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7

8 **Space cannot substitute for time – an integrated experimental assessment of climate-change effects on**
9 **litter decomposition**

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34

35 Abstract

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

48

49 Introduction

50 Climate is changing alarmingly quick with possibly dramatic consequences for single species to global
51 biogeochemical cycles (IPCC 2014; Ripple *et al.* 2020). The global carbon cycle is strongly affected by both
52 anthropogenic and natural processes. Litter decomposition, for example, releases roughly the same
53 amount of CO₂ into the atmosphere as anthropogenic CO₂ production (Raich & Schlesinger 1992;
54 Couteaux *et al.* 1995), and is therefore highly important for the understanding of global carbon and
55 nutrient cycles (Berg & McLaugherty 2003). However, since biological processes themselves are affected
56 by climate change directly and indirectly (Cornelissen *et al.* 2007; Cornwell *et al.* 2008; Suding *et al.*
57 2008), modeling the carbon cycle is highly complex and uncertain (Ostle *et al.* 2009). Direct effects have
58 been studied a lot, mostly with respect to precipitation (or humidity) and temperature (Couteaux *et al.*
59 1995). These studies reveal unequivocally that in wet (Aerts 1997; Yahdjian *et al.* 2006; Suseela &
60 Tharayil 2018) and warm climates (Couteaux *et al.* 1995) decomposition is faster than in dry and cold
61 environments (Stark & Firestone 1995; Chapin III *et al.* 2011; Baker *et al.* 2018). Indirect effects of climate
62 on decomposition operate via the vegetation, e.g. via growth rates, litter quality, or plant species
63 composition (Cornelissen *et al.* 2007; Cornwell *et al.* 2008; Suseela & Tharayil 2018).

64 An important indirect effect of climate on decomposition is via plant litter quality, i.e. the combination of
65 chemical (holocellulose:lignin ratio, carbon (C)/nitrogen (N) content, and phosphorus (P) concentration;
66 Cornwell *et al.*, 2008; Graça and Poquet, 2014) and physiognomic traits (leaf dry matter content, specific
67 leaf area (SLA), and leaf toughness; Meentemeyer, 1978; Couteaux, Bottner and Berg, 1995; Hobbie,
68 1996; Aerts, 1997; Cornwell *et al.*, 2008; Andresen *et al.*, 2010; Melillo, Aber and Muratore, 2014).
69 Because many of these leaf traits may also represent specific adaptations to climatic conditions, they
70 strongly vary among different climates (Graça & Poquet 2014). For example, small, tough leaves with
71 thick cuticulae represent well-known adaptations to drought and are thus common in plants inhabiting

72 arid environments (Anonymous 1932; Cunningham *et al.* 1999; Wright *et al.* 2004). Therefore, plants in
73 dryclimates usually have a lower litter quality (Wright *et al.* 2004; Graça & Poquet 2014; Pugnaire *et al.*
74 2019; Xu *et al.* 2020) which inhibits break down by the decomposer community (Pérez-Harguindeguy *et*
75 *al.* 2000; Zhang *et al.* 2008). *Vice-versa*, in wetter climates, plant species often exhibit 'soft' leaves, low C/
76 N-ratio, and high SLA (Wright *et al.* 2004) because costly adaptations to drought are not needed,
77 however, the vegetation is denser, and light is scarcer, which results in leaves with high SLA to increase
78 photosynthetic ability (Kunstler *et al.* 2016; Gruntman *et al.* 2017). Overall, it has been repeatedly
79 concluded that along climatic gradients from dry to wet conditions, leaf traits should change, from small,
80 spiny, tough leaves with low SLA and low litter quality with high lignin and carbon content and low
81 phosphorus content to soft leaves with opposite traits (Wright *et al.* 2001, 2004). This suggests that
82 direct and indirect climate effects on litter decomposition amplify each other, i.e. decomposition will be
83 slower in dry climates due to lower litter quality (Aerts 1997) and to less precipitation (Austin & Vitousek
84 2000).

85 However, while these assumptions are backed up by many previous studies (Aerts 1997; Zhang *et al.*
86 2008) exceptions to this rule have been found, too (Pérez-Harguindeguy *et al.* 2007). This is because
87 plant litter quality is also determined by factors that operate independently of climate, like
88 biogeographic history, biotic interactions, nutrient availability, or disturbance (Woodward & Diament
89 1991; Chapman *et al.* 2003; Wiens & Donoghue 2004; Chapman 2006; Bhalawe *et al.* 2012; Zhu *et al.*
90 2016). Despite these exceptions, dynamic vegetation models (e.g. LPJ, MC1, HYBRID, ORCHIDEE and
91 TRIFFID) or terrestrial carbon cycle models (e.g. ED, CTEM), and their derivatives assume that conditions
92 in climatically similar ecosystems have selected for plants with similar traits (and therefore similar
93 decomposition) and that they therefore will respond similarly to climate change. These models have
94 commonly assumed increasing litter decomposition rates with wetter climates (Patton 1996; Friend *et al.*
95 1997; Cox 2001; Smith 2001). If not backed up by solid evidence, the generalization used in the models
96 can cause serious dissimilarities between the modeled and the real climate-change effects, especially as

97 decomposition accounts for approximately half of the CO₂ release into the atmosphere (Raich &
98 Schlesinger 1992; Couteaux *et al.* 1995).

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

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

120 **Experiment-for-time: reciprocal translocations along gradients.** Reciprocal translocations along climate
121 gradients (litter collected at each site is decomposed at each site of a climate gradient) combine common

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

133 **Experiment-for-time approach: *in situ* climate manipulations.** Field experiments can manipulate the
134 climate factor of interest (e.g. precipitation, temperature) while the response of the ecological factor
135 (e.g. decomposition) is studied. *In situ* climate experiments of litter decomposition are not very common,
136 and have studied the effect of manipulated precipitation (e.g. Yahdjian, Sala and Austin, 2006; Andresen
137 *et al.*, 2010; Zhou *et al.*, 2018) or temperature (e.g. Andresen *et al.*, 2010). Most of these studies found
138 that reduced precipitation significantly reduced litter decomposition (Yahdjian & Sala 2002; Brandt *et al.*
139 2007; Andresen *et al.* 2010; Santonja *et al.* 2017; Zheng *et al.* 2017; Zhou *et al.* 2018), and due to the
140 experimental approach, these relationships are causal. However, their mechanistic insight comes at a
141 cost. As they usually manipulate only one factor, may have side effects (Leuzinger *et al.* 2011; Kreyling *et*
142 *al.* 2017) and be less 'realistic' than observations. They are also costly and often restricted to one site.
143 Furthermore, it is unclear whether short-term mechanistic relationships between independent (e.g.
144 climate) and dependent (e.g. ecosystem process) variables can be extrapolated to longer time scales.
145 Tielbörger *et al.* (2014) developed an approach that combines the best of all the above-mentioned
146 approaches and that directly tests for the validity of the space-for-time approach. This approach requires

147 a multi-site setup along a climate gradient. The rationale of the approach is that by manipulating climate
148 at a given site and including an adjacent site with similar specific climatic conditions as within the
149 manipulation, the gradient can be used directly as a hypothesis for the direction and magnitude of
150 change within the climate manipulations. Thus, this approach has two controls, an *in situ* control where
151 all environmental conditions, except for the manipulated one, are similar, and a spatial control where
152 specific climatic conditions are similar. By applying this approach to an aridity gradient in Israel,
153 Tielbörger et al. (2014) showed a large mismatch between space (plant communities differed largely
154 among sites) and experimental drought (no effect in species composition, abundance or productivity).
155 Here, we expanded this approach with reciprocal transplants to study climate change effects on litter
156 decomposition along an even more extreme climate gradient. We combined the space-for-time
157 observations with a) a fully reciprocal translocation of native and a standard litter, b) a small-scale
158 humidity gradient by comparing drier with wetter expositions, and c) *in situ* drought treatments,
159 simulating precipitation conditions of the adjacent drier site. This allowed us to directly and
160 experimentally test for the applicability of space-for-time approaches in carbon cycle studies, and to
161 separate the effects of climate alone from the indirect climatic effects on litter quality.
162 We used a prominent climate gradient ranging from extremely arid to wet temperate conditions in the
163 Chilean coastal cordillera. Because litter decomposition correlates very weakly to air temperature above
164 6.7 °C (Bradford *et al.* 2016), and because regional climate scenarios predict a decrease in precipitation
165 by approximately 10% (IPCC 2014) we focused on the influence of drought on litter decomposition. Our
166 gradient encompasses a 100-fold difference in precipitation, ensuring a large effect size.
167 We tested the overarching hypothesis that space can substitute for time. Namely, we assumed that *in*
168 *situ* litter decomposition accelerates from arid to humid climates due to a) climatic conditions (i.e. more
169 humidity) and b) higher litter quality at wetter sites. We expected that the higher decomposition under
170 wetter conditions would be reflected in the decomposition of translocated litter among sites, between
171 expositions within sites, as well as in the experimentally manipulated plots.

172 Materials and methods

173 Study sites

174 Our study was conducted in Chile at four sites along a large climate gradient that runs from the arid
175 Atacama Desert to the humid temperate forest (26° - 38° S, Error: Reference source not found, Figure 1).
176 The sites were selected to be within the same geographical unit (the Chilean coastal cordillera) and share
177 a common granitoid bedrock (Oeser *et al.* 2018). Thus, the main difference between the four sites is the
178 climate, with increasing precipitation from north to south. With the exception of the (cooler) temperate
179 site, average temperatures were relatively similar, whereas annual precipitation (AP) increased along the
180 gradient and differed approx. 100-fold between the wettest (2158 mm y⁻¹) and the driest (22 mm y⁻¹) site
181 (Figure 1a, Übernickel, K., Ehlers, T. A., Ershadi, M. R., Paulino, L., Fuentes Espoz, J. P., Maldonado, A.,
182 Oses-Pedraza, R., von Blanckenburg, F. (2020) 'Time series of meteorological station data in the
183 EarthShape study areas of the Coastal Cordillera, Chile', GFZ Data Services.
184 <https://doi.org/10.5880/fidgeo.2020.043>., for additional information see: Bernhard *et al.*, 2018; Oeser *et*
185 *al.*, 2018).

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

195 species), bamboo, shrubs, grasses and annual herbs (Bernhard et al., 2018; Oeser et al., 2018;
196 Wolodarsky-Franke & Diaz Herrera, 2011).

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

201 **2) Drought manipulation with rainout shelters.** We installed drought treatments (according to Yahdjian
202 and Sala, 2002) on wet and the dry expositions at the semi-arid and mediterranean sites. At the semi-
203 arid site, where plants were small, the shelters covered representative sections of the overall vegetation.
204 At the mediterranean site, the shelters were erected between large trees, but included small shrubs and
205 herbaceous vegetation.

206 The treatment reduced the precipitation by 75%, approximating both the mean annual precipitation of
207 the adjacent drier site (arid and semi-arid, respectively. Figure 1b) and scenarios for future extreme
208 droughts events in the region (Quintana and Aceituno, 2012; Garreaud *et al.*, 2017). Continuous soil
209 moisture measurements indicated that the treatments were highly effective in reducing soil moisture
210 (i.e. 15-35%) and that these drought conditions were similar to soil moisture at the adjacent drier site
211 (Supplementary data: Figure MM1, Table MM2). Our data also showed very small side-effects of the
212 shelters on soil temperature (on average +0.1°C compared to controls).

213 **3) Species selection and litter bag preparation.** At each site, we selected five abundant and
214 representative native species . Senescent leaves, attached to the plant to minimize contamination with
215 on-site soil microbes (Stone 1987), were collected during the dry season (December 2016 - January 2017,
216 Error: Reference source not found). For evergreen species, green leaves were collected. In addition,
217 Lipton® green tea (*Camellia sinensis*, EAN Nr.: 8 722700 055525, from here on “tea”) was used as a
218 standard litter (Keuskamp *et al.* 2013; Djukic *et al.* 2018) to help separating litter origin and climate
219 effects. The collected litter and tea bags were dried to a stable weight for 72 hours at 40°C, and

220 depending on leaf size, leaf weight and availability of dry litter 1, 2 or 2.5 g (± 0.005 g the exact initial
221 weight was recorded) were bagged in 2 mm polyester mesh. When leaves were very small, brittle, or
222 had the tendency to pass through the mesh, an additional layer of 2 mm mesh was used. No significant
223 differences in decomposition were detected when both types of bags were used (Supplementary data:
224 Table MM4). Litterbags and teabags were placed at ground level in the field between 11 and 29 May
225 2017, just before the first rains of the season (May – August).

226 **4) Reciprocal translocations along the gradient (between and within sites).** Litterbags of all species
227 were fully reciprocally distributed along the climate gradient and placed in the independent plots on dry
228 and wet exposition (20 species * 3 replicates * 3 retrievals * 3 plots * 2 expositions * 4 sites), together
229 with two tea bags per plot (2 replicates * 3 retrievals * 3 plots * 2 expositions * 4 sites). Litter and tea
230 bags were collected at three points in time to account for the temporal dynamics of decomposition: after
231 3, 6, and 12 months (93 ± 1 ; 195 ± 4 ; 366 ± 5 days), respectively. Due to a snow event at the temperate site,
232 the 3-month batch was retrieved after 9 months (280.5 ± 0.5 days). Overall, 4320 litterbags and 144 tea
233 bags were used in the reciprocal translocations.

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

240 All retrieved bags were dried at 40°C for at least 72 hours until stable weight, after which the remaining
241 litter was weighed. Mass loss was calculated as a proportion of the initial weight: $(\text{dry weight}_{\text{initial}} - \text{dry}$
242 $\text{weight}_{\text{end}}) / \text{dry weight}_{\text{initial}}$.

243 **6) Litter quality.** Total carbon (C_t , detection limit 0.1 weight percent (wt %)) and nitrogen (N_t , detection
244 limit 0.03 (wt %)) contents of homogenized (planetary ball mill, Pulverisette 5, Fritsch) initial litter

245 samples (i.e. before decomposition) were analyzed with an Element Analyzer (Vario EL III, Elementar
246 Analysensysteme GmbH). The outcomes were used to calculate C/N mass ratios of the respective litter as
247 proxy for litter quality (i.e., low values are expected to decompose fast, high values slow). For details
248 regarding detection limits and quality control see table MM5 in the supplementary data.

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

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

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

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

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

269 All statistical analyses were performed in JMP 14.

270 Results

271 As the qualitative patterns of all retrievals were similar, we only show the decomposition after 12
272 months. For remaining results see supplementary material (Figures R1-4, Tables R1-3).

273 **Space-for-time: observations along the gradient (decomposition of local litter at home).** After six
274 months, litter decomposition rates of local litter, “at home”, decreased with increasing precipitation
275 ($p=0.02$, supplementary data: Table R1 (space-for-time) and Figure R1a, c and e). After 12 months, this
276 pattern remained, but was not statistically significant anymore ($p=0.11$, Figure 2. Mean \pm SE mass loss
277 (i.e. ratio between mass loss and initial weight, in proportion) of 20 species from 4 climates (Origin,
278 different colors) along a climate gradient in Chile after 12 months shown in each climate (AR=arid,
279 SA=semi-arid, ME=mediterranean, TE=temperate). The left panel (a) represent litter mass loss of local
280 litter at the home site (i.e. space-for-time). Significant differences ($p<0.05$) of litter decomposing at home
281 were not found, as indicated above the bars ($n=3$). The right panel (b) represents the litter mass loss of
282 reciprocally translocated litter (i.e. experiment for time) and is broken up into bars from each origin
283 (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing precipitation from left to
284 right. Significant differences in mass loss ($p<0.05$) between climates are indicated above the bars in
285 underlined italic letters ($n=3$), a, Table : space-for-time).

286 **Space-for-time: litter quality.** Analyses of carbon and nitrogen concentrations showed that average
287 initial litter quality gradually decreased, i.e. increasing C/N ratios (from 31 to 98), from the driest to the
288 wettest site ($p<0.05$, Figure 2;

289 **Experiment-for-time: reciprocal translocations along the gradient (decomposition among climates).**
290 The mass loss of litter from the 20 species and that of tea increased markedly with increasing
291 precipitation ($p<0.01$, Figure 2. Mean \pm SE mass loss (i.e. ratio between mass loss and initial weight, in
292 proportion) of 20 species from 4 climates (Origin, different colors) along a climate gradient in Chile after
293 12 months shown in each climate (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate). The left

294 panel (a) represent litter mass loss of local litter at the home site (i.e. space-for-time). Significant
295 differences ($p < 0.05$) of litter decomposing at home were not found, as indicated above the bars ($n=3$).
296 The right panel (b) represents the litter mass loss of reciprocally translocated litter (i.e. experiment for
297 time) and is broken up into bars from each origin (AR=arid, SA=semi-arid, ME=mediterranean,
298 TE=temperate), with increasing precipitation from left to right. Significant differences in mass loss
299 ($p < 0.05$) between climates are indicated above the bars in underlined italic letters ($n=3$), (b) and 4; Table
300). The mass loss in the temperate site was twice as high as in the arid site. This pattern was confirmed for
301 all litter origins (Figure 2. Mean \pm SE mass loss (i.e. ratio between mass loss and initial weight, in
302 proportion) of 20 species from 4 climates (Origin, different colors) along a climate gradient in Chile after
303 12 months shown in each climate (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate). The left
304 panel (a) represent litter mass loss of local litter at the home site (i.e. space-for-time). Significant
305 differences ($p < 0.05$) of litter decomposing at home were not found, as indicated above the bars ($n=3$).
306 The right panel (b) represents the litter mass loss of reciprocally translocated litter (i.e. experiment for
307 time) and is broken up into bars from each origin (AR=arid, SA=semi-arid, ME=mediterranean,
308 TE=temperate), with increasing precipitation from left to right. Significant differences in mass loss
309 ($p < 0.05$) between climates are indicated above the bars in underlined italic letters ($n=3$), (b): bars with
310 similar color; Table). Furthermore, the litter from the two driest sites decomposed faster than the litter
311 from the temperate site in each site, and the litter from the mediterranean climate always fell in
312 between.

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

311 **Experiment-for-time: *in situ* climate manipulations (decomposition in drought treatments).**
312 Decomposition of local litter (five local species at each of the sites with drought treatment) and tea was
313 markedly lower in drought plots compared to controls ($p < 0.01$). With one exception (dry exposition at

314 the semi-arid site), these differences were significant. For tea, the drought treatment decreased mass
315 loss significantly only on the dry exposition (semi-arid $p < 0.01$, mediterranean $p < 0.05$; Error: Reference
316 source not found; Table).

317 Discussion

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

324 **Space-for-time: observations along the gradient.** Decomposition of local litter decreased with increasing
325 precipitation, and these differences decreased with increasing decomposition time. This is surprising,
326 given that climate has been suggested to be the main predictor of litter decomposition among
327 ecosystems, with wetter climates promoting faster decomposition (Fan *et al.*, 2014; Aerts, 1997). With
328 precipitation being the most important predictor (Walse *et al.* 1998; Austin 2002), and a 100-fold
329 difference in precipitation between the arid and the temperate site, we expected a much larger mass
330 loss of the local species at the wetter than at the drier site. In our arid site, the lack of moisture could
331 partially have been compensated by photo-degradation, which can account for up to 50% of carbon loss
332 in arid and semi-arid ecosystems (Montaña *et al.* 1988; Moorhead & Reynolds 1989; Steinberger *et al.*
333 1990; Austin & Vivanco 2006; Day *et al.* 2018), thus increasing litter decomposition. However, Canessa *et*
334 *al.* (2021), who worked at the same sites, showed that the effect photodecomposition in the arid sites
335 was marginal. Also, this phenomenon cannot explain the lowest decomposition rates of local litter at the
336 wettest site. There, lower temperatures could play a role (Couteaux *et al.* 1995; Wu *et al.* 2020), but in

337 subtropical and temperate areas (with temperatures $> 6.7^{\circ}\text{C}$) like our study sites, decomposition does
338 not strongly depend on temperature (Bradford et al. 2016). These explanations can also only explain
339 differences between the most extreme sites, but not the consistent trend from dry to wet sites.

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

351 Initial nutrient composition is important for the decomposition rate (Couteaux, Bottner and Berg, 1995;
352 Andresen et al., 2010; Manzoni, 2008), and can be linked with climate (Chen et al. 2013; Graça & Poquet
353 2014). It is commonly thought that species from temperate, humid climates produce high quality litter
354 (but see Santiago and Mulkey, 2005) and decompose quickly (Aerts 1997), while species from arid
355 climates produce low quality litter (tough and waxy leaves; Anonymous, 1932), as a response to drought
356 (Schulze et al. 1998; Niinemets 2001; Wright et al. 2001, 2004; Graça & Poquet 2014; Pugnaire et al.
357 2019). This was confirmed in several studies showing that local litter in humid sites decomposed quicker
358 than local litter in dry sites (Meentemeyer 1978; Berg et al. 1993; Couteaux et al. 1995; Aerts 1997; Fan
359 et al. 2014). Our counterintuitive findings could be explained by e.g. biogeographic, phylogenetic history
360 and biotic interactions, which all influence litter quality and therefore local litter decomposition
361 (Woodward & Diament 1991; Chapman et al. 2003; Wiens & Donoghue 2004; Chapman 2006; Bhalawe

362 *et al.* 2012; Zhu *et al.* 2016). Also, along our gradient the soil pH decreases with increasing precipitation
363 (Bernhard *et al.*, 2018) and a decrease in soil pH increases leaf dry matter content (Laughlin *et al.* 2015),
364 which negatively affects litter decomposition (Cortez *et al.* 2007). Additionally, the succulent and soft-
365 leaved species at the arid site reflects an alternative adaptation to aridity and enables persistence
366 through highly irregular arid conditions (Griffiths & Males 2017). Overall, while litter quality probably
367 explains the unexpected findings of local litter decomposition, it is still remarkable that this biotic factor
368 could override a climate gradient with a 100-fold difference in precipitation. The experimental
369 approaches enabled us to separate these unexpected biotic effects from the direct effect of
370 precipitation.

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

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

391 **Experiment-for time - *in situ* climate manipulations.** Our experimental drought experiments confirmed
392 the causal relationship between litter decomposition and moisture. Namely, decomposition in the
393 drought treatment was markedly lower in drought plots compared to controls. This corresponds with
394 previous studies that looked at litter decomposition under experimental drought (e.g. Andresen et al.,
395 2010; Jentsch et al., 2011; Wu et al., 2020; L. Yahdjian et al., 2006). The results of our drought
396 experiment, designed to manipulate precipitation, confirmed the results from the reciprocal
397 translocation experiment: decomposition was slower under the drought treatments and similar to the
398 decomposition in the adjacent drier site. This indicates that, despite the fact that decreasing litter quality
399 decreases decomposition of local litter decreased towards the wetter sites, precipitation was still a main
400 driver of decomposition rates along our gradient.

401 The combination of a fully reciprocal translocation experiment with litter of 20 common species from
402 four distinct ecosystems and one standard litter, using dry and wet exposition within the sites, with an
403 additional on-site drought treatment in two ecosystems, is a comprehensive approach to study the
404 influence of climate, and single climatic factors (i.e. precipitation or soil moisture), on litter
405 decomposition. Only with this approach, combining space-for-time observations with experiments and
406 manipulations, we could disentangle the indirect climate effects from direct effects of precipitation. We
407 found a clear causal and positive relationship between precipitation and decomposition, but this pattern
408 disappeared when we used the space-for-time approach only. Therefore, we suggest that space-for-time
409 observations in litter decomposition should be treated with caution, as has been suggested for plant
410 traits, species distributions or bioclimatic envelope models (e.g. Sandel *et al.* 2010; Sternberg *et al.* 2011;
411 Plischoff *et al.* 2012; Tielbörger *et al.* 2014), especially when used to predict responses to climate change.

412 This conclusion is important because the space-for-time assumption is also fundamental for global
413 vegetation models that attempt to simulate the carbon cycle (Scheiter *et al.* 2013) and which could be
414 biased for a large fraction of South American vegetation. We thus strongly advocate an experimental
415 approach, combined with 'space' or 'time', to study climate change effects on biogeochemical processes
416 and the global carbon and nutrient cycle and separate biotic effects from climate-only effects.

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677 **Tables**

678 *Table 1. Results of linear mixed models (Least Squares) on mass loss of litter decomposing at home and*
 679 *initial C/N ratio (space-for-time, local litter, 5 species per site) for the effect of origin, and for litter*
 680 *translocated to all sites (experiment-for-time, native litter, 20 species per site and standard litter (green*
 681 *tea)) after 12 months for the effects of origin (only for litter), location, exposition and their interactions,*
 682 *including species, plot and their interaction as random factors when applicable. Significant results are in*
 683 *bold.*

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

685

686 *Table 2. Results of linear mixed models on decomposition fraction of local litter (5 species) and standard*687 *litter (green tea) after 12 months for the effects of treatment (drought vs. control), location (semi-arid vs.*688 *mediterranean), exposition (dry vs. wet) and all their interactions, including species, plot and their*689 *interaction as random factors. Significant results are in bold.*

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

690

691

692 Figures

693 *Figure 1. Climate gradient and experimental drought setup. Shown is a land-cover map showing the study*
694 *site locations (a: U.S. Central Intelligence Agency, 1972), and the experimental setup of the drought*
695 *experiment (b). The rainout shelters reduce the percentage of rain which reaches the plot under the*
696 *rainout shelter (dark arrow) by 75%, which mimics the average annual precipitation that falls in the*
697 *adjacent drier site (light arrows). The drought treatment therefore has two controls: one at the same site,*
698 *where climate is the same, and one at the drier adjacent site, where precipitation is similar as under the*
699 *rainout shelter, but other aspects of the climate and environment are different. The setup included three*
700 *replicate plots (three control and three experimental drought treatments) at both exposures (dry and*
701 *wet) at each climate (semi-arid and mediterranean).*

702

703 *Figure 2. Mean \pm SE mass loss (i.e. ratio between mass loss and initial weight, in proportion) of 20 species*
704 *from 4 climates (Origin, different colors) along a climate gradient in Chile after 12 months shown in each*
705 *climate (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate). The left panel (a) represent litter*
706 *mass loss of local litter at the home site (i.e. space-for-time). Significant differences ($p < 0.05$) of litter*
707 *decomposing at home were not found, as indicated above the bars ($n=3$). The right panel (b) represents*
708 *the litter mass loss of reciprocally translocated litter (i.e. experiment for time) and is broken up into bars*
709 *from each origin (AR=arid, SA=semi-arid, ME=mediterranean, TE=temperate), with increasing*
710 *precipitation from left to right. Significant differences in mass loss ($p < 0.05$) between climates are*
711 *indicated above the bars in underlined italic letters ($n=3$), significant differences between origins of litter*
712 *are indicated directly above the bars ($n=3$) (NOTE: letters of significance can only be compared within*
713 *climates, not between). See Table for corresponding statistics.*

714

715 *Figure 2. Mean \pm SE C/N of the initial litter (five species per site, n=5) per origin (AR=arid, SA=semi-arid,*
716 *ME=mediterranean, TE=temperate). Significant differences in initial C/N ratio ($p<0.05$) between the*
717 *origins of the litter are indicated above the bars in letters. See R5 for corresponding statistics and C and N*
718 *values.*

719
720 *Figure 3. Mean \pm SE mass loss (i.e. ratio between mass loss and initial weight) along a climate gradient in*
721 *Chile after 12 months shown in each climate (Location of decomposition, AR=arid, SA=semi-arid,*
722 *ME=mediterranean, TE=temperate), with increasing precipitation from left to right for all native litter*
723 *combined (a) and standard litter (Lipton green tea, b). Dark bars show the mass loss from the reciprocal*
724 *translocation of 20 species (n=3), or tea (n=2) along the climate gradient (significant differences in*
725 *uppercase) at both expositions (dry vs wet: significant differences, $p<0.05$, in lowercase). Lighter bars in*
726 *the SA and ME climate show the mass loss of the 5 local species (n=3) and tea (n=2) in the drought*
727 *experiment (significant differences between drought and control plots, $p<0.05$, in italic. NOTE: letters of*
728 *significance can only be compared within climates, not between). See Table 2 for corresponding statistics.*