter) may have benefited the overall litter decomposition of the mixture (Hättenschwiler et al., 2005). In contrast, at the AF site a variance in recalcitrance traits (mainly total phenolics) permitted mixtures with similar (e.g. *Cristaria inegerrima + N. crassulifolia*) and very different (*C. integerrima + Frankenia chilensis*) quality. Here, for example, the presence of inhibitory compounds in *F. chilensis* (rich in phenolics and lignin) could have reduced the decomposition of *C. integerrima* (with high litter quality) and thus, of the whole mixture (Schimel et al., 1998). Therefore, a larger diversity in one of these sets of litter traits could explain that one of the two possible mechanisms involved (nutrient transference or decomposition inhibition) dominated, leading to contrasting results between these two arid sites. Plants from arid and semi-arid areas are known to have high phenolics content as chemical defences to herbivory and environmental stress (Bär Lamas et al., 2016; Hättenschwiler & Vitousek 2000). However, in arid areas with some fog or dew input, succulent species with high litter quality are also common (Griffiths and Males 2017), as is the case of our study sites (e.g. *Nolana* species). This wide range in key litter traits likely provided enough variation to observe diversity effects on mixtures decomposition. In contrast, in sites such as the ME, where most of the species are sclerophyllous and rich in secondary compounds, FDis values were lower, potentially limiting strong litter mixture effects. To this end, to understand the role of these two sets of traits, we recommend to use a functionally variable set of standardised litter mixtures across different climate zones.

An alternative explanation for the observed differences between AD and AF may rely on the different (micro)climatic conditions of these sites. At the AF, the fog input, which increases superficial moisture (Lehnert et al., 2018; Jung et al., 2020), may facilitate nutrient movements within the litter mixtures, favouring more positive mixture effects with higher trait dispersion. In the higher-rainfall sites, a quick loss of nutrients due to increased leaching rates (Powers et al., 2009; Schreeg et al., 2013) could have limited nutrient transfer among litter types, which may

explain the lack of mixture effects. Kou et al. (2020) found a significant (although weak) negative correlation between litter mixture effects and precipitation in forests, with smaller mixture effects at higher rainfall sites. Thus, rainfall might have an effect, but it is unlikely to be the dominant factor in determining the strength of mixture effects. In addition, the rather low nutrient limitation of these sites, compared to the arid end of our gradient (Bernhard et al., 2018), probably also influenced the low importance of nutrient trait diversity for mixtures decomposition. Altogether, these findings suggest that the mechanistic explanation of litter mixture effects relies on species-specific litter compounds and nutrient contents, which should be studied in relation to functional dispersion and climatic conditions.

The inclusion of all these traits (i.e. nutrient and recalcitrance traits) in one single index (FDis all) was able to predict both positive and negative mixture effects and thus could provide an approach to evaluate diversity effects on litter decomposition. However, this approach does not reveal the nature of the traits that drive mixture effects and positive and negative effects might in some cases cancel out. We therefore recommend the use of different sets of traits with particular expected functions. To better understand the mechanisms of litter mixture effects, a mechanism-based selection of traits should be used for functional diversity measures in future studies.

5.5 Conclusions

Our study of litter diversity effects on decomposition, based on litter mixtures of species across a large climatic gradient, showed that non-significant litter mixture effects dominated, although both positive and negative mixture effects also occurred, mainly in the arid climates. At these sites, functional diversity and not species richness determined these litter mixture effects. We highlight that the dominance of specific processes, e.g. nutrient transfer among litters or decomposition inhibition within mixtures, are dependent on the diversity of litter functional traits (i.e. litter quality) and climate (e.g. moisture, rainfall). The evaluation of functional diversity indices that include litter traits related to these processes separately (e.g. C/N, K vs. lignin, phenolics) provides an approach to evaluate the mechanisms behind litter mixture effects in different climates. Still, other controlling factors for non-additive mixture effects need further investigation, as much of the variation observed remains unexplained. Overall, with the very large range of climatic conditions, species and mixture types covered here, our results suggest that litter diversity effects are rather the exception than the rule and may have relatively little impact on decomposition processes across large spatial scales. Additional efforts using functionally variable litter mixtures are needed to further test this hypothesis and to reveal the necessary conditions and driving mechanisms of diversity effects on the decomposition process.

5.6 Acknowledgements

RC and LB express their deep gratitude to all students, technical assistants, colleagues and park rangers who helped during field and laboratory work. Peter Chifflard and Martin Reis are

acknowledged for their involvement in the initial project proposal. We are grateful to the Chilean National Forest Corporation (CONAF) and Comunidad Agrícola Quebrada de Talca who permitted the access to the study sites. This study was funded by the German Research Foundation (DFG) in the Priority Program SPP-1803 “EarthShape: Earth Surface Shaping by Biota” (grant BA 3843/6-1 to MYB; TI 338/14-1&2 to KT). All authors declare that there is no conflict of interest.

5.7 Authors’ contributions

MYB conceived the ideas and designed methodology, in coordination with KT, AS and RR; RC and LB developed the experiment and collected the data; RC and SH provided laboratory results, RC and MBB analysed the data, RC led the writing of the manuscript, supervised by MYB. All authors contributed critically to the drafts and gave final approval for publication.

5.8 Data availability

Should the manuscript be accepted, all data supporting the results will be archived in the Dryad public repository. Other data sources are correspondingly cited in the reference list.

Chapter 6

Synthesis and outlook

To understand the functioning of ecosystems, researchers need to consider the linkages between aboveground and belowground processes (Hooper et al., 2000). One important process by which the aboveground biota influences the belowground ecosystem is litter input to soils and its decomposition. The results of this process create feedbacks that in turn affect the aboveground biota (Berg & McClaugherty, 2008). Thus, understanding the drivers of litter decomposition adds to the knowledge of overall ecosystem function (e.g. nutrient cycling, soil formation) and the benefits that people derive from them. Particularly in the context of global change, the interactions among drivers require a better understanding across ecosystems. In this doctoral thesis, I aimed to investigate the interactive effects of plant traits (i.e. litter quality) and climate on litter decomposition along the Chilean coastal range.

6.1 The importance of litter quality for decomposition

Using litter transplant experiments, in Chapters 3 and 4 I revealed how both the intrinsic nature of litter (i.e. litter quality) and the environmental conditions (particularly soil moisture) contribute significantly to litter decay. Although in the last decades several decomposition studies have undoubtedly highlighted these two factors as the main drivers of decomposition, the present work disentangles their relative contribution over time as well as their interactions. My analyses indicated that litter quality is more relevant than litter origin in determining decomposition rates (Chapter 3). Moreover, contrary to previous findings (e.g. García-Palacios et al., 2013), I demonstrated that litter traits can drive litter decomposition in (semi-) arid ecosystems and thus, interact with climatic factors (Chapter 4). Additionally, I showed that litter quality effects, although present throughout the decomposition process, are of particular in importance during the first year of litter decay, when the highest decomposition rates occur (Coûteaux et al., 1995). Also importantly, my study emphasizes the critical role of representative ranges in litter trait variability (i.e. inter- and intraspecific variation) to accurately predict litter quality effects on decomposition.

These interactions between litter quality and climate, and the variation in the importance of litter quality are of high relevance for decomposition models that aim to better understand and predict the consequences of global changes for soil dynamics. For example, in the context of climate change, it is expected that the increase in atmospheric CO_2 leads to a decrease in litter quality (i.e. an increase in C:N ratios; Cotrufo et al., 1994). This change could decrease litter consumption by detritivores, slow the decomposition process, increase carbon storage and the need of external inorganic nitrogen to allow decomposition (Cotrufo et al., 1998; Wetzel & Tuchman, 2005), ultimately altering carbon and nutrient cycles.

Furthermore, not only atmospheric CO_2 can alter the composition of plant litter. Indirectly, alterations of the richness and composition of plant communities that contribute litter to soils can also modify decomposition rates. Land-use change (Echeverría et al., 2006; Turner et al., 2007) and alien plant invasion (Seebens et al., 2015) have incredibly expanded in the last decades, modifying biodiversity (Chapin III et al., 2000). In Chapter 5, I showed that litter quality effects can also depend on the functional diversity of litter in some ecosystems.

Previous studies had found varying effects of litter diversity on decomposition (Gessner et al., 2010), although a positive effect of diversity is more commonly observed (i.e. higher decomposition with increasing litter diversity; Kou et al., 2020; Liu et al; 2020). However, Hättenschiler et al. (2015) pointed out the need for a better understanding of the mechanisms that explain litter mixture effects. In my study, litter mixture effects were rare, but when they occurred, they were driven by the functional dispersion (FDis) values based on particular litter traits: FDis defined by nutrient transfer and recalcitrance traits lead to increased and decreased litter mass loss, respectively. Thus, this study highlights how litter traits can reflect the underlying mechanisms that drive mixture effects in decomposition. The divergent litter quality observed in the most arid ecosystems of the Chilean climatic gradient was crucial to reveal these findings, and thus, highlight the need of using diverse site-specific litter mixtures to understand diversity effects on decomposition. More detailed studies of how present and real changes in diversity affect decomposition will be crucial to improve local conservation policies and to understand other potential changes in biodiversity associated with global change, such as changes in species distribution and functional composition.

Overall, the important control of litter quality on decomposition, highlighted in all three studies within this thesis, is an indication of how shifts in plant community composition and plant traits spectrum can impact soil carbon processes. Other aspects of litterfall that were not included here can add to the understanding of litter quality controls of decomposition. For instance, how the spatial and temporal variation in litterfall determines decomposition rates, how these patterns vary across ecosystems or with primary productivity, and how global changes will affect these drivers themselves and, in turn, affect decomposition, carbon and nutrient dynamics in soils.

6.2 The importance of climate for litter decomposition.

6.2.1 The study of climatic gradients and representative ranges

Because of the strong climate dependency of decomposition, this factor has also received important attention in the context of climate change. I showed that soil microclimatic parameters such as soil moisture and temperature can accurately predict litter decay, especially in advanced decomposition stages (Chapter 4). This study is one of the few showing that litter decomposition increases with soil moisture across different ecosystems (e.g. Petraglia et al., 2019). Because decomposition is a process that occurs near the ground surface, the use of microclimatic parameters is of particular relevance when studying decomposition across ecosystems differing in vegetation and soil characteristics (Lembrechts et al., 2020) and can potentially improve global decomposition models.

Climate change predictions for the studied Chilean coastal range show, on the one hand, a decrease in rainfall (and therefore in soil moisture) and an increase of extreme climatic events (IPCC 2013). This will probably decrease decomposition rates, enhance soil carbon storage, but also limit nutrient cycling. On the other hand, an increase in the mean annual temperature (IPCC 2013) could have opposite effects and enhance litter decomposition, although decomposition between 10 and 20 °C is not strongly driven by temperature (Bradford et al., 2016). My results also suggest that soil temperature is less significant for litter decomposition than soil moisture for this gradient. Although climate change effects could be directly tested by the use of other experimental setups (e.g. rain-out shelters or controlled laboratory

experiments), the use of a large climatic gradient, together with the translocation experiment, gave me very important insights on the effects of climate on litter decomposition.

While litter decomposition has been studied for decades, a strong bias towards temperate and boreal forests exists (Berg and McClaugherty, 2003), limiting our understanding of climate effects on a global scale. In fact, only in the last decade more studies in underrepresented ecosystems and across ecosystems were developed (Djukic et al., 2018). This study is an example of how the use of representative ranges of climate is relevant to understand climatic influences on litter decay, as the drivers of litter decomposition varied between the arid and the wet end of the gradient (Chapter 4). To observe such interaction would not have been possible if the temperate sites would not have been included.

The use of large climatic gradients with contrasting ecosystems is a practical tool for studying the correlation of a certain response factor to climatic variables. However, these should be carefully evaluated, as they might present confounding factors that make it difficult to unravel causal relationships. One of the limitations of this thesis is the lack of control and data of the decomposer communities, whose abundance probably correlates to soil moisture (Bernhard et al., 2018). The identification of the different species or groups present in decomposer communities, as well as their activity (e.g. respiration rates), could have given important insights for a better understanding of litter quality-decomposer interactions in Chapter 3, and could potentially have improved the decomposition models in Chapter 4.

6.2.3 Litter decomposition in arid areas

With this work, I contributed with essential data to the knowledge of so far highly underrepresented arid and semi-arid areas, where an additional variable (i.e. UV radiation) can influence decomposition (Austin & Vivanco, 2006). Although the analyses in Chapter 4 determined that photodegradation did not strongly determine mass loss patterns in the arid climate zones, this does not mean that it did not occur. The conclusions about this particular process are in fact limited, as I did not directly measure nor control radiation. Furthermore, the data of these climate zones should be carefully evaluated, as the two most arid sites belong to a very particular desert, the coastal Atacama Desert, which receives (to a greater or lesser degree) an input of coastal fog that causes a superficial moisture and sustains life in this ecosystem (Lehnert et al., 2018). This fog input probably increased the proportion of microbial decomposition compared to other arid areas.

Additionally, this climate exerts an important selection on litter quality, favoring succulent plant forms with water-storing tissues that tolerate high temperatures and strong saline conditions (Griffiths & Males, 2017). In contrast to sclerophylly, these adaptations produce nutrient-rich leaves, which on average decompose faster than leaves of other study sites (Chapter 2). Thus, even though decomposition in arid and dry ecosystems is expected to be slow due to a moisture limitation (Djukic et al., 2018), in this coastal desert the high litter quality produced by some succulent species compensates for the climatic limitations and thus, similar decomposition rates as in wetter climates (e.g. mediterranean or temperate sites) occurred.

Taken as a whole, the results from the drier end of the Chilean coastal range, in particular those from the desert sites, question the premise that in arid ecosystems decomposition rates and nutrient cycling are slow. This study suggests that litter in these ecosystems is diverse, but on

average of high quality. This fact, together with the important fog input and the high radiation, can potentially increase nutrient cycling and increase the available nutrient resources for below and aboveground communities. A deeper understanding of transport pathways and the fate of elements during litter decomposition could help to better interpret nutrient cycling in this arid ecosystem, how this process could influence biogenic weathering.

6.3 Final conclusions

This thesis is an integrated assessment of the main litter decomposition drivers across a large climatic gradient and over time. I showed that local litter is not favored by local decomposer communities but decomposes as expected based on litter quality (slow for low-quality and quick for high-quality litter). Additionally, any type of litter decomposes faster towards the wettest end of the gradient. The inclusion of a large range of climates and litter traits permitted to accurately explain litter mass loss based on soil moisture and a combination of leaf functional traits, as well as the interaction of these factors. Importantly, I disentangled the relative importance of climate vs. litter quality effects over time (increasing and decreasing their importance after the first year of decomposition, respectively). Litter quality effects on decomposition were also related to functional dispersion in dry ecosystems, as litter mixtures at this sites decomposed either faster or slower than predicted by single-species decomposition.

Overall, these findings contribute to understanding how the interactive effects of vegetation (via litter quality and diversity) and climate determine litter decomposition. Current shifts in climate will likely cause changes in plant and decomposer communities and, as a consequence, affect all decomposition drivers. This thesis suggests that potential shifts in litter quality and diversity may strongly alter decomposition rates. While the direct effects of climate on decomposition are now well understood and global efforts have led to measure litter decomposition across several ecosystems, a deeper understanding of its indirect effects (via vegetation and decomposers) is still needed to correctly predict litter decomposition. Furthermore, this knowledge is key to understanding the feedbacks from litter decomposition to plant productivity, soil formation, atmospheric CO_2 concentrations and climate.

Acknowledgements

This doctorate thesis is the product of a large personal and academic process, along which I received the support of many persons, to who I am deeply grateful.

I thank my parents and siblings for they encouragement, buoyancy and advice in every stage. You took part of this story not only by cheering me up, but also by participating in my fieldwork. You are simply the best! But certainly, your support comes from even earlier, and thus, I believe my thanks to you will never be enough. Thanks for making me who I am now.

To my supervisor, Maaike Bader, who trusted me from the beginning and after a first push, gave me the confidence to go my own way, while keeping an eye on me to correct me when necessary. Your enthusiastic and curious spirit, dedication and kindness are my example to follow. Thank you for your knowledge and for guiding me to develop and strengthen my skills.

Thanks to an incredible woman, friend and scientist, Liesbeth van den Brink. I really don't know what I would've done without you this last five years. You were the best partner for this project and even a better friend for life. You stood beside at each phase, and I'm proud to say that we grew up in this journey together. I'm looking forward to our next challenges!

To my boyfriend and partner, Justus, who accompanied me in the last years in every success and fail, cheered me up and always believed in me. Thanks for your patience, kindness, craziness and love. Thanks to you and your family for opening your heart to me.

To Alfredo Saldaña and Rodrigo Ríos, my "unofficial" supervisors. Thank you for your help in the logistics, fieldwork campaigns, tips, statistical advice, scientific discussions and even more important, for your empathy and affection.

Thanks to my collaborators in Tübingen, Munich and Montpellier, and to the EarthShape group for your cooperation, ideas and support. In particular, I am thankful to Katja Tielbörger, Yvonne Oelman, Harald Neidhart and Stephan Hättenschwiler for your knowledge and patience. Your advice was key, especially in the last stages of this process.

Thanks to the DFG for the funding of this research and to MARA (University of Marburg) for their "Doctoral Completion Scholarship". Thanks to CONAF and Comunidad Agrícola Quebrada de Talca for providing access to the study sites.

I am deeply grateful to my friends and colleagues Rocío Fernández and Daniela Aros. You were a fundamental part of this work. Thanks for your support, endurance and enthusiasm. To all my field and laboratory technicians: Dani Mardones, Titi Silva, Nico Burger, Nico Valenzuela, Rodrigo Aravena, Naty Ramos, Sambo Fuentes, Adri Lozada, Negro Vidal, Isi Sepúlveda, Maida Bustos, Diana Osses and many others. Also, thanks to the (by then) students Rebecca Pieters, Louise Wraase, Lea Dzierzawa and Lorena Mattes, who joined the field campaigns and filled them with joy. Thanks to all the park rangers who eagerly participated in this research, for their knowledge and for their priceless daily work in nature conservation. Thanks to Christiane Enderle for her assistance with the maps of Chile.

To Eyvar and a group of strong woman, Nada, Lirey, Élodie, Adriana, Glenda and Mónica. Could I have wished a better group to work with? Thank you for your ideas, discussions, backing, smiles, motivation and diversity. Each one of you has enriched my life.

To my WG and Marburg friends, who made life and this process even more beautiful than I expected. Thanks for being so open minded and generous, and for keeping me dreaming of a better world.

References

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, 79, 439-449. doi: 10.2307/3546886

Alberti, G., Nock, C., Fornasier, F., Scherer-Lorenzen, M., De Nobili, M., Peressotti, A., ... & Bauhus, J. (2017). Tree functional diversity influences belowground ecosystem functioning. Applied Soil Ecology, 120, 160-168. https://doi.org/10.1016/j.apsoil.2017.07.038

Austin, A. T. 2011. Has water limited our imagination for aridland biogeochemistry? Trends in Ecology and Evolution. 26: 229–235. https://doi.org/10.1016/j.tree.2011.02.003

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

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

Austin, A. T., Vivanco, L., González-Arzac, A., & Pérez, L. I. (2014). There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems. New Phytologist, 204(2), 307-314. https://doi.org/10.1111/nph.12959

Ayres, E., Dromph, K. M., & 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), 183-186. https://doi.org/10.1016/j.soilbio.2005.04.018

Ayres, E., Steltzer, H., Berg, S., & Wall, D. H. (2009a). 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), 901-912. https://doi.org/10.1111/j.1365-2745.2009.01539.x

Ayres, E., Steltzer, H., Simmons, B. L., Simpson, R. T., Steinweg, J. M., Wallenstein, M. D., ... & Wall, D. H. (2009b). Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry, 41(3), 606-610. https://doi.org/10.1016/j.soilbio.2008.12.022

Azen, R., & Budescu, D. V. (2006). Comparing Predictors in Multivariate Regression Models: An Extension of Dominance Analysis. Journal of Educational and Behavioral Statistics, 31(2), 157-180. https://doi.org/10.3102/10769986031002157

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters, 9, 1146-1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Bär Lamas, M. I., Carrera, A. L., & Bertiller, M. B. (2016). Meaningful traits for grouping plant species across arid ecosystems. Journal of Plant Research, 129(3), 449-461. https://doi.org/10.1007/s10265-016-0803-6

Barantal, S., Schimann, H., Fromin, N., & Hättenschwiler, S. (2014). C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter

diversity effects on decomposition. Proceedings of the Royal Society B: Biological Sciences, 281(1796), 20141682. https://doi.org/10.1098/rspb.2014.1682

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear Mixed-Effects Models Using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Becking, B. 1934. Geobiologie of inleiding tot de milieukunde (DE Canfield, Ed.). - W.P. van Stockum & Zoon.

Berg, B. 2014. Decomposition patterns for foliar litter - A theory for influencing factors. Soil Biology and Biochemistry. 78: 222–232. https://doi.org/10.1016/j.soilbio.2014.08.005

Berg, B., Berg, M. P., Bottner, P., Box, E., Breymeyer, A., De Anta, R. C., ... & Madeira, M. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry, 20(3), 127-159. https://doi.org/10.1007/BF00000785

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

Bernhard, N., Moskwa, L. M., Schmidt, K., Oeser, R. A., Aburto, F., Bader, M. Y., ... & Brucker, E. (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. Catena, 170, 335-355. https://doi.org/10.1016/j.catena.2018.06.018

Bonanomi, G., Capodilupo, M., Incerti, G., & Mazzoleni, S. (2014). Nitrogen transfer in litter mixture enhances decomposition rate, temperature sensitivity, and C quality changes. Plant and Soil, 381(1-2), 307-321. https://doi.org/10.1007/s11104-014-2119-4

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., & Wood, S. A. (2016). Understanding the dominant controls on litter decomposition. Journal of Ecology, 104(1), 229-238. https://doi.org/10.1111/1365-2745.12507

Bradford, M. A., Veen, G. C., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., ... & Manrubia-Freixa, M. (2017). A test of the hierarchical model of litter decomposition. Nature Ecology & Evolution, 1(12), 1836-1845. https://doi.org/10.1038/s41559-017-0367-4

Briones, M. J. I., & Ineson, P. (1996). Decomposition of eucalyptus leaves in litter mixtures. Soil Biology and Biochemistry, 28(10-11), 1381-1388. https://doi.org/10.1016/S0038-0717(96)00158-7

Bustos, C. E., & Soares, F. C. (2020) Dominance analysis for general, generalized and mixed linear models. R package version 1.3.0. https://CRAN.R-project.org/package=dominanceanalysis

Butenschoen, O., Krashevska, V., Maraun, M., Marian, F., Sandmann, D., & Scheu, S. (2014). Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay. Soil Biology and Biochemistry, 77, 121-128. https://doi.org/10.1016/j.soilbio.2014.06.019

Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., ... & Marland, G. (2007). Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences, 104(47), 18866-18870. https://doi.org/10.1073/pnas.0702737104

Canessa, R., van den Brink, L., Saldaña, A., Rios, R. S., Hättenschwiller, S., Mueller, C. W., ... & Bader, M. Y. (2021). Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. Journal of Ecology, 109:447–458. https://doi.org/10.1111/1365-2745.13516

Canessa, R., van den Brink, L., Saldaña, A., Rios, R. S., Hättenschwiller, S., Mueller, C. W., ... & Bader, M. Y. (2020). Data from: Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. Dryad Digital Repository. https://doi.org/10.5061/dryad.ttdz08kwb

Carrera, A. L. & Bertiller, M. B. 2013. Combined effects of leaf litter and soil microsite on decomposition process in arid rangelands. Journal of Environmntal Management. 114: 505–511. https://doi.org/10.1016/j.jenvman.2012.10.059

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... & Mack, M. C. (2000). Consequences of changing biodiversity. Nature, 405(6783), 234-242. https://doi.org/10.1038/35012241

Clay, N. A., Donoso, D. A., & Kaspari, M. (2015). Urine as an important source of sodium increases decomposition in an inland but not coastal tropical forest. Oecologia, 177(2), 571-579. https://doi.org/10.1007/s00442-014-3183-4

Cornelissen, J. H. C., & Thompson, K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. New Phytologist, 135(1), 109-114. https://doi.org/10.1046/j.1469-8137.1997.00628.x

Cornelissen, J. H., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S., Alatalo, J., ... & MOL Team. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters, 10(7), 619-627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., ... & Quested, H. M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters, 11(10), 1065-1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Cotrufo, M. F., Briones, M. J. I., & Ineson, P. (1998). Elevated CO2 affects field decomposition rate and palatability of tree leaf litter: importance of changes in substrate quality. Soil Biology and Biochemistry, 30(12), 1565-1571. https://doi.org/10.1016/S0038-0717(98)00032-7

Cotrufo, M. F., Ineson, P., & Rowland, A. P. (1994). Decomposition of tree leaf litters grown under elevated CO 2: effect of litter quality. Plant and Soil, 163(1), 121-130. https://doi.org/10.1007/BF00033948

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

Currie, W. S., Harmon, M. E., Burke, I. C., Hart, S. C., Parton, W. J., & Silver, W. (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(6), 1744-1761. https://doi.org/10.1111/j.1365-2486.2009.02086.x

Cunningham, S. A., Summerhayes, B., & Westoby, M. (1999). Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological

Monographs, 69(4), 569-588. https://doi.org/10.1890/0012-9615(1999)069[0569:EDILSA]2.0.CO;2

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

De Wit, R. & Bouvier, T. 2006. "Everything is everywhere, but, the environment selects"; what did Baas Becking and Beijerinck really say? Environmental Microbiology. 8: 755–758. https://doi.org/10.1111/j.1462-2920.2006.01017.x

Dias, A. T. C., Cornelissen, J. H., & Berg, M. P. (2017). Litter for life: assessing the multifunctional legacy of plant traits. Journal of Ecology, 105(5), 1163-1168. https://doi.org/10.1111/1365-2745.12763

Duan, J., Wang, S., Zhang, Z., Xu, G., Luo, C., Chang, X., ... & Du, M. (2013). Non-additive effect of species diversity and temperature sensitivity of mixed litter decomposition in the alpine meadow on Tibetan Plateau. Soil Biology and Biochemistry, 57, 841-847. https://doi.org/10.1016/j.soilbio.2012.08.009

Dyer, M. L., Meentemeyer, V., & Berg, B. (1990). Apparent controls of mass loss rate of leaf litter on a regional scale: litter quality vs. climate. Scandinavian Journal of Forest Research, 5(1-4), 311-323. https://doi.org/10.1080/02827589009382615

Echeverría, C., Coomes, D., Salas, J., Rey-Benayas, J. M., Lara, A., & Newton, A. (2006). Rapid deforestation and fragmentation of Chilean temperate forests. Biological Conservation, 130(4), 481-494. https://doi.org/10.1016/j.biocon.2006.01.017

Ehlers, T. A., von Blanckenburg, F., & Übernickel, K. (2019). EarthShape weather data collection. Retrieved from: https://esdynamics.geo.uni-tuebingen.de/earthshape/index.php?id=68. Last accessed 2 December 2019.

Evans, S. E., Wallenstein, M. D., & Burke, I. C. (2014). Is bacterial moisture niche a good predictor of shifts in community composition under long-term drought?. Ecology, 95(1), 110-122. https://doi.org/10.1890/13-0500.1

Freschet, G. T., Aerts, R., & Cornelissen, J. H. (2012a). A plant economics spectrum of litter decomposability. Functional Ecology, 26(1), 56-65. https://doi.org/10.1111/j.1365-2435.2011.01913.x

Freschet, G. T., Aerts, R., & Cornelissen, J. H. (2012). Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. Journal of Ecology, 100(3), 619-630. https://doi.org/10.1111/j.1365-2745.2011.01943.x

Fujii, S., Cornelissen, J. H., Berg, M. P., & Mori, A. S. (2018). Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. Functional Ecology, 32(3), 840-852. https://doi.org/10.1111/1365-2435.13027

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

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

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

Garreaud, R. D., Boisier, J. P., Rondanelli, R., Montecinos, A., Sepúlveda, H. H., & Veloso-Aguila, D. (2020). The Central Chile Mega Drought (2010–2018): A climate dynamics perspective. International Journal of Climatology, 40(1), 421-439. https://doi.org/10.1002/joc.6219

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

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. & Hattenschwiler, S. (2010). Diversity meets decomposition. Trends in Ecology and Evolution, 25, 372-380. https://doi.org/10.1016/j.tree.2010.01.010

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., & Parton, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology, 6(7), 751-765. https://doi.org/10.1046/j.1365-2486.2000.00349.x

Gießelmann, U. C., Martins, K. G., Brändle, M., Schädler, M., Marques, R., & Brandl, R. (2011). Lack of home-field advantage in the decomposition of leaf litter in the Atlantic Rainforest of Brazil. Applied Soil Ecology, 49, 5-10. https://doi.org/10.1016/j.apsoil.2011.07.010

González-Bonorino, F. 1971. Metamorphism of the crystalline basement of central Chile. Journal of Petrology. 12: 149–175. https://doi.org/10.1093/petrology/12.1.149

Gottschall, F., Davids, S., Newiger-Dous, T. E., Auge, H., Cesarz, S., & Eisenhauer, N. (2019). Tree species identity determines wood decomposition via microclimatic effects. Ecology and Evolution, 9(21), 12113-12127. https://doi.org/10.1002/ece3.5665

Griffiths, H., & Males, J. (2017). Succulent plants. Current Biology, 27(17), R890-R896. https://doi.org/10.1016/j.cub.2017.03.021

Gripp, A. R., de Assis Esteves, F., Carneiro, L. S., Guariento, R. D., Figueiredo-Barros, M. P., Coq, S., ... & Caliman, A. (2018). Weak to no effects of litter biomass and mixing on litter decomposition in a seasonally dry tropical forest. Pedobiologia, 68, 20-23. https://doi.org/10.1016/j.pedobi.2018.02.003

Haines-Young, R. (2009). Land use and biodiversity relationships. Land Use Policy, 26, S178-S186. https://doi.org/10.1016/j.landusepol.2009.08.009

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., ... & McKie, B. G. (2014). Consequences of biodiversity loss for litter decomposition across biomes. Nature, 509(7499), 218-221. https://doi.org/10.1038/nature13247

Harmon, M. E., Silver, W. L., Fasth, B., Chen, H. U. A., Burke, I. C., Parton, W. J., ... & Lidet. (2009). Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Global Change Biology, 15(5), 1320-1338. https://doi.org/10.1111/j.1365-2486.2008.01837.x

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M. M., Roy, J., & Bonal, D. (2008). High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytologist, 179(1), 165-175. https://doi.org/10.1111/j.1469-8137.2008.02438.x

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics, 36, 191-218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hättenschwiler, S., & Vitousek, P. M. (2000). The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends in Ecology and Evolution, 15(6), 238-243. https://doi.org/10.1016/S0169-5347(00)01861-9

He, Z., Yu, Z., Huang, Z., Davis, M., & Yang, Y. (2016). Litter decomposition, residue chemistry and microbial community structure under two subtropical forest plantations: A reciprocal litter transplant study. Applied Soil Ecology, 101, 84-92. https://doi.org/10.1016/j.apsoil.2016.01.015

Hobbie, S. E., Shevtsova, A. and Chapin, F. S. I. 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. Oikos, 84: 417–434. https://doi.org/10.2307/3546421

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., ... & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature, 486(7401), 105-108. https://doi.org/10.1038/nature11118

Hooper, D. U., Bignell, D. E., Brown, V. K., Brussard, L., Dangerfield, J. M., Wall, D. H., ... & Van Der Putten, W. H. (2000). Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks. Bioscience, 50(12), 1049-1061. https://doi.org/10.1641/0006-3568(2000)050[1049:IBAABB]2.0.CO;2

Hoorens, B., Aerts, R., & Stroetenga, M. (2003). Does initial litter chemistry explain litter mixture effects on decomposition? Oecologia, 137(4), 578-586. https://doi.org/10.1007/s00442-003-1365-6

INIA. (2019) Red Agrometeorológica del Instituto Nacional de Investigación Agropecuaria, Chile. Retrieved from: http://agromet.inia.cl/estaciones.php. Last accessed 11 March 2019.

I. P. O. C. Change (2014). Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Jung, P., Baumann, K., Lehnert, L. W., Samolov, E., Achilles, S., Schermer, M., ... & Büdel, B. (2020). Desert breath - How fog promotes a novel type of soil biocenosis, forming the coastal Atacama Desert's living skin. Geobiology, 18(1), 113-124. https://doi.org/10.1111/gbi.12368

Kaspari, M., Clay, N. A., Donoso, D. A., & Yanoviak, S. P. (2014). Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. Ecology, 95(4), 795-800. https://doi.org/10.1890/13-1274.1

Knorr, W., Prentice, I. C., House, J. I., & Holland, E. A. (2005). Long-term sensitivity of soil carbon turnover to warming. Nature, 433(7023), 298-301. https://doi.org/10.1038/nature03226

Koch, G. W., Vitousek, P. M., Steffen, W. L., & Walker, B. H. (1995). Terrestrial transects for global change research. Vegetatio, 121(1-2), 53-65. https://doi.org/10.1007/BF00044672

Kou, L., Jiang, L., Hättenschwiler, S., Zhang, M., Niu, S., Fu, X., ... & Wang, H. (2020). Diversity-decomposition relationships in forests worldwide. Elife, 9:e55813. https://doi.org/10.7554/eLife.55813

Kuiters, A. T., & Sarink, H. M. (1986). Leaching of phenolic compounds from leaf and needle litter of several deciduous and coniferous trees. Soil Biology and Biochemistry, 18(5), 475-480. https://doi.org/10.1016/0038-0717(86)90003-9

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91(1), 299-305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P. & Shipley, B. (2014). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://rdrr.io/cran/FD/

Laskowski, R., Niklinska, M., & Maryanski, M. (1995). The dynamics of chemical elements in forest litter. Ecology, 76(5), 1393-1406. https://doi.org/10.2307/1938143

Lehnert, L. W., Thies, B., Trachte, K., Achilles, S., Osses, P., Baumann, K., ... & Karsten, U. (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), 254-269. https://doi.org/10.4209/aaqr.2017.01.0021

Leimu, R. & Fischer, M. 2008. A meta-analysis of local adaptation in plants. PLoS One 3: e4010. https://doi.org/10.1371/journal.pone.0004010

Leppert, K. N., Niklaus, P. A., & Scherer-Lorenzen, M. (2017). Does species richness of subtropical tree leaf litter affect decomposition, nutrient release, transfer and subsequent uptake by plants? Soil Biology and Biochemistry, 115, 44-53. https://doi.org/10.1016/j.soilbio.2017.08.007

Liu, J., Liu, X., Song, Q., Compson, Z. G., LeRoy, C. J., Luan, F., ... & Yang, Q. (2020). Synergistic effects: a common theme in mixed-species litter decomposition. New Phytologist, 227(3):757-765. https://doi.org/10.1111/nph.16556

Lu, W., Liu, N., Zhang, Y., Zhou, J., Guo, Y., & Yang, X. (2017). Impact of vegetation community on litter decomposition: evidence from a reciprocal transplant study with 13C labeled plant litter. Soil Biology and Biochemistry, 112, 248-257. https://doi.org/10.1016/j.soilbio.2017.05.014

Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2020). Assessment of Regression Models Performance. CRAN. R package version 0.4.8.1. https://easystats.github.io/performance

Luebert, F. & Pliscoff, P. 2006. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago de Chile.

Lummer, D., Scheu, S., & Butenschoen, O. (2012). Connecting litter quality, microbial community and nitrogen transfer mechanisms in decomposing litter mixtures. Oikos, 121(10), 1649-1655. https://doi.org/10.1111/j.1600-0706.2011.20073.x

Luo, W., & Azen, R. (2013). Determining Predictor Importance in Hierarchical Linear Models Using Dominance Analysis. Journal of Educational and Behavioral Statistics, 38(1), 3-31. https://doi.org/10.3102/1076998612458319

Macel, M., Lawson, C. S., Mortimer, S. R., Šmilauerova, M., Bischoff, A., Crémieux, L., ... & Steinger, T. (2007). Climate vs. soil factors in local adaptation of two common plant species. Ecology, 88(2), 424-433. https://doi.org/10.1890/0012-9658(2007)88[424:CVSFIL]2.0.CO;2

MacLean, R. C. 2005. Adaptive radiation in microbial microcosms. Journal of Evolutionary Biology. 18: 1376–1386. https://doi.org/10.1111/j.1420-9101.2005.00931.x

Makkonen, M., Berg, M. P., Handa, I. T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P. M., & Aerts, R. (2012). Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecology Letters, 15(9), 1033-1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x

Martiny, J. B. H., Bohannan, B. J., Brown, J. H., Colwell, R. K., Fuhrman, J. A., Green, J. L., ... & Staley, J. T. (2006). Microbial biogeography: putting microorganisms on the map. Nature Reviews Microbiology, 4(2), 102-112. https://doi.org/10.1038/nrmicro1341

May, R. M. (2011). Why should we be concerned about loss of biodiversity. Comptes Rendus Biologies, 334, 346–350. https://doi.org/10.1016/j.crvi.2010.12.002

McClaugherty, C. A. (1983). Soluble polyphenols and carbohydrates in throughfall and leaf litter decomposition. Acta oecologica. Série Oecologia generalis Montreuil, 4(4), 375-385.

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature, 341(6238), 142-144. https://doi.org/10.1038/341142a0

Meentemeyer, V. (1978). Macroclimate and lignin control of litter decomposition rates. Ecology, 59(3), 465-472. https://doi.org/10.2307/1936576

Melillo, J. M., Aber, J. D., Linkins, A. E., Ricca, A., Fry, B., & Nadelhoffer, K. J. (1989). Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil, 115(2), 189-198. https://doi.org/10.1007/BF02202587

Moreno, T. & Gibbons, W. (2007). The Geology of Chile. The Geological Society of London.

Moskwa, L-M, Oses, R., Wagner, D. (2020). Distribution of microbial generalists and habitat specialists in soils along a climate gradient in the Chilean Coastal Cordillera. Preprint (Version 1), Research Square. https://doi.org/10.21203/rs.3.rs-41494/v1

Naeem, S., Duffy, J. E. & Zavaleta, E. The functions of biological diversity in an age of extinction. Science, 336, 1401–1406 (2012). https://doi.org/10.1126/science.1215855

Oeser, R. A., Stroncik, N., Moskwa, L. M., Bernhard, N., Schaller, M., Canessa, R., ... & Fuentes, J. P. (2018). Chemistry and microbiology of the Critical Zone along a steep climate and vegetation gradient in the Chilean Coastal Cordillera. Catena, 170, 183-203. https://doi.org/10.1016/j.catena.2018.06.002

Parsons, S. A., Congdon, R. A., & Lawler, I. R. (2014). Determinants of the pathways of litter chemical decomposition in a tropical region. New Phytologist, 203(3), 873-882. https://doi.org/10.1111/nph.12852

Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., ... & Carbognani, M. (2019). Litter decomposition: effects of temperature driven by soil moisture and vegetation type. Plant and Soil, 435(1-2), 187-200. https://doi.org/10.1007/s11104-018-3889-x

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry, 101(1-3), 133-149. https://doi.org/10.1007/s10533-010-9439-0

Preston, C. M., Nault, J. R., Trofymow, J. A., Smyth, C., & CIDET Working Group. (2009). Chemical changes during 6 years of decomposition of 11 litters in some Canadian forest sites. Part 1. Elemental composition, tannins, phenolics, and proximate fractions. Ecosystems, 12(7), 1053-1077. https://doi.org/10.1007/s10021-009-9266-0

Powers, J. S., Montgomery, R. A., Adair, E. C., Brearley, F. Q., DeWalt, S. J., Castanho, C. T., ... & González-Iturbe, J. A. (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(4), 801-811. https://doi.org/10.1111/j.1365-2745.2009.01515.x

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., & Solomon, A. M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19(2), 117-134. https://doi.org/10.2307/2845499

R Core Team. (2019). R: A Language and Environment for Statistical Computing. Vienna, Austria. R Foundation for Statistical Computing. https://www.R-project.org/

Raich, J. W., & Potter, C. S. (1995). Global patterns of carbon dioxide emissions from soils. Global Biogeochemical Cycles, 9(1), 23-36. https://doi.org/10.1029/94GB02723

Raich, J. W., & Schlesinger, W. H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B, 44(2), 81-99. https://doi.org/10.3402/tellusb.v44i2.15428

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences, 94(25), 13730-13734. https://doi.org/10.1073/pnas.94.25.13730

Robertson G. P. & Paul E. A. (1999) Decomposition and soil organic matter dynamics. In: Sala, O. E., Jackson, R. B., Mooney, H. A., Howarth, R. W. (Eds) Methods of ecosystem science. Springer, New York.

Santonja, M., Milcu, A., Fromin, N., Rancon, A., Shihan, A., Fernandez, C., ... & Hättenschwiler, S. (2019). Temporal shifts in plant diversity effects on carbon and nitrogen dynamics during litter decomposition in a Mediterranean shrubland exposed to reduced precipitation. Ecosystems, 22(5), 939-954. https://doi.org/10.1007/s10021-018-0315-4

Scherer-Lorenzen, M. (2008). Functional diversity affects decomposition processes in experimental grasslands. Functional Ecology, 22(3), 547-555. https://doi.org/10.1111/j.1365-2435.2008.01389.x

Scheu, S., Albers, D., Alphei, J., Buryn, R., Klages, U., Migge, S., ... & Salamon, J. A. (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), 225-238. https://doi.org/10.1034/j.1600-0706.2003.12131.x

Schimel, J. P., Cates, R. G., & Ruess, R. (1998). The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. Biogeochemistry, 42(1-2), 221-234. https://doi.org/10.1023/A:1005911118982

Schimel, J. P., & Hättenschwiler, S. (2007). Nitrogen transfer between decomposing leaves of different N status. Soil Biology and Biochemistry, 39(7), 1428-1436. https://doi.org/10.1016/j.soilbio.2006.12.037

Schlesinger, W. H., & Andrews, J. A. (2000). Soil respiration and the global carbon cycle. Biogeochemistry, 48(1), 7-20. https://doi.org/10.1023/A:1006247623877

Schlesinger, W. H. & Pilmanis, A. 1998. Plant-soil interactions in deserts. Biogeochemistry 42: 169–187. https://doi.org/10.1023/A:1005939924434

Scholes, M. C., Powlson, D. S., & Tian, G. L. (1997). Input control of organic matter dynamics. Geoderma, 79(1-4), 25-47. https://doi.org/10.1016/S0016-7061(97)00037-2

Schreeg, L. A., Mack, M. C., & Turner, B. L. (2013). Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species. Ecology, 94(1), 94-105. https://doi.org/10.1890/11-1958.1

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., ... & Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. Global change biology, 21(11), 4128-4140. https://doi.org/10.1111/gcb.13021

Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G., ... & Rustad, L. (2000). Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis: Ecosystem responses to global warming will be complex and varied. Ecosystem warming experiments hold great potential for providing insights on ways terrestrial ecosystems will respond to upcoming decades of climate change. Documentation of initial conditions provides the context for understanding and predicting ecosystem responses. Bioscience, 50(10), 871-882. https://doi.org/10.1641/0006-3568(2000)050[0871:GWATEA]2.0.CO;2

Simberloff, D. (2015). Non-native invasive species and novel ecosystems. F1000prime reports, 7. https://dx.doi.org/10.12703%2FP7-47

Snijders, T. A. B., & Bosker, R. J. (1994). Modeled Variance in Two-Level Models. Sociological Methods & Research, 22(3), 342–363. https://doi.org/10.1177/0049124194022003004

St. John, M. G., Orwin, K. H., & Dickie, I. A. (2011). No 'home'versus 'away'effects of decomposition found in a grassland–forest reciprocal litter transplant study. Soil Biology and Biochemistry, 43(7), 1482-1489. https://doi.org/10.1016/j.soilbio.2011.03.022

Strickland, M. S., Osburn, E., Lauber, C., Fierer, N., & Bradford, M. A. (2009). Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology, 23(3), 627-636. https://doi.org/10.1111/j.1365-2435.2008.01515.x

Suding, K. N., Lavorel, S., Chapin Iii, F. S., Cornelissen, J. H., DIAz, S., Garnier, E., ... & Navas, M. L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology, 14(5), 1125-1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Sun, Y., & Zhao, S. (2016). Leaf litter decomposition in urban forests: test of the home-field advantage hypothesis. Annals of Forest Science, 73(4), 1063-1072. https://doi.org/10.1007/s13595-016-0577-y

Suseela, V., & 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), 1428-1451. https://doi.org/10.1111/gcb.13923

Swift et al. 1979. Decomposition in terrestrial ecosystems. Blackwell Publishing.

Tenney FG, Waksman SA. (1929). Composition of natural organic materials and their decomposition in the soil. IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. Soil Science, 28:55–84

Thompson, M. V., Palma, B., Knowles, J. T., & Holbrook, N. M. (2003). Multi-annual climate in Parque Nacional Pan de Azúcar, Atacama Desert, Chile. Revista Chilena de Historia Natural, 76(2), 235-254. https://doi.org/10.4067/S0716-078X2003000200009

Trofymow, J. A., Moore, T. R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., ... & Duschene, L. (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Canadian Journal of Forest Research, 32(5), 789-804. https://doi.org/10.1139/x01-117

Turner, B. L., Lambin, E. F., & Reenberg, A. (2007). The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences, 104(52), 20666-20671. https://doi.org/10.1073/pnas.0704119104

Übernickel, K. Ehlers, T. A., Ershadi, M.R., Paulino, L., Fuentes Espoz, J. P., Maldonado, A., Oses-Pedraza, R., von Blanckenburg, F. (2020). Time series of meteorological station data in the EarthShape study areas in the Coastal Cordillera, Chile. GFZ Data Services. https://doi.org/10.5880/fidgeo.2020.043

Vanlauwe, B., Vanlangenhove, G., Merckx, R., & Vlassak, K. (1995). Impact of rainfall regime on the decomposition of leaf litter with contrasting quality under subhumid tropical conditions. Biology and Fertility of Soils, 20(1), 8-16. https://doi.org/10.1007/BF00307835

Veen, G. F., Freschet, G. T., Ordonez, A., & Wardle, D. A. (2015). Litter quality and environmental controls of home-field advantage effects on litter decomposition. Oikos, 124(2), 187-195. https://doi.org/10.1111/oik.01374

Wallenstein, M. D., Haddix, M. L., Ayres, E., Steltzer, H., Magrini-Bair, K. A., & Paul, E. A. (2013). Litter chemistry changes more rapidly when decomposed at home but converges during decomposition–transformation. Soil Biology and Biochemistry, 57, 311-319. https://doi.org/10.1016/j.soilbio.2012.09.027

Wang, Q., Zhong, M., & He, T. (2013). Home-field advantage of litter decomposition and nitrogen release in forest ecosystems. Biology and Fertility of Soils, 49(4), 427-434. https://doi.org/10.1007/s00374-012-0741-y

Wardle, D. A., Bonner, K. I., & Nicholson, K. S. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos, 79:247-258. https://doi.org/10.2307/3546010

Weathers, K. C., Strayer D. L., & Likens, G. E. (2013). Fundamentals of Ecosystem Science. Academic Press. Croydon, UK.

Wetzel, R. G., & Tuchman N. C. Effects of atmospheric CO2 enrichment and sunlight on degradation of plant particulate and dissolved organic matter and microbial utilization. Archiv für Hydrobiologie 162.3 (2005): 287-308. https://doi.org/10.1127/0003-9136/2005/0162-0287

Wickings, K., Grandy, A. S., Reed, S. C., & Cleveland, C. C. (2012). The origin of litter chemical complexity during decomposition. Ecology Letters, 15(10), 1180-1188. https://doi.org/10.1111/j.1461-0248.2012.01837.x

Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology, 268, 40-47. https://doi.org/10.1016/j.agrformet.2018.12.018

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... & Flexas, J. (2004). The worldwide leaf economics spectrum. Nature, 428(6985), 821-827. https://doi.org/10.1038/nature02403

Wu, D., Li, T., & Wan, S. (2013). Time and litter species composition affect litter-mixing effects on decomposition rates. Plant and Soil, 371(1-2), 355-366. https://doi.org/10.1007/s11104-013-1697-x

Xu, X., & Hirata, E. (2005). Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: N and P dynamics. Plant and Soil, 273(1-2), 279-289. https://doi.org/10.1007/s11104-004-8069-5

Yuan, X., Niu, D., Wang, Y., Boydston, A., Guo, D., Li, X., ... & Fu, H. (2019). Litter decomposition in fenced and Grazed grasslands: a test of the home-field advantage hypothesis. Geoderma, 354, 113876. https://doi.org/10.1016/j.geoderma.2019.07.034

Zhang, D., Hui, D., Luo, Y., & Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology, 1(2), 85-93. https://doi.org/10.1093/jpe/rtn002

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., ... & Hattenschwiler, S. (2020). Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. Journal of Ecology. https://doi.org/10.1111/1365-2745.13452

Zhou, S., Huang, C., Xiang, Y., Tie, L., Han, B., & Scheu, S. (2018a). Effects of reduced precipitation on litter decomposition in an evergreen broad-leaved forest in western China. Forest Ecology and Management, 430, 219-227. https://doi.org/10.1016/j.foreco.2018.08.022

Zhou, Z., Wang, C., & Luo, Y. (2018b). Response of soil microbial communities to altered precipitation: A global synthesis. Global Ecology and Biogeography, 27(9), 1121-1136. https://doi.org/10.1111/geb.12761

Zukswert, J. M., & Prescott, C. E. (2017). Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. Oecologia, 185(2), 305-316. https://doi.org/10.1007/s00442-017-3951-z

Supporting Information

Appendix Chapter 2

Appendix S2-1. *List of plant species in Fig. 2-2.*

1) *Tetragonia maritima*
2) *Cristaria integerrima*
3) *Copiapoa cinerea*
4) *Cistanthe grandiflora*
5) *Frankenia chilensis*
6) *Nolana mollis*
7) *Nolana crassulifolia*
8) *Nolana paradoxa*
9) *Eulychnia breviflora*
10) *Euphorbia lactiflua*
11) *Nolana divaricata*
12) *Echinopsis deserticola* with *Usnea eulychnioides*
13) *Cordia decandra*
14) *Porlieria chilensis*
15) *Flourensia thurifera*
16) *Gutierrezia resinosa*
17) *Haplopappus decurrens*
18) *Baccharis linearis*
19) *Jubaea chilensis*
20) *Kageneckia oblonga*
21) *Aristeguietia salvia*
22) *Retanilla trinervia*
23) *Colliguaja odorifera*
24) *Lithraea caustic*
25) *Araucaria araucana* and *Nothofagus* spp.
26) *Festuca sp.* and *Nothofagus spp.,* covered *with Usnea* sp.
27) *Nothofagus antarctica*
28) *Gaultheria mucronata*
29) *Viola maculata*
30) *Gevuina avellana*
31) *Lapageria rosea*
32) *Chusquea quila*
33) *Eucryphia cordifolia*
34) *Drimys winteri*
35) *Aextoxicon punctatum*

Appendices Chapter 3

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.

Species	Origin	K [mg/g]	P [mg/g]	C [mg/g]	N [mg/g]	C/N
Heliotropium pycnophyllum	arid	20.3	0.49	252	11.0	22.9
Nolana crassulifolia		12.7	0.57	284	8.99	31.5
Nolana mollis		9.79	0.19	207	3.96	52.3
Ophryosporus triangularis		19.6	1.54	415	18.9	22.0
Tetragonia maritima		22.9	0.87	26	11.2	23.5
Cordia decandra	semi-arid	21.3	1.23	389	19.6	19.9
Flourensia thurifera		22.5	0.64	444	8.73	50.9
Lobelia tupa		28.8	3.35	435	10.3	42.0
Maytenus boaria		15.2	1.89	407	17.7	22.9
Senna cumingii		16.5	1.94	414	18.4	22.5
Aristeguietia salvia	mediterranean	23.7	1.38	426	13.3	32.0
Cestrum parqui		46.5	1.29	420	12.8	32.8
Jubaea chilensis		6.83	0.59	492	9.65	51.0
Podantus mitiqui		28.4	1.47	434	9.49	45.7
Quillaja saponaria		6.85	0.55	441	4.85	90.8
Chusquea culeou	temperate	11.2	1.40	429	14.6	29.5
Festuca sp.		8.34	1.16	447	3.12	143
Notofagus antarctica		5.41	0.94	482	10.9	44.5
Usnea sp.		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

Table S3-4. Linear mixed models for relative N loss and relative P loss of reciprocally translocated litter decomposing at four sites along a steep climatic gradient in Chile. DF = degrees of freedom, F = F statistic, p = statistical significance.

Response	Factor	DF	F	p
N loss (%)	Site	3	61.236	<.0001 ***
	Origin	3	1.3337	0.3061
	Site*Origin	9	0.9995	0.4397
	Litter quality	2	1.0093	0.3913
	Site*Litter quality	6	3.4871	0.0022 **
P loss (%)	Site	3	66.214	<.0001 ***
	Origin	3	1.1591	0.3627
	Site*Origin	9	2.2595	0.0178 *
	Litter quality	2	0.2828	0.7582
	Site*Litter quality	6	9.859	<.0001 ***

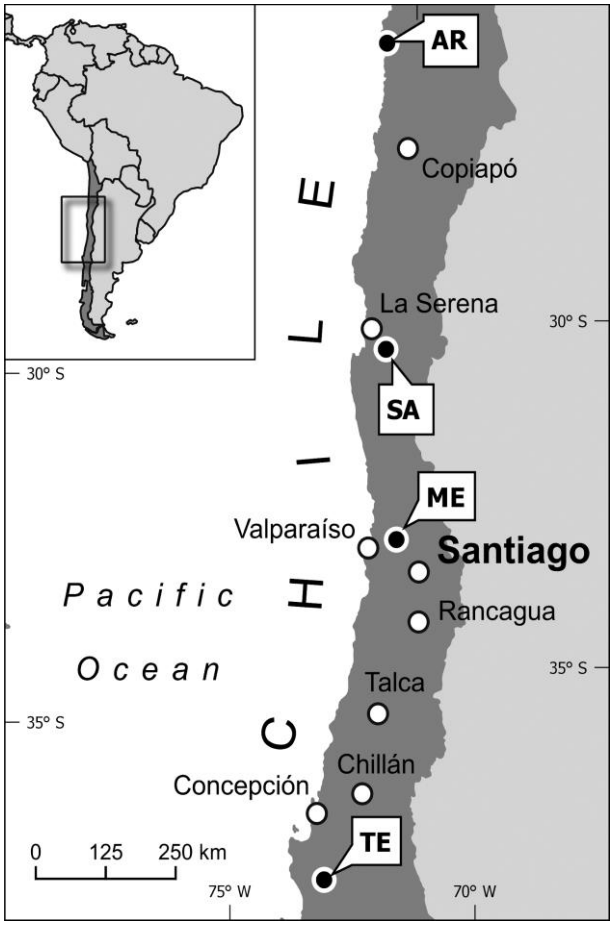

Figure S3-1. Location of the study sites in Chile. AR = Arid; SA = Semi-Arid; ME = Mediterranean; TE = Temperate.

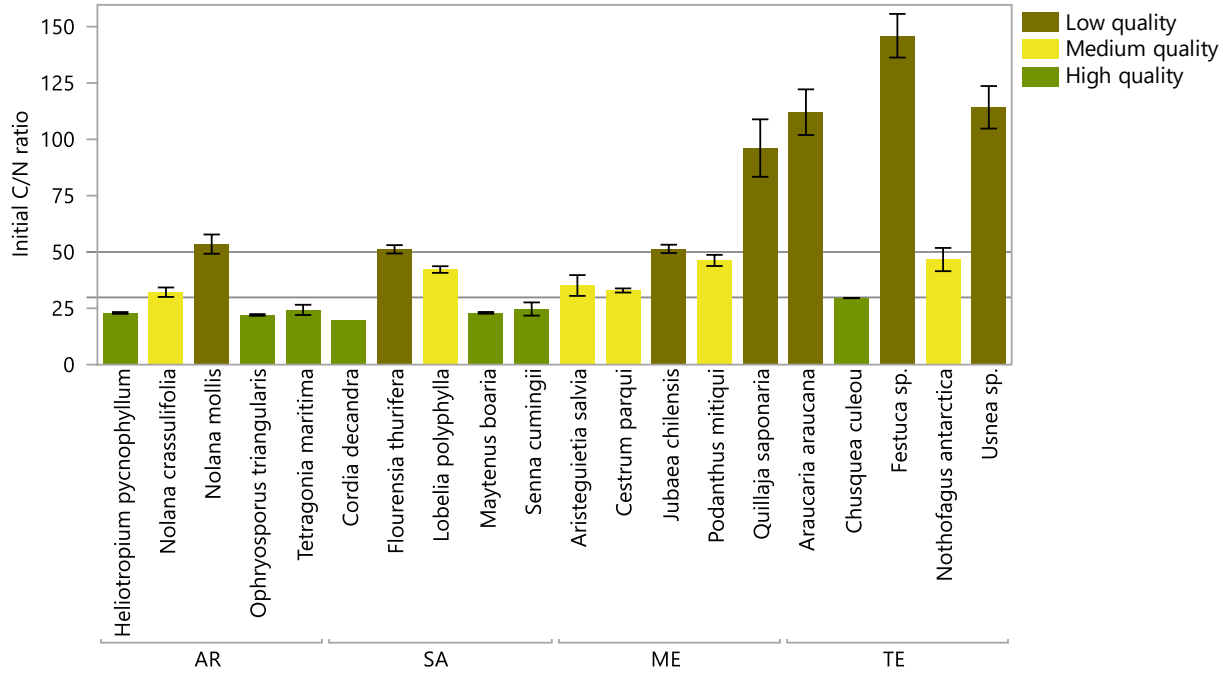

Figure S3-2. Initial litter carbon to nitrogen ratio (C/N) from 20 species used in a reciprocal litter transplant experiment along the coastal cordillera of Chile. Species are ordered per origin (AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate), and classified in three litter quality categories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

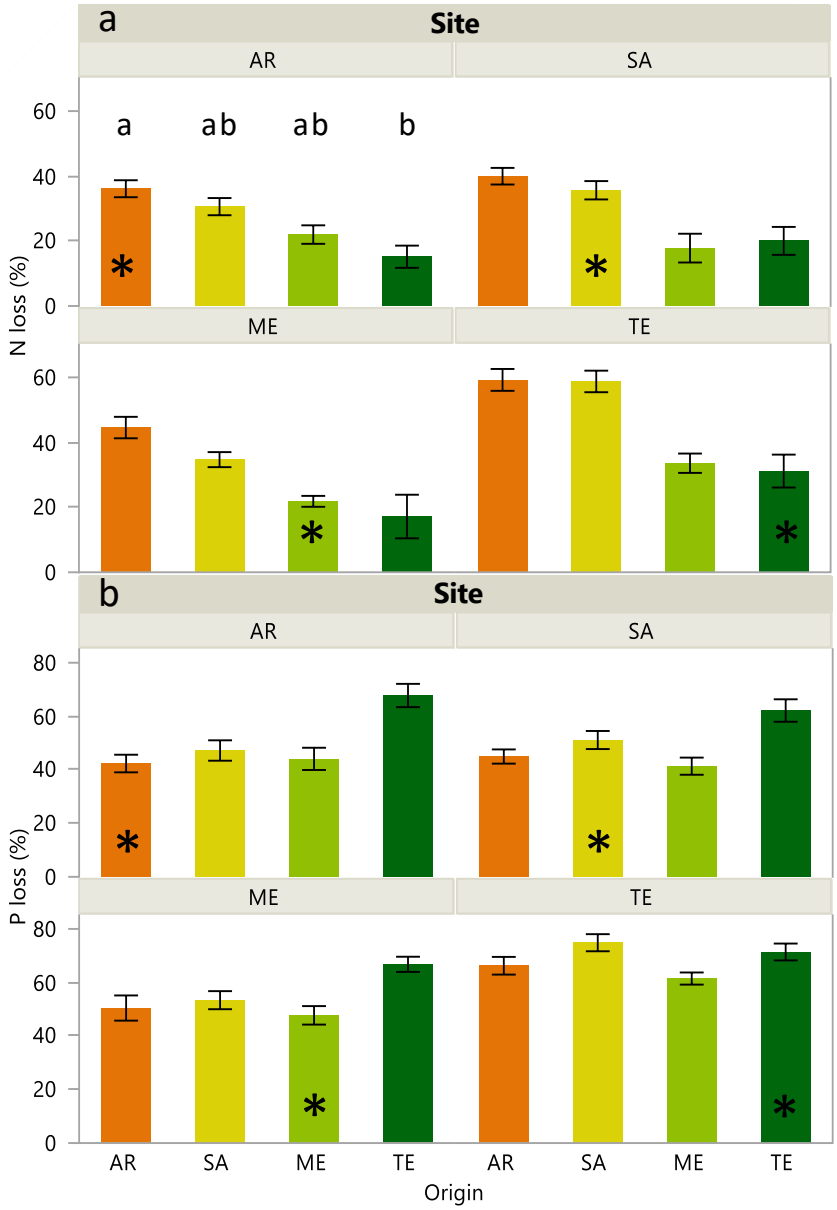

Figure S5-3. (a) N loss (%) and (b) P loss (%) after 12 months of decomposition for litter from 19 plant species from different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile **(**AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate). Error bars represent the standard error. Significance is expressed per site with different letters. * = litter decomposing "at home".

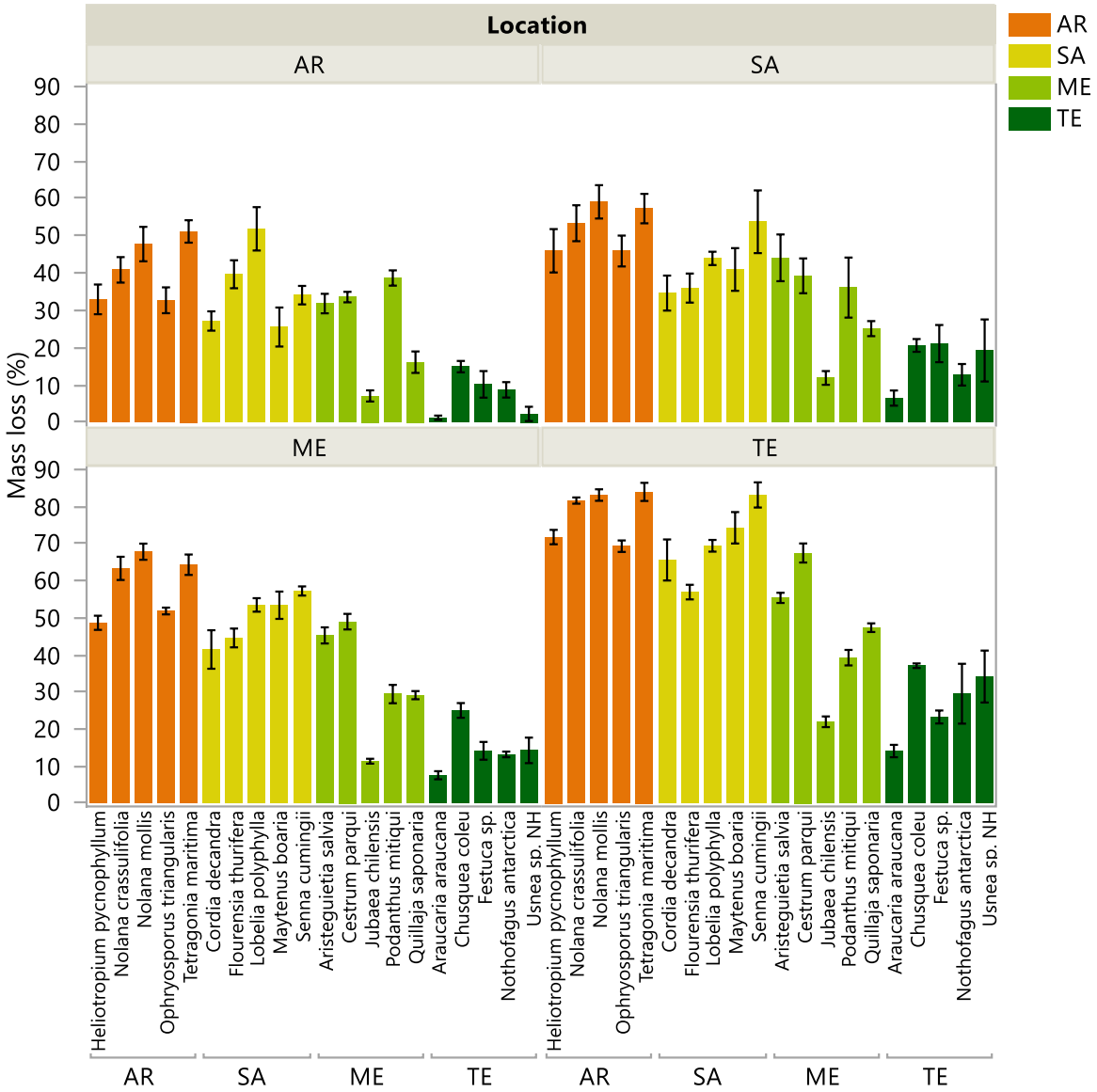

Figure S3-4. Litter mass loss (%) after 12 months of decomposition for litter from 20 plant species with different origin (colours) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile (AR = arid, SA = semi-arid, ME = mediterranean, TE = temperate humid). Error bars represent standard error.

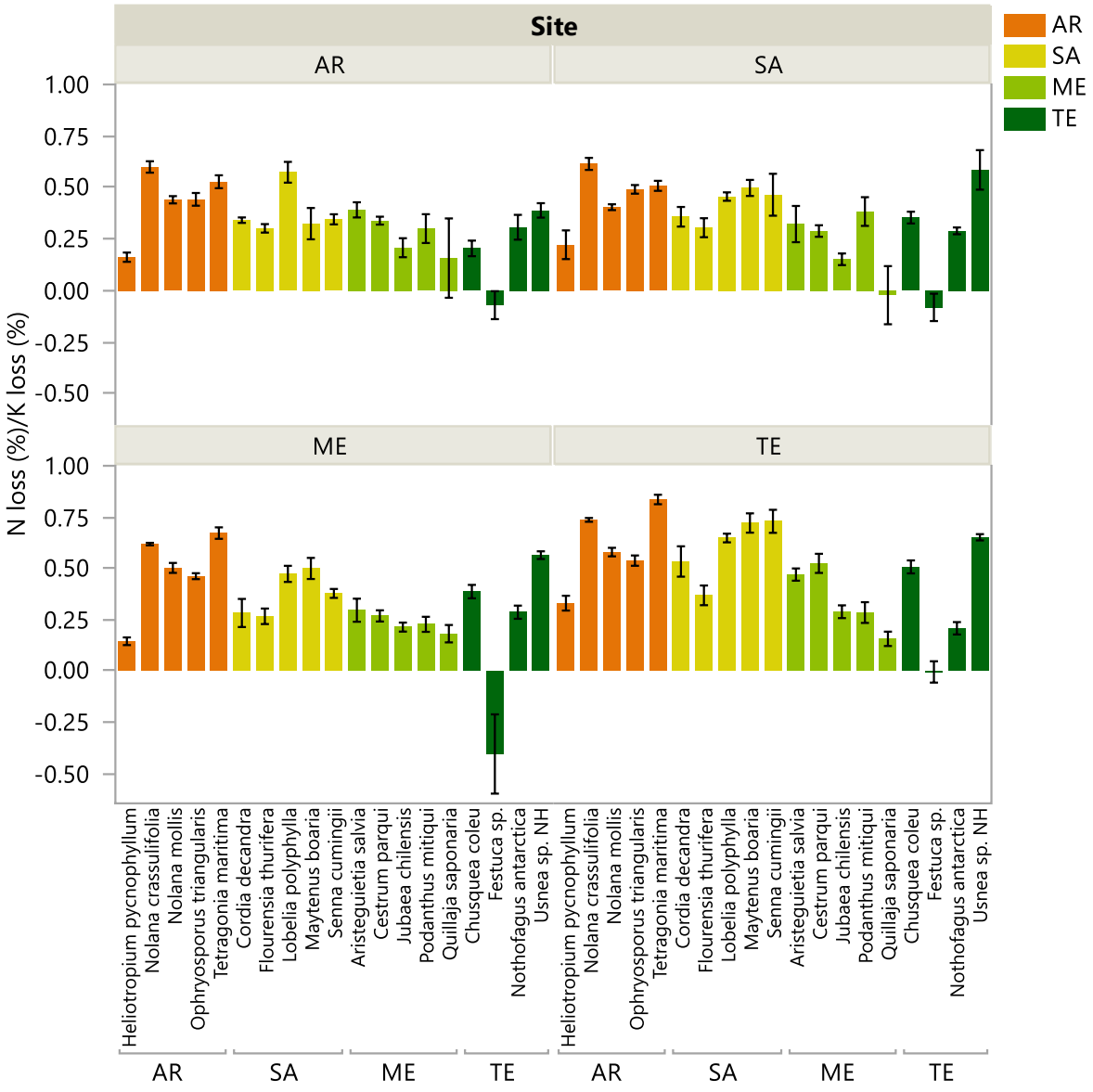

Figure S3-5. Relative N/K loss after 12 months of decomposition for litter from 19 plant species with different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile **(**AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate). Error bars represent the standard error. No significant effects within sites were observed (Tukey HSD tests). * = litter decomposing at their "home site". *Festuca* sp. gained in N during the experiment which led to negative relative N/K loss.

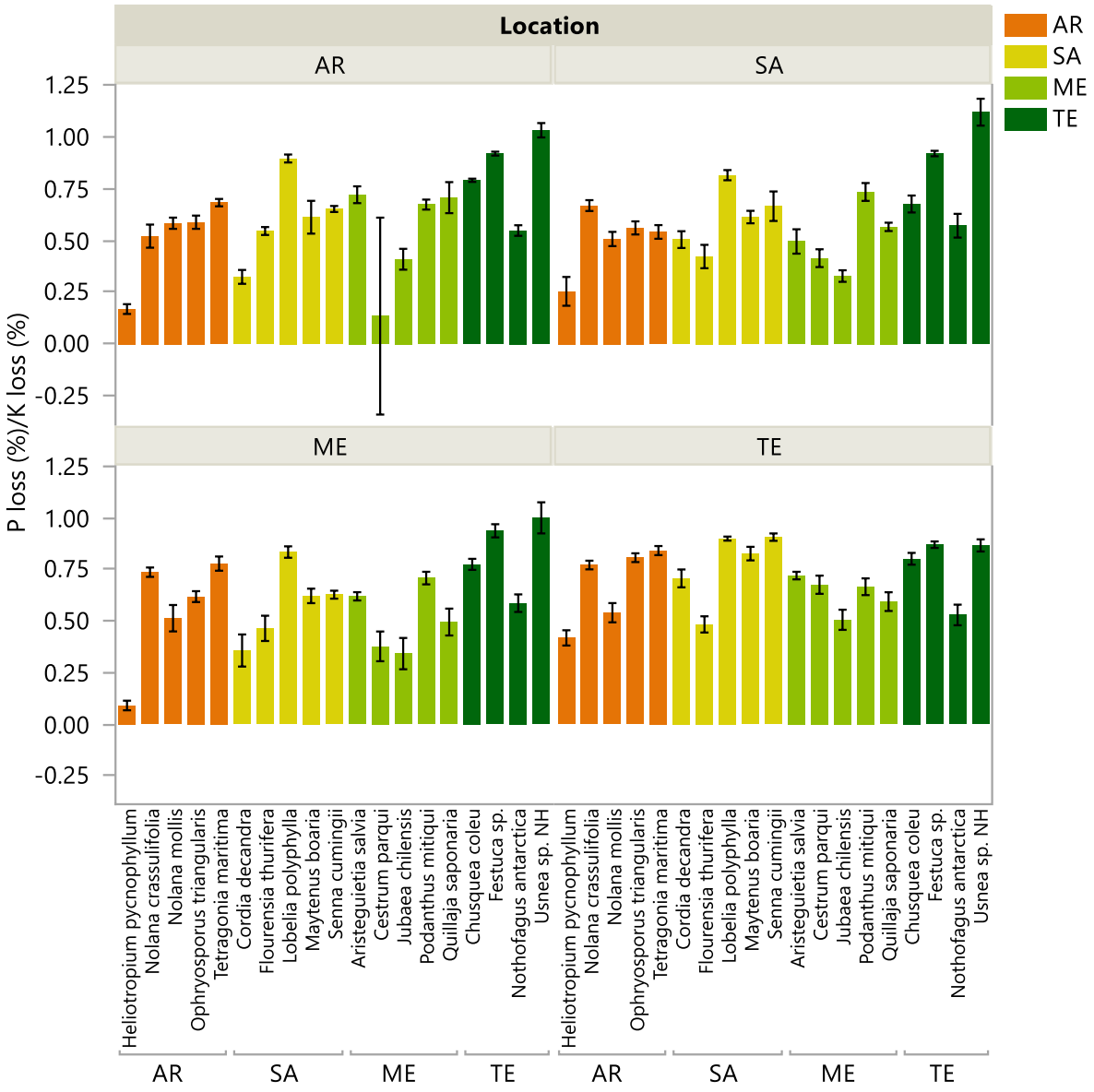

Figure S3-6. Relative P/K loss after 12 months of decomposition for litter from 19 plant species with different origins (colors) and placed reciprocally at these sites (panels) along the coastal cordillera of Chile. AR = Arid, SA = Semi-arid, ME = Mediterranean, TE = Temperate. Error bars represent the standard error. No significant effects within sites were observed (Tukey HSD tests). * = litter decomposing at their "home site".

Appendices Chapter 4

Appendix S4-1. *Plant functional traits measurement methods.*

Physical traits

The force required to punch a leaf (Fp, equivalent to leaf toughness) was measured for five healthy individuals located near the study plots, using ten leaves per individual. When it was impossible to obtain the leaves without heavily damaging the individual (*Cistanthe sp, Cristaria integerrima, Festuca sp*), we harvested as many leaves as possible and increased the number of individual plants until reaching 50 leaves per species in total, sampling from the spatially closest individuals. Upon harvest, leaves were wrapped in wet absorbing paper and placed in plastic bags, to avoid shrinkage and folding. Within the next eight hours, Fp was measured as maximum force to fracture, using a digital force gauge (IMADA, DS2-50N) attached to a 3 mm diameter cylindrical probe (IMADA, FR-EC-3J), mounted on a vertical manual test stand (IMADA, KV-50N), averaging two random punches per leaf, avoiding the midrib. For specific leaf area (SLA), ten additional leaves were collected from the same individuals, scanned and analyzed using the Image J software (https://imagej.nih.gov/ij/) to estimate leaf area. These leaves were then dried at 70 °C for 72 h and weighed to get dry mass using an analytical scale. SLA was then calculated as the area (cm^2) divided by the dry mass (g) of a leaf. Species-specific mean traits were calculated as average values across all individuals from a species for each site.

Chemical traits

For each species, five subsamples (10 g each) of the dried leaf material used for the litter transplant experiment were milled to fine powder. For each subsample, carbon and nitrogen concentration (and thus C/N ratio) were determined at the University of Oldenburg, Germany, using a CHNS Analyzer (FLASHEA, 1112 Series; CE Elantech, Inc., Lakewood, USA). For each subsample, Al, Ca, Fe, K, Mg, Mn and P content were obtained by elemental analysis according to Jackson (1958) and Lim & Jackson (1982). Briefly, about 100 mg of milled samples were weighed in platinum beakers and treated with 1:1 mixture of 60% perchlorid acid (HClO4) and 65% nitric acid (HNO3). Samples were stepwise heated up to 150°C on a sand bath and left until the organic matter was oxidized. Subsequently, the temperature was increased to 300°C to vaporize the acid and 40% hydrofluoric acid (HF) was applied and left overnight. Afterwards, HClO4 was added, heated to 300°C to vaporize the acid again. Finally, 37% hydrochloric acid (HCl) was added and the sample was heated. The final sample was filtrated, and the total amount of the elements was analyzed by ICP-OES (Varian Vista-Pro).
From three subsamples, total phenolics were measured colorimetrically using the Folin-Ciocalteau reagent following Marigo (1973) with gallic acid as a standard. From a 0.5 g sample of ground leaf material, total phenolics were extracted with 30 mL of a solution containing 50% methanol and 50% distilled water, shaken for 2 h and filtered (filter number 112, Durieux, Torcy, France).

Tannins were measured according to Hagerman & Butler (1978) with the modified version of the protein precipitation method using the microplate assay (see Ann Hagerman's "tannin handbook", http://www.users.miamioh.edu/hagermae/). Tannins were extracted from a 0.1 g sample of ground leaf material with 1 mL of the same solvent used for the total phenolics extraction and left under ultrasound exposure for 30 min (samples within 15 mL Falcon tubes placed in a water bath). After extraction, the samples were centrifuged at 2000 rpm for 15 min and the supernatant kept for further tannin analyses. Microplates were prepared with 75 µl BSA (Bovine Serum Albumin) protein and buffer solutions (1:5) per well to which 25 µl of sample solution was added and mixed immediately with a microplate shaker for 10 min. After 15 min incubation, microplates were centrifuged for 1 h 15 min at 3700 rpm, and all supernatant was removed. 200 µl of SDS (sodium dodecyl sulfate) / TEA (triethanolamin) solution was added to each well and shaken for 10 min until precipitates were completely re-dissolved. 50 µl of ferric chloride was then added to each well, shaken, quickly centrifuged (500 rpm) for 1 min and then read with the microplate reader at 510 nm wavelength.

A combined sample of each species was subjected to ^{13}C cross polarization magic angle spinning nuclear magnetic resonance (^{13}C CPMAS-NMR) spectroscopy (Bruker AvanceIII200 spectrometer, Bruker, Billerica, MA, USA). Finely ground samples were spun in a zirconium oxide rotor at 6.8 kHz and analyzed with a recycle delay time of 1.0 s and 2500 scans for each sample – to obtain a sufficient signal to noise ratio some samples required more scans: *Nolana crassulifolia, Nolana paradoxa, Tetragonia maritima, Porlieria chilensis* (5000 each), and *Frankenia chilensis* (7500). The NMR spectra were integrated according to chemical shift regions: 0 – 45 alkyl C, 45 – 60 N-alkyl/methoxyl C, 60 – 95 O-alkyl C, 95 – 110 Di-O-Alkyl C, 110 – 145 aromatic C, 145 – 165 phenolic and 165 – 215 amide/carboxyl C (Nelson & Baldock 2005). Based on the NMR spectra, the relative content of carbohydrates (including cellulose, hemicellulose, muco-polysaccharides and smaller molecular weight saccharides), proteins, lignin and lipids were obtained using a molecular mixing model (Nelson & Baldock 2005). According to Bonanomi et al. (2013), a decomposition proxy based on the integrated NMR spectra was calculated as the ratio between 70-75 ppm (O-alkyl C in carbohydrates) and 52-57 ppm (methoxyl C in lignin).

References in Appendix S4-1

Bonanomi, G., Incerti, G., Giannino, F., Mingo, A., Lanzotti, V., & Mazzoleni, S. (2013). Litter quality assessed by solid state C-13 NMR spectroscopy predicts decay rate better than C/N and Lignin/N ratios. Soil Biology & Biochemistry, 56, 40-48. doi: 10.1016/j.soilbio.2012.03.003

Hagerman A.E., & Butler L.G. (1978) Protein precipitation method for the quantitative determination of tannins**.** Journal of Agricultural and Food Chemistry, 26(4), 809-812. doi: 10.1021/jf60218a027

Jackson, M.L. (1958). Soil chemical analysis. London. Constable & Co. Ltd.

Lim, C.H., & Jackson, M.L. (1982). Dissolution for total elemental analysis. In: A. Page, R. H. Miller, & R. R. Keeney (Eds.) *Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties* (pp. 1-12). Madison, Wisconsin, USA: American Society of Agronomy, Inc.

Marigo, G. (1973). Sur une méthode de fractionnement et d'estimation des composées phénoliques chez les végéteaux. Analysis, 2, 106-110.
Nelson, P. N., & Baldock, J. A. (2005). Estimating the molecular composition of a diverse range of natural organic materials from solid-state C-13 NMR and elemental analyses. Biogeochemistry, 72(1), 1-34. doi: 10.1007/s10533-004-0076-3

Table S4-1. Selected linear mixed models, explained variance of their predictors and model estimates for litter mass loss (%, logit transformation) of the 30 plant species used in a reciprocal litter translocation experiment along the Coastal Cordillera of Chile. One linear model was selected for each decomposition stage, testing the relative importance of mean soil moisture (MSM) and traits for litter mass loss and their interaction, including site as a random factor. Explained variance of predictors was approached as the S&B R^2 at level 1 (Snijders & Bosker, 1994) using dominance analysis (Azen & Bodescu, 2006). Relative importance of traits to MSM (RI Traits) was calculated as the explained variance of Traits (R^2 Traits) divided by the explained variance of MSM. MSM, mean soil moisture; Fp, force to punch; SLA, specific leaf area.

Explained variance					
Selected predictors	Decomposition stages (months)				
	3	6	9	12	24
MSM	0.12	0.10	0.24	0.18	0.32
Na	0.23	0.23	0.14	0.17	0.06
Mg	0.11		0.10	0.13	0.07
K	0.07	0.08	0.05		
Fp	0.08	0.07	0.06		0.05
SLA	0.02	0.03	0.02		0.01
Protein	0.09	0.11	0.10	0.10	0.06
Lignin/N	0.03	0.04	0.03		
Tannins	0.02		0.01		
Carbohydrates		0.02		0.03	
Lignin		0.02			
Lipids				0.01	
Fe					0.02
Mn	<0.01		<0.01		
MSM:K	0.02				
MSM:Na		0.01	0.01	0.01	
MSM:Carbohydrates		<0.01			
MSM:Protein			0.01	0.03	0.03
MSM:Fp			<0.01		0.02
MSM:Mg			0.01		
Model estimates					
df	452	464	460	465	473
R^2	0.76	0.74	0.8	0.74	0.64
R^2 Traits	0.64	0.60	0.52	0.45	0.27
RI Traits	5.44	6.18	2.19	2.50	0.84

Table S4-2. Selected linear models, explained variance of their predictors and model estimates for litter mass loss (%, logit transformation) of the 30 plant species used in a reciprocal litter translocation experiment during two years along the Coastal Cordillera of Chile. One linear model was selected for each decomposition stage, testing the relative importance of climate and traits for litter mass loss and their interaction. Explained variance was approached as the R^2 using dominance analysis (Azen & Bodescu, 2006). Relative importance of traits to mean soil moisture (MSM) (RI Traits) was calculated as the explained variance of Traits (R^2 Traits) divided by the explained variance of MSM. Notable changes (Δ>0.02) in the R^2 of predictors or total R^2 in comparison to mixed models (Table S1) are marked in bold. MSM, mean soil moisture; Fp, force to punch; SLA, specific leaf area.

Explained variance					
Selected predictors	Decomposition stages (months)				
	3	6	9	12	24
MSM	0.11	0.10	**0.21**	0.17	**0.28**
Na	0.23	0.22	0.14	0.17	0.06
Mg	0.11		0.10	0.13	0.07
K	0.07	0.08	0.05		
Fp	0.08	0.07	0.06		0.05
SLA	0.02	0.03	0.02		0.01
Protein	0.09	0.12	0.10	0.10	0.06
Lignin/N	0.03	0.04	0.03		
Tannins	0.02		0.01		
Carbohydrates		0.03		0.03	
Lignin		0.02			
Lipids				0.01	
Fe					0.02
Mn	<0.01		<0.01		
MSM:K	0.02				
MSM:Na		0.01	0.01	0.02	
MSM:Carbohydrates		<0.01			
MSM:Protein			0.02	0.03	0.03
MSM:Fp			<0.01		0.02
MSM:Mg			0.01		
Model estimates					
df	454	466	462	467	475
R^2	0.75	**0.71**	**0.77**	**0.66**	**0.60**
R^2 Traits	0.64	0.60	0.52	0.45	0.27
RI Traits	**6.0**	**6.29**	**2.49**	**2.64**	**0.96**

Table S4-3. Mean and standard deviation of litter mass loss (% of initial weight) after 3, 6, 9, 12 and 24 months of decomposition for 30 species under different climate regimes along the Coastal Cordillera of Chile. AD, Arid-Dry; AF, Arid-Fog; SA, Semi-Arid; ME, Mediterranean; TU, Temperate Upland and TL, Temperate Lowland.

	Decomposition stage (months)									
	3		6		9		12		24	
Climate	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
AD	15.0	26	22.5	26.2	21.5	26.2	31.8	25.7	40.5	26.3
AF	20.0	26.3	27.6	26.3	27.8	26.3	35.1	25.8	46.1	26.4
SA	19.5	26.4	20.6	26.4	21.8	26.5	27.5	25.7	48.1	26.5
ME	22.7	26.3	26.5	26.4	27.0	26.4	32.7	25.6	47.3	26.4
TU	32.8	26.6	35.3	26.6	40.3	26.6	43.9	26.1	67.9	26.7
TL	33.7	26.5	45.2	26.5	57.7	26.5	62.6	26.7	84.9	26.7

Table S4-4. Pearson correlations between decomposition and different plant functional traits (PFT). Numbers in brackets represent degrees of freedom. Significance code: *** $p<0.001$.

PFT	*r* (df)	PFT	*r* (df)
Fp	-0.39 (897)***	Total phenolics	0.10 (867)***
SLA	0.10 (897)***	Al	0.17 (897)***
Carbohydrates	-0.24 (897)***	Ca	0.42 (897)***
Lignin	-0.11 (897)***	Fe	0.12 (897)***
Lipids	0.17 (897)***	Mg	0.55 (897)***
Proteins	0.50 (897)***	Mn	0.06 (897)
C/N	-0.48 (897)***	Na	0.57 (867)***
Lignin/N	-0.32 (897)***	P	0.23 (897)***
Tannins	-0.13 (867)***		

Table S4-5. Results of a linear mixed model of litter mass loss (%, logit transformed) after 6 and 12 months of decomposition in 30 plant species along a desert-to-temperate climatic gradient in Chile, aimed at testing explicitly for interactive effects that may indicate additional decomposition through photodegradation, especially in lignin-rich species at the dry end of the gradient. SE, standard error; df, degrees of freedom.

	6 months					12 months				
Fixed Effects	Estimate	SE	df	t value	p value	Estimate	SE	df	t value	p value
Intercept	-0.93	0.48	15.71	-1.94	0.07	0.07	0.76	16.77	0.09	0.93
Lignin	-0.02	0.01	500.7	-1.53	0.13	-4E-03	0.02	499.7	-0.24	0.81
MSM	1.05	1.7	29.16	0.62	0.54	-1.31	2.62	201.78	-0.5	0.62
Lignin:MSM	2.7E-05	0.05	500.7	1E-03	1	-0.02	0.07	499.68	-0.35	0.73
Random Effects	Variance	SD				Variance	SD			
Climate *(Intercept)*	0.22	0.47				1.36	1.17			
Residual	1.65	1.29				2.37	1.54			

Table S4-6. Functional traits (mean ± SD in parentheses) of the initial litter of 30 plant species used in a fully-reciprocal litter transplant and decomposition experiment in the Coastal Cordillera of Chile. O, species origin site; AD, Arid Dry; AF, Arid Fog; SA, Semi-Arid; ME, Mediterranean; TU, Temperate Upland; TL, Temperate Lowland; Fp, force to punch; SLA, specific leaf area; Carb, carbohydrates; Lig, lignin; Lip, lipids; Prot, proteins; C/N, carbon to nitrogen ratio; Lig/N, lignin to nitrogen ratio; Tan, tannins; Phen, total phenolics; Al, aluminium; Ca, calcium; Fe, iron; Mg, magnesium; Na, sodium; P, phosphorus. Carb, Lig, Lip, Prot and Phen data were obtained after a combination of samples and, therefore, have no SD. For Tan n=3, for all other traits n=5.

Species	O	Mean trait (SD)																
		Fp (N cm^{-2})	SLA (g cm^{-1})	Carb (%)	Lig (%)	Lip (%)	Prot (%)	C/N	Lig/N	Tan (mg g^{-1})	Phen (mg g^{-1})	Al (mg g^{-1})	Ca (mg g^{-1})	Fe (mg g^{-1})	Mg (mg g^{-1})	Mn (mg g^{-1})	Na (mg g^{-1})	P (mg g^{-1})
Cistanthe grandiflora	AD	10.47 (1.4)	68.98 (27)	41.31	12.46	31.77	11.05	25.63 (4.1)	9.33 (1.4)	NA	NA	0.31 (0.1)	14.96 (1.3)	0.23 (0.1)	22.32 (3.1)	0.39 (0.1)	72.97 (3.1)	0.54 (0.1)
Cristaria integerrima	AD	7.66 (1.7)	87.69 (16.7)	57.23	14.87	5.22	16.94	16.06 (4.2)	6.66 (2.1)	0.57 (1)	11.86	1.65 (0.1)	42.88 (3.2)	1.21 (0.1)	17.27 (0.7)	0.22 (0)	6.66 (1.7)	1.08 (0.1)
Frankenia chilensis	AD	2.52 (0.8)	39.48 (5.8)	39.07	32.25	16.10	11.22	24.76 (0.8)	27.49 (4)	47.63 (11.2)	123.11	0.84 (0.3)	75.17 (12.8)	0.71 (0.2)	20.79 (0.5)	0.8 (0.3)	19.51 (1.9)	0.44 (0)
Nolana mollis	AD	17.34 (4.2)	66.71 (6.4)	59.35	13.09	11.09	11.12	23.87 (6.5)	12.03 (3.1)	0 (0)	13.03	0.68 (0.4)	10.09 (2.7)	0.46 (0.2)	16.06 (3.6)	0.26 (0.1)	83.86 (7.2)	0.39 (0.1)
Tetragonia maritima	AD	14.09 (2.8)	74.13 (9.3)	60.67	13.71	11.39	14.23	21.89 (10)	9.9 (5.9)	0 (0)	21.69	0.47 (0.1)	14.6 (1.8)	0.55 (0.1)	23.46 (2.2)	0.38 (0.2)	62.49 (7.8)	0.46 (0.1)
Eulychnia breviflora	AF	333.3 (0)	9.9 (0.8)	93.54	5.14	0.00	1.10	210.63 (26.3)	23.54 (3.1)	1.3 (1.5)	3.49	0.19 (0)	0.7 (0.1)	0.37 (0.2)	0.31 (0.1)	0.04 (0)	0.45 (0.1)	0.01 (0)
Euphorbia lactiflua	AF	7.59 (0.5)	106.66 (16)	37.41	42.74	8.71	9.56	28.70 (0.2)	24.49 (1.7)	64.8 (13.3)	193.06	0.78 (0.2)	10.15 (1)	0.87 (0.6)	3.28 (0.3)	0.18 (0)	2.83 (0.7)	0.85 (0.1)

Nolana crassulifolia	AF	9.01 (2.4)	80.11 (9.3)	47.92	12.23	25.42	11.71	23.41 (2.9)	8.2 (0.8)	0 (0)	11.04	0.45 (0.1)	15.01 (2.4)	0.35 (0.1)	29.91 (4)	0.48 (0.1)	29.71 (12.2)	0.67 (0.2)
Nolana paradoxa	AF	4.39 (1.3)	203.8 (99.2)	57.19	14.33	12.75	15.73	17.70 (3.9)	9.52 (3)	0 (0)	13.38	0.59 (0.1)	23.73 (1.6)	0.47 (0.1)	10.8 (1.1)	0.15 (0)	105.63 (2.5)	0.57 (0.1)
Usnea sp.	AF	1.79 (0.5)	91.41 (15.9)	77.96	7.06	6.13	5.39	44.70 (4.1)	6.25 (0.9)	0 (0)	4.51	1.31 (0.2)	0.72 (0.1)	1.33 (0.2)	0.76 (0.1)	0.02 (0)	1.58 (0.5)	0.19 (0)
Cordia decandra	SA	15.01 (3.5)	43.16 (2.8)	49.73	27.63	6.10	10.48	26.01 (6.1)	20.81 (8.6)	16 (2.4)	34.52	1.52 (0.3)	67.47 (14.4)	1.15 (0.2)	8.04 (0.4)	0.11 (0)	3.35 (2.6)	0.96 (0.3)
Flourensia thurifera	SA	15.74 (2.5)	86.84 (8.5)	57.25	21.73	9.91	7.35	36.38 (9.5)	16.2 (3.3)	28.77 (5.2)	46.23	1.4 (0.2)	21.93 (2.2)	1.26 (0.2)	4.27 (0.9)	0.16 (0)	4.99 (0.7)	1.24 (0.2)
Gutierrezia resinosa	SA	11.49 (1)	70.06 (13.8)	44.75	23.04	23.16	6.86	41.11 (7)	18.86 (4.1)	34.53 (1.7)	43.67	2.18 (0.3)	19.68 (0.7)	1.78 (0.3)	4.98 (0.5)	0.24 (0.1)	7.24 (1.6)	1.26 (0.3)
Haplopappus decurrens	SA	56.14 (9.5)	66.76 (2.8)	63.41	20.30	8.40	4.27	61.10 (10.2)	23.48 (6.7)	0.77 (1.3)	44.71	0.69 (0.1)	15.21 (1)	0.62 (0)	2.26 (0.3)	0.15 (0)	10.96 (1)	0.68 (0.2)
Porlieria chilensis	SA	55.29 (15)	57.49 (4.1)	41.90	16.33	30.94	10.84	27 (5.4)	8.43 (1.8)	0.93 (0.2)	46.84	0.52 (0.2)	19.72 (4.3)	0.54 (0.2)	3.96 (0.7)	0.12 (0)	1.56 (0.6)	0.73 (0.1)
Acacia caven	ME	10.51 (0.7)	89.44 (16.8)	43.04	26.04	19.29	10.44	26.55 (3.7)	13.47 (1.9)	8.5 (0.4)	84.30	1.46 (0.5)	23.9 (3.8)	0.98 (0.3)	3.01 (0.5)	0.08 (0)	0.13 (0.1)	0.48 (0.1)
Aristeguietia salvia	ME	6.97 (0.6)	154.88 (28.6)	45.38	19.11	25.92	6.90	41.71 (9.1)	17.65 (5.4)	0 (0)	28.83	3.28 (0.8)	21.94 (2.3)	1.97 (0.4)	3.8 (0.3)	0.31 (0.1)	0.44 (0.2)	0.9 (0.1)
Colliguaja odorifera	ME	14.16 (1)	83.3 (12.6)	42.50	49.49	2.88	3.62	75.44 (13.4)	78.09 (11.3)	388.73 (61.4)	198.60	0.23 (0.1)	6.9 (2.3)	0.21 (0.1)	1.86 (0.3)	0.09 (0)	NA	0.51 (0.2)

Jubaea chilensis	ME	210.37 (32.7)	30.08 (6.7)	60.07	24.62	10.42	4.21	61.86 (5.9)	29.58 (4.4)	20.2 (7.6)	21.27	0.3 (0.1)	7.32 (0.7)	0.28 (0.1)	1.69 (0.2)	0.14 (0)	0.53 (0.2)	0.49 (0)
Lithraea caustica	ME	15.46 (1.1)	61.5 (4)	44.11	38.29	13.73	3.87	67.42 (25.9)	49.18 (20)	599.57 (126.2)	176.34	0.49 (0.2)	12.46 (3.1)	0.5 (0.2)	2.73 (0.5)	0.12 (0)	0.31 (0)	0.37 (0.2)
Araucaria araucana	TU	125.82 (31.7)	25.83 (5)	57.65	25.29	13.30	3.65	69.52 (7.1)	30.26 (2.1)	89.87 (9.5)	27.56	0.12 (0)	13.97 (1.5)	0.28 (0.1)	2.49 (0.4)	0.54 (0.2)	0.35 (0.1)	0.43 (0)
Festuca sp.	TU	83.54 (15)	55.04 (6.7)	75.50	20.56	0.57	1.54	156.75 (11.2)	68 (5.5)	0 (0)	4.46	0.67 (0.2)	1.5 (0.4)	0.66 (0.2)	0.4 (0.1)	0.18 (0.1)	0.48 (0.2)	0.25 (0)
Gaultheria mucronata	TU	61.19 (6.9)	58.8 (4)	45.49	31.12	19.25	4.14	67.29 (6.3)	37.11 (8.6)	113.07 (15.1)	83.23	0.37 (0)	7.46 (0.3)	0.31 (0.1)	2.28 (0.1)	1.03 (0.2)	0.32 (0.2)	0.61 (0)
Nothofagus dombeyi	TU	27.84 (2)	93.74 (6.9	43.07	19.90	23.86	13.17	22.27 (4.9)	7.7 (2.1)	68.8 (17.5)	115.48	0.56 (0.4)	4.69 (1.3)	0.59 (0.2)	1.12 (0.2)	1.43 (0.3)	1 (0.3)	0.84 (0.1)
Nothofagus obliqua	TU	6.90 (2.2	187.57 (54.1)	55.67	23.81	15.07	5.45	50.08 (8.4)	20.66 (4.2)	78.77 (9.2)	67.46	0.31 (0)	5.1 (0.3)	0.41 (0)	1.53 (0.1)	0.71 (0.2)	0.34 (0.1)	0.8 (0.2)
Drimys winteri	TL	20.71 (1.3)	122.55 (27.8)	44.12	32.04	19.46	3.98	71.79 (15.4)	44.34 (9.9)	101.77 (17)	26.53	0.57 (0.2)	5.64 (1.6)	0.38 (0.1)	3.01 (0.6)	0.8 (0.3)	0.48 (0.1)	0.35 (0.1)
Greigia sphacelata	TL	197.58 (40.3)	53.79 (9.7)	71.82	19.00	6.85	2.34	107.2 (8.4)	38.17 (3.4)	0 (0)	7.46	0.51 (0.1)	3.12 (1.2)	0.37 (0.1)	1.77 (0.4)	0.22 (0.1)	0.51 (0.1)	0.3 (0.1)
Laureliopsis philippiana	TL	18.60 (2.1)	179.34 (46.6)	56.74	21.19	12.70	9.36	32.58 (13.7)	14.24 (5.7)	5.4 (1.8)	34.96	1.12 (0.2)	14.15 (2)	0.63 (0.1)	5.12 (0.8)	0.54 (0.2)	1.33 (0.2)	0.8 (0.2)
Lophosoria quadripinnata	TL	20.45 (0.7)	115.6 (13.6)	53.60	29.73	10.56	6.10	43.68 (3.9)	26.16 (4.3)	0 (0)	11.33	1.22 (0.6)	4.78 (0.8)	0.82 (0.3)	1.67 (0.2)	0.36 (0.1)	0.51 (0.1)	0.59 (0.2)

Nothofagus obliqua	TL	11.42 (1.4)	247.26 (40.6)	50.94	27.53	12.43	9.10	32.94 (12.2)	17.56 (7.3)	75.27 (3.6)	44.57	0.61 (0.2)	6.28 (0.5)	0.5 (0.2)	2.12 (0.2)	0.67 (0.3)	0.14 (0)	0.51 (0.1)

Appendices Chapter 5

Table S5-1. Description of sites across the climatic gradient considered in this study. Meteorological data represent environmental conditions during the study period (June 2017-May 2019). AD = Arid-Dry, AF = Arid-Fog, SA =Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland, MAT = mean air temperature, AP = annual precipitation, MST = mean soil temperature, MSM = mean soil moisture.

Site (Climate)	Dominant vegetation	Latitude / Longitude	Elevation (m)	MAT (C°)	AP (mm)	MST (°C)	MSM (m^3/m^3)
AD	Very open desert scrub	-25.95 / -70.61	538	14.4*	13§	17.8	0.11
AF	Open coastal desert scrub	-26.01 / -70.61	798	10.5†	13§	15.4	0.14
SA	Semi-arid mediterranean scrub	-30.05 / -71.1	798	14.3‡	62‡	16.8	0.17
ME	Mediterranean sclerophyllous forest	-32.95 / -71.06	719	15.9‡	139‡	13.9	0.17
TU	Temperate upland rainforest with conifers	-38.01 / -73.01	1206	6.7*	2167*	7.1	0.29
TL	Temperate lowland rainforest	-38.01 / -73.18	426	11.9‡	814	9.5	0.35

* Übernickel, K. et al. 2020. Time series of meteorological station data in the EarthShape study areas in the Coastal Cordillera, Chile. GFZ Data Services. https://doi.org/10.5880/fidgeo.2020.043.

† Laboratory for Climatology and Remote Sensing, University of Marburg, Germany, personal communication, April 2020; data represent one year of records (April 2017-March 2018).

‡ INIA. (2020). Red Agrometeorológica del Instituto Nacional de Investigación Agropecuaria, Chile. Retrieved from: http://agromet.inia.cl/estaciones.php. Last accessed 2 October 2020.
Stations Gabriela Mistral, La Cruz and La Isla were used for SA, ME and TL, respectively.

§ Thompson, M. V., Palma, B., Knowles, J. T., & Holbrook, N. M. (2003). Multi-annual climate in Parque Nacional Pan de Azúcar, Atacama Desert, Chile. Revista Chilena de Historia Natural, 76(2), 235-254. http://dx.doi.org/10.4067/S0716-078X2003000200009. AP for AF is assumed to be the same as for AD.

Table S5-2. Species composition of litter mixtures used in this study, belonging to 6 climate zones. The results of t-tests (p-value) comparing the observed and predicted mass loss are shown for each decomposition period. n=3 except when differently indicated. Bold values represent p<0.05. (+) and (-) indicate that the observed mass loss of the mixture was significantly higher or lower than predicted, respectively.

Site	Species richness	Litter mixture species composition	p-value		
			Decomposition stage (months)		
			6	12	20
AD	2	*Nolana mollis* I.M. Johnst., *Tetragonia maritima* Barnéoud	0.59	0.24	0.06 (n=2)
AD	2	*N. mollis, Cristaria integerrima* Phil.	0.39	0.10	**0.02 (-)** (n=2)
AD	2	*N. mollis, Frankenia chilensis* C.Presl ex Schult. & Schult.f.	0.22	0.10	**0.05 (-)** (n=2)
AD	2	*C. integerrima, Nolana crassulifolia* Poepp.	0.33	**0.03 (-)**	0.58 (n=2)
AD	2	*C. integerrima, F. chilensis*	**<0.01 (-)**	**<0.01 (-)**	**<0.01 (-)** (n=2)
AD	2	*Nolana elegans* (Phil.) Reiche, *N. crassulifolia*	0.50	0.26	0.81 (n=2)
AD	2	*N. elegans, N. mollis*	0.87	0.49	0.38 (n=2)
AD	4	*F. chilensis, N. elegans, C. integerrima, T. maritima*	0.22	**<0.01 (-)**	0.09 (n=2)
AD	4	*C. integerrima, N. crassulifolia, N. mollis, T. maritima*	0.39	0.36	0.24 (n=2)
AD	6	*F. chilensis, N. elegans, C. integerrima, N. crassulifolia, N. mollis, T. maritima*	**<0.01 (-)**	**<0.01 (-)**	**0.04 (-)** (n=2)

AF	2	*Echinopsis deserticola* (Werderm.) Friedrich & G.D.Rowley, *N. crassulifolia*	0.15	0.77	0.15
AF	2	*E. deserticola, Nolana divaricata* I.M. Johnst.	0.06	0.08	0.84
AF	2	*E. deserticola, Usnea eulychnioides*	0.09 (n=2)	0.26	0.72
AF	2	*Euphorbia lactiflua* Phil., *N. crassulifolia*	0.57	0.98	0.53
AF	2	*E. lactiflua, N. paradoxa* Lindl.	0.79	0.48	0.76
AF	2	*E. lactiflua, Solanum remyanum* Phil.	0.81	0.41	0.13
AF	2	*N. divaricata, N. paradoxa*	**0.04 (-)**	**<0.01 (-)**	0.10 (n=2)
AF	2	*S. remyanum, U. eulychnioides*	0.41	0.36	0.76
AF	4	*S. remyanum, U. eulychnioides, N. divaricata, N. paradoxa*	0.51	**<0.01 (-)**	**<0.01 (-)**
AF	4	*E. deserticola, E. lactiflua, N. paradoxa, U. eulychnioides*	0.71	0.78	0.38
AF	6	*Eulychnia breviflora* Phil., *E. lactiflua, N. crassulifolia, N. paradoxa, N. divaricata, U. eulychnioides*	0.18	0.11	0.41
SA	2	*Haplopappus decurrens* J.Rémy, *Porlieria chilensis* I.M. Johnst.	0.78	0.66	0.79
SA	2	*H. decurrens, Cordia decandra* Hook. & Arn.	0.47	**0.04 (-)**	0.28
SA	2	*H. decurrens, Gutierrezia resinosa* (Hook. & Arn.) S.F.Blake	**<0.01 (+)**	0.16	0.50
SA	2	*H. decurrens, Senna cumingii* (Hook. & Arn.) H.S.Irwin & Barn	0.42	0.45	0.53
SA	2	*Flourensia thurifera* (Molina) DC., *C. decandra*	**0.03 (-)**	0.09	0.98 (n=2)
SA	2	*F. thurifera, S. cumingii*	0.27	0.25 (n=2)	0.27
SA	2	*G. resinosa, Baccharis paniculata* DC.	0.74	0.46	0.63
SA	2	*G. resinosa, S. cumingii*	0.17	0.43	0.69
SA	4	*G. resinosa, B. paniculata, F. thurifera, C. decandra*	0.07	0.34	0.18
SA	4	*S. cumingii, G. resinosa, F. thurifera, H. decurrens*	**0.05 (+)**	0.32	0.35
SA	6	*S. cumingii, B. paniculata, F. thurifera, C. decandra, P. chilensis, H. decurrens*	0.96	0.33	0.86
ME	2	*Jubaea chilensis* (Molina) Baill., *Kageneckia oblonga* Ruiz & Pav.	**0.04 (+)**	0.98	0.16

ME	2	*J. chilensis, Lithraea caustica* (Molina) Hook. & Arn.	0.56	0.94	0.43
ME	2	*J. chilensis, Retanilla trinervia* (Gillies & Hook.) Hook. & Arn.	0.20	**0.01 (+)**	0.31
ME	2	*Cryptocarya alba* (Molina) Looser, *K. oblonga*	0.60	0.96	0.98
ME	2	*C. alba, Colliguaja odorifera* Molina	0.62	0.27	0.86
ME	2	*C. alba, Podanthus mitiqui* Lindl.	0.23	**<0.01 (+)**	0.06
ME	2	*C. alba, Stellaria media* (L.) Vill.	0.90	0.75	0.78
ME	2	*L. caustica, Acacia caven* (Molina) Molina	0.32	0.34	0.50
ME	2	*Aristeguietia salvia* (Colla) R.M.King & H.Rob., *L. caustica*	0.30	0.27	0.21
ME	2	*A. salvia, R. trinervia*	0.27	0.29	0.45
ME	4	*R. trinervia, A. salvia, A. caven, S. media*	0.10	0.61	0.77
ME	4	*A. salvia, C. odorifera, Quillaja saponaria* Molina, J. chilensis	0.88	0.15	0.58
ME	1	*J. chilensis, C. alba, A. caven, C. odorifera, R. trinervia, Geranium robertianum* L.	0.60	0.06	0.50
TU	2	*Araucaria araucana* (Molina) K.Koch, *Gaultheria mucronata* (L.f.) Hook. & Arn.	0.91	0.58	0.80 (n=2)
TU	2	*Nothofagus dombeyi* (Mirb.) Oerst., *A. araucana*	0.53 (n=2)	0.83	0.82 (n=2)
TU	2	*A. araucana, Nothofagus obliqua* (Mirb.) Oerst.	0.70	0.99	NA
TU	2	*Festuca sp., Chusquea culeou* É.Desv.	0.11 (n=2)	0.15	0.88 (n=2)
TU	2	*Festuca sp., N. dombeyi*	0.09	0.21	0.76 (n=2)
TU	2	*Usnea sp., Festuca sp.*	0.70	0.11	**<0.01 (+)** (n=2)
TU	2	*N. dombeyi, N. obliqua*	0.09	0.20	0.44 (n=2)
TU	2	*N. dombeyi, Viola maculata* Cav.	0.48	**<0.01 (+)**	NA
TU	2	*Nothofagus antarctica* (G.Forst.) Oerst., *Usnea sp.*	0.66	0.49	0.21 (n=2)

TU	4	*Usnea sp., N. antarctica, N. obliqua, V. maculata*	0.34 (n=2)	0.18	0.06 (n=2)
TU	4	*N. obliqua, N. dombeyi, G. mucronata, A. araucana*	0.51	0.40	0.64 (n=2)
TU	6	*Usnea sp., N. obliqua, N. dombeyi, Festuca sp., G. mucronata, A. araucana*	0.43	0.25	0.98 (n=2)
TL	2	*Lapageria rosea* Ruiz & Pav., *Greigia sphacelata* (Ruiz & Pav.) Regel	0.31	0.38 (n=2)	NA
TL	2	*Laureliopsis philippiana* (Looser) Schodde, *G. sphacelata*	0.87	0.48 (n=2)	NA
TL	2	*N. obliqua, G. sphacelata*	0.64	0.16 (n=2)	NA
TL	2	*Aextoxicon punctatum* Ruiz & Pav., *L. rosea*	0.57	0.26 (n=2)	NA
TL	2	*A. punctatum, Gevuina avellana* Molina	0.07	0.57 (n=2)	NA
TL	2	*N. obliqua, A. punctatum*	0.21	0.66 (n=2)	NA
TL	2	*L. philippiana, Drimys winteri* J.R.Forst. & G.Forst.	0.59	0.75 (n=2)	NA
TL	2	*L. philippiana, N. obliqua*	0.09	0.90 (n=2)	NA
TL	4	*Chusquea quila* Kunth, L. philippiana, *Lophosoria quadripinnata* (J.F. Gmel.) C. Chr., D. winteri	0.62	0.70 (n=2)	NA
TL	4	*G. sphacelata, A. punctatum, L. quadripinnata, N. obliqua*	0.19	0.55 (n=2)	NA
TL	6	*G. sphacelata, A. punctatum, L. rosea, G. avellana, C. quila, N. obliqua*	**0.02 (-)** (n=2)	0.64 (n=2)	NA

Table S5-3. Variation in litter mixture effects in relation to either species richness or functional dispersion (FDis) of litter mixtures and six sites (i.e. climates) along an arid-to-temperate-humid gradient in Chile, as well as their interaction. Differences are based on linear least squares models for 68 litter mixtures decomposing after 20 months. FDis all includes all measured traits, while FDis+ and FDis– include only those traits considered to cause positive and negative diversity effects, respectively. DF = degrees of freedom, SS = sum of squares, MS = mean of squares, F = F-statistics, p = p-value. Values in bold represent significant differences under a critical α-value=0.05.

Factor	SS	DF	F	p
Richness	<0.01	1	0.01	0.94
Site	0.63	4	6.42	**<0.001**
Richness*Site	0.02	4	0.16	0.96
FDis all	0.01	1	0.59	0.44
Site	0.6	4	6.64	**<0.001**
FDis all*Site	0.23	4	2.49	**0.05**
FDis+	0.01	1	0.29	0.59
Site	0.61	4	6.58	**<0.001**
FDis+*Site	0.18	4	1.89	0.12
FDis–	0.03	1	1.51	0.22
Site	0.65	4	7.13	**<0.001**
FDis–*Site	0.21	4	2.29	0.06

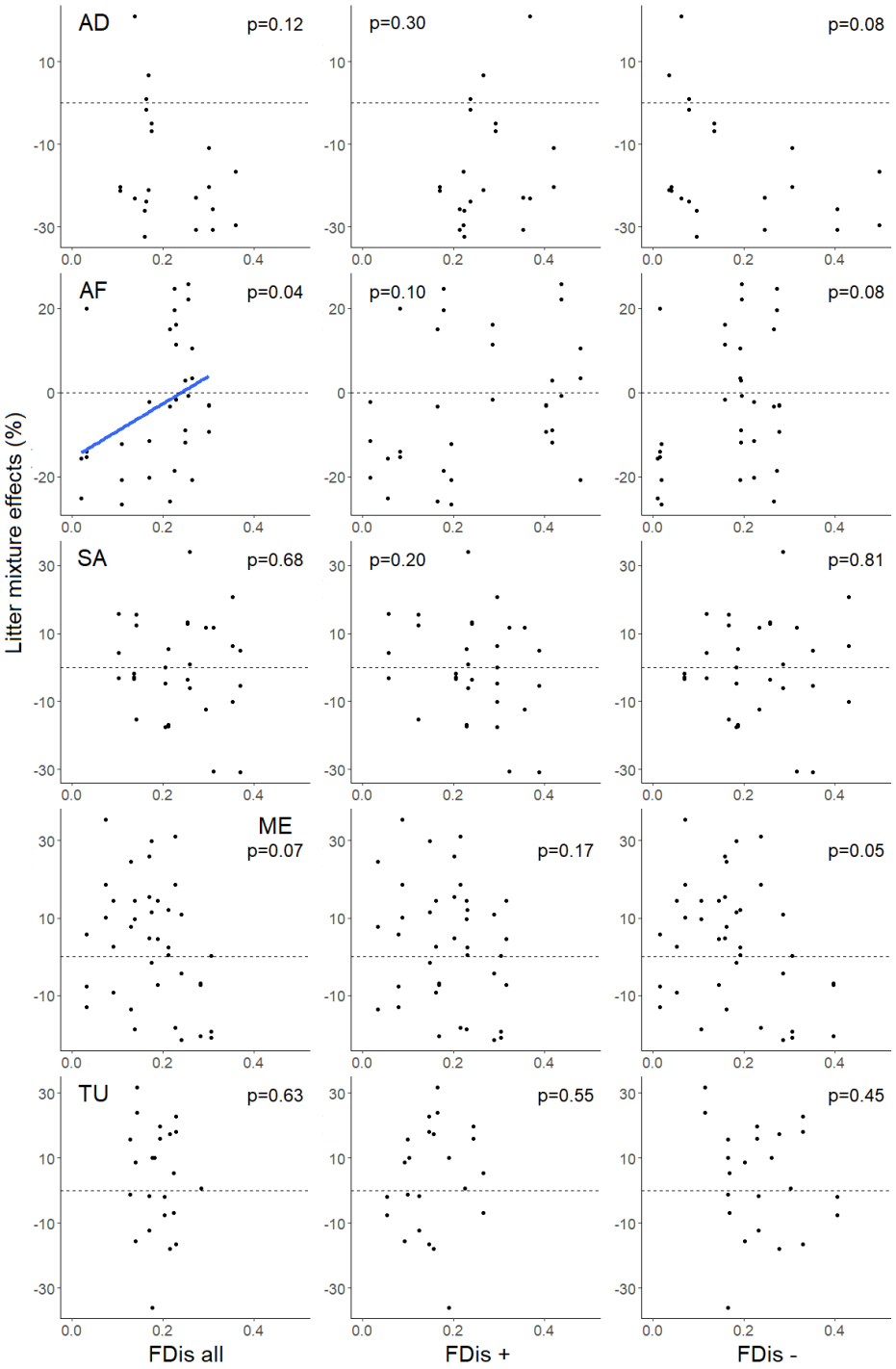

Figure S5-1. Pearson correlations between different FDis values (columns) and litter mixture effects (%) after 20 months of decomposition (colours) using different litter mixtures that decomposed along a climatic gradient in Chile (lines, AD = Arid-Dry, AF = Arid-Fog, SA = Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland). A solid line represents a significant correlation (α-value=0.05).

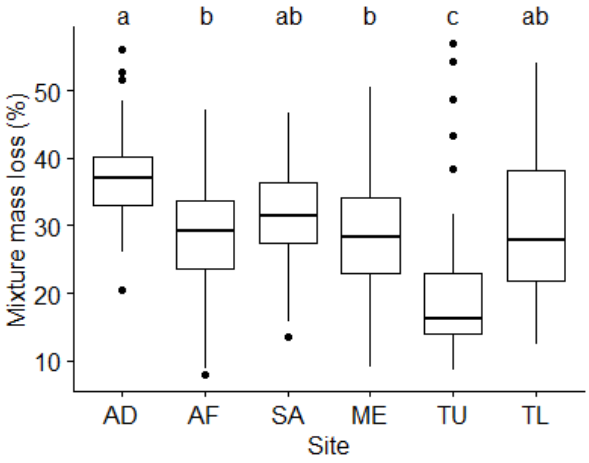

Figure S5-2. Observed litter mass loss (%) of mixtures after 6 months of decomposition at different study sites along a climatic gradient in Chile. AD = Arid-Dry, AF = Arid-Fog, SA =Semi-Arid, ME = Mediterranean, TU = Temperate Upland, TL = Temperate Lowland. Different letters represent different groups after a Tukey HSD test at α-value=0.05, as an ANOVA yielded significant variation among sites ($F_{5, 212} = 9.46$, $p < 0.01$).