



# UNIVERSITÀ DI PARMA

## ARCHIVIO DELLA RICERCA

University of Parma Research Repository

Litter decomposition: effects of temperature driven by soil moisture and vegetation type

This is the peer reviewed version of the following article:

*Original*

Litter decomposition: effects of temperature driven by soil moisture and vegetation type / Petraglia, A.; Cacciatori, C.; Chelli, S.; Fenu, G.; Calderisi, G.; Gargano, D.; Abeli, T.; Orsenigo, S.; Carbognani, M.. - In: PLANT AND SOIL. - ISSN 0032-079X. - 435:1-2(2019), pp. 187-200. [10.1007/s11104-018-3889-x]

*Availability:*

This version is available at: 11381/2866937 since: 2021-11-01T09:42:28Z

*Publisher:*

Springer International Publishing

*Published*

DOI:10.1007/s11104-018-3889-x

*Terms of use:*

Anyone can freely access the full text of works made available as "Open Access". Works made available

*Publisher copyright*

note finali coverpage

(Article begins on next page)

02 May 2026

## Metadata of the article that will be visualized in OnlineFirst

Article Title	<b>Litter decomposition: effects of temperature driven by soil moisture and vegetation type</b>	
Article Sub-Title		
Article Copyright Year	<b>Springer Nature Switzerland AG 2018 (This will be the copyright line in the final PDF)</b>	
Journal Name	<b>Plant and Soil</b>	
Author	Family Name	<b>Petraglia</b>
	Particle	
	Given Name	<b>Alessandro</b>
	Suffix	
	Division	Department of Chemistry, Life Sciences and Environmental Sustainability
	Organization	University of Parma
Address	Parco Area delle Scienze 11/A, I-43124 Parma, Italy	
Author	Family Name	<b>Cacciatori</b>
	Particle	
	Given Name	<b>Cecilia</b>
	Suffix	
	Division	Department of Chemistry, Life Sciences and Environmental Sustainability
	Organization	University of Parma
Address	Parco Area delle Scienze 11/A, I-43124 Parma, Italy	
Author	Family Name	<b>Chelli</b>
	Particle	
	Given Name	<b>Stefano</b>
	Suffix	
	Division	School of Biosciences and Veterinary Medicine, Plant Diversity and Ecosystems Management Unit
	Organization	University of Camerino
Address	Camerino, Italy	
Author	Family Name	<b>Fenu</b>
	Particle	
	Given Name	<b>Giuseppe</b>
	Suffix	
	Division	Department of Life and Environmental Sciences
	Organization	University of Cagliari
Address	Cagliari, Italy	
Author	Family Name	<b>Calderisi</b>
	Particle	
	Given Name	<b>Giulia</b>

	Suffix	
	Division	Department of Life and Environmental Sciences
	Organization	University of Cagliari
	Address	Cagliari, Italy
Author	Family Name	<b>Gargano</b>
	Particle	
	Given Name	<b>Domenico</b>
	Suffix	
	Division	Department of Biology, Ecology and Earth Sciences
	Organization	University of Calabria
	Address	Cagliari, Italy
Author	Family Name	<b>Abeli</b>
	Particle	
	Given Name	<b>Thomas</b>
	Suffix	
	Division	Department of Life Sciences
	Organization	University of Trieste
	Address	Trieste, Italy
Author	Family Name	<b>Orsenigo</b>
	Particle	
	Given Name	<b>Simone</b>
	Suffix	
	Division	Department of Agricultural and Environmental Sciences - Production, Landscape, Agroenergy
	Organization	University of Milan
	Address	Milan, Italy
Corresponding Author	Family Name	<b>Carbognani</b>
	Particle	
	Given Name	<b>Michele</b>
	Suffix	
	Division	Department of Chemistry, Life Sciences and Environmental Sustainability
	Organization	University of Parma
	Address	Parco Area delle Scienze 11/A, I-43124 Parma, Italy
e-mail	michele.carbognani@unipr.it	
Schedule	Received	21 April 2018
	Revised	
	Accepted	13 November 2018
Abstract	We examined the importance of litter quality and microclimate on early-stage litter mass loss, analysed the importance of interactions among environmental factors in determining key decomposition parameters and compared the variation in decomposition rates in vegetation types and sites with similar climate.	

Following the Tea-Bag Index approach, 464 tea-bags were incubated in the soil in 79 sites, distributed across Italy, which included six vegetation types and a broad range of microclimatic conditions.

Litter type exerted a stronger control on mass loss compared to climatic factors. The effects of soil moisture were not the same for high and lower quality litter. In addition, the effects of temperature on the decomposition rate depended on soil moisture. The stabilization factor was strongly temperature-dependent, but the influence of temperature differed among vegetation types: those dominated by small-size plants showed a strong decrease in the potential amount of plant material entering into the soil stock under warmer temperatures. The lowest variation in decomposition rate was found in sites characterised by low temperatures, and, among the vegetation types, in alpine snowbeds.

The role of litter quality and of the interactions among environmental conditions can potentially determine significant shifts in the expected patterns of ecosystem carbon fluxes.

---

Keywords (separated by '-')	Tea-bag index - Litter quality - Microclimate - Vegetation type - Decomposition constant - Stabilization factor
--------------------------------	---

---

Foot note information	Alessandro Petraglia and Cecilia Cacciatori equally to this work and should be considered co-first authors Responsible Editor: Feike A. Dijkstra. The online version of this article ( <a href="https://doi.org/10.1007/s11104-018-3889-x">https://doi.org/10.1007/s11104-018-3889-x</a> ) contains supplementary material, which is available to authorized users.
--------------------------	---

## Electronic supplementary material

### ESM 1

(DOCX 142 kb)

# Litter decomposition: effects of temperature driven by soil moisture and vegetation type

Alessandro Petraglia · Cecilia Cacciatori · Stefano Chelli · Giuseppe Fenu ·  
Giulia Calderisi · Domenico Gargano · Thomas Abeli · Simone Orsenigo ·  
Michele Carbognani

Received: 21 April 2018 / Accepted: 13 November 2018  
© Springer Nature Switzerland AG 2018

## Abstract

**Aims** We examined the importance of litter quality and microclimate on early-stage litter mass loss, analysed the importance of interactions among environmental factors in determining key decomposition parameters and compared the variation in decomposition rates in vegetation types and sites with similar climate.

**Methods** Following the Tea-Bag Index approach, 464 tea-bags were incubated in the soil in 79 sites, distributed across Italy, which included six vegetation types and a broad range of microclimatic conditions.

**Results** Litter type exerted a stronger control on mass loss compared to climatic factors. The effects of soil moisture were not the same for high and lower quality litter. In addition, the effects of temperature on the decomposition rate depended on soil moisture. The stabilization factor was strongly temperature-dependent, but the influence of temperature differed among vegetation types: those dominated by small-size plants showed a strong decrease in the potential amount of plant material entering into the soil stock under warmer temperatures. The lowest variation in decomposition rate was found in sites characterised by low

Alessandro Petraglia and Cecilia Cacciatori equally to this work and should be considered co-first authors

Responsible Editor: Feike A. Dijkstra.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s11104-018-3889-x>) contains supplementary material, which is available to authorized users.

A. Petraglia · C. Cacciatori · M. Carbognani (✉)  
Department of Chemistry, Life Sciences and Environmental  
Sustainability, University of Parma, Parco Area delle Scienze 11/A,  
I-43124 Parma, Italy  
e-mail: michele.carbognani@unipr.it

S. Chelli  
School of Biosciences and Veterinary Medicine, Plant Diversity  
and Ecosystems Management Unit, University of Camerino,  
Camerino, Italy

G. Fenu · G. Calderisi  
Department of Life and Environmental Sciences, University of  
Cagliari, Cagliari, Italy

D. Gargano  
Department of Biology, Ecology and Earth Sciences, University of  
Calabria, Cagliari, Italy

T. Abeli  
Department of Life Sciences, University of Trieste, Trieste, Italy

S. Orsenigo  
Department of Agricultural and Environmental Sciences -  
Production, Landscape, Agroenergy, University of Milan,  
Milan, Italy

temperatures, and, among the vegetation types, in alpine snowbeds.

**Conclusions** The role of litter quality and of the interactions among environmental conditions can potentially determine significant shifts in the expected patterns of ecosystem carbon fluxes.

**Keywords** Tea-bag index · Litter quality · Microclimate · Vegetation type · Decomposition constant · Stabilization factor

### Abbreviations

GWC Gravimetric water content  
 LMM Linear mixed-effect model  
 MAP Mean annual cumulative precipitation  
 MAT Mean annual air temperature  
 SOC Soil Organic Carbon  
 TBI Tea-Bag Index

### Introduction

Decomposition processes play a key role in linking organic and inorganic components of natural ecosystems and are equally significant in the completion of the carbon cycle. Litter decomposition represents a fundamental component in such processes since plants, as primary producers, are the main source of organic carbon in terrestrial ecosystems.

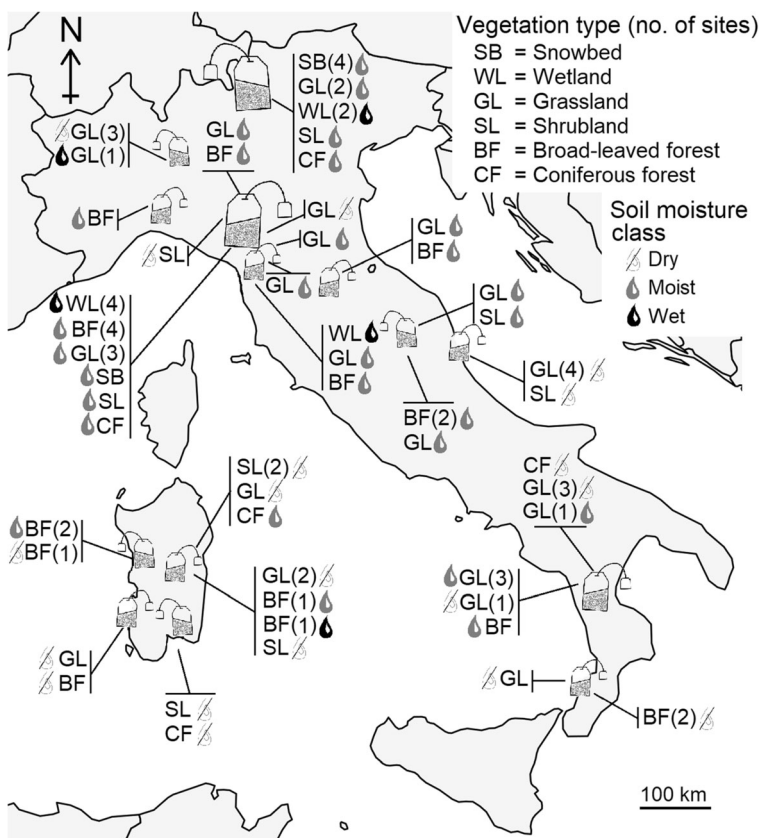
Decomposition has been widely studied for over a century, but it was the introduction of the litter bags technique (Bocock and Gilbert 1957) that triggered the proliferation of a wide range of systematic studies, which were also motivated by the growing concern about global climate change (e.g. Cornwell et al. 2008). Research undertaken in recent decades has tried to identify the main drivers of litter decomposition as well as highlighting the importance of such factors across a wide range of environmental conditions at different spatial scales (e.g. Gholz et al. 2000; Cornelissen et al. 2007; García-Palacios et al. 2013, 2016; Parton et al. 2007; Zhang et al. 2008). This research identifies climatic factors and litter quality as key drivers of litter decomposition on both a regional and global scale (Aerts 1997; Austin and Vitousek 2000; Cornwell et al. 2008; García-Palacios et al. 2013; Zhang et al. 2008).

Climate can affect litter decomposition directly, by regulating the activity of decomposers, and indirectly through changes in plant species composition and abundance and, as a result, in variation in litter quality and quantity. The decomposability of the litter depends also on the specific physical and chemical properties of plant tissues (i.e. their quality as a resource for decomposers) due to their responsiveness to microbial mineralization (Jagadamma et al. 2014). However, the lack of a widespread implementation of an easy-to-use and well-standardized method for estimating litter decomposition has hampered investigations aimed at understanding the relative importance of climatic factors and litter quality. In order to overcome the conceptual and practical setbacks involved in the use of local litter, Keuskamp et al. (2013) have recently proposed the use of the Tea-Bag Index (TBI), a method based on commercially available tea as a standard plant material. The TBI can be a useful tool to increase understanding of decomposition processes through an assessment of the relative importance of different drivers and through pinpointing the role of the interactions among environmental factors.

The function of the principal climatic factors (i.e. temperature and precipitation) and litter quality has been investigated independently in the past. The potential interactions among these agents is poorly known, despite their potential importance in the carbon balance of terrestrial ecosystems (Wu et al. 2011), in particular under changing climatic conditions and vegetation dynamics. Although the importance of the interactions between temperature and soil moisture on soil respiration rates has recently been demonstrated (Sierra et al. 2017; Tucker and Reed 2016; Wang et al. 2016), research on the role of the interactions among drivers of litter decomposition processes (i.e. litter quality, vegetation properties and climatic features) remains limited. The few available studies on the influence of interactions among environmental factors on litter decomposition are based on the interaction between mean annual air temperature (MAT) and mean annual cumulative precipitation (MAP) (Taylor et al. 2017) and on the interactions between litter quality and MAT, MAP, land-use and biome (Djukic et al. 2018). Furthermore, in most studies on litter decomposition, the main climatic variables tested were treated as constant across large areas and within biomes (e.g. Cornelissen et al. 2007; Cornwell et al. 2008). Topographic variability and vegetation cover, however, should be taken into consideration as these factors can potentially influence local

138	microclimatic conditions (e.g. Wundram et al. 2010;	provides a wide range of contrasting climatic regimes	183
139	Graham et al. 2012) and their spatial variation occurs	within relatively small areas. Moreover, the historical	184
140	at finer scales compared to the ones provided by high-	influence of human land-use offers a variety of natural	185
141	resolution gridded climatic datasets. Variations in soil	and semi-natural habitats within short distances and,	186
142	slope and aspect coupled with plant shading and tran-	consequently, experiencing the same climatic regime.	187
143	spiration are able to determine detailed patterns of soil	The study sites were located at an elevation ranging	188
144	temperature and moisture conditions on a very small	from 0 to 2681 m a.s.l. and comprised different zones,	189
145	spatial scale. In addition, historical land-use coupled	ranging from the coastal areas of the southern peninsular	190
146	with the occurrence of azonal vegetation types such as	regions and Sardinia, characterised by a typical Medi-	191
147	those associated with specific site conditions (e.g.	terranean climate, to the alpine tundra environment in	192
148	waterlogging, high salt content, long-lasting snow-cov-	the Rhaetian Alps (Table 1).	193
149	er, frequent disturbance) contribute to a substantial plant	Each site was assigned one of six vegetation types -	194
150	cover differentiation of the landscape. It is, therefore,	snowbed, wetland, grassland, shrubland, broad-leaved	195
151	unknown how much variation in litter decomposition	forest, coniferous forest – on the basis of the composi-	196
152	occurs at a local level, such as in sites characterised by	tion and structure of its plant communities.	197
153	similar climate but with different vegetation types.	Soil temperature was recorded hourly at each site by	198
154	We measured early-stage mass loss and decomposi-	a Pendant sensor (Onset, Cape Cod, MA, USA) placed	199
155	tion parameters following the TBI approach (Keuskamp	in the soil at a depth of 8 cm, while soil water content	200
156	et al. 2013) in order to investigate the effects of litter	was estimated through direct observations of the phys-	201
157	quality, microclimatic conditions, vegetation types and	ical features of the soil - i.e. friability, ductility,	202
158	their interactions on litter decomposition and also to	waterlogging - carried out during the burying of the	203
159	estimate the variation occurring in sites with similar	tea-bags in the soil and their subsequent retrieval. An	204
160	climate and among different vegetation types. This	estimate of the percentage of gravimetric water content	205
161	was achieved by calculating the decomposition rate	(GWC) of the soil was undertaken in order to assign a	206
162	constant $k$ , representing the turnover time of the labile	categorical class of soil moisture to each site. Three	207
163	fraction of material (i.e. the short-term dynamics of new	categories of soil moisture were identified: dry (roughly	208
164	inputs) and the stabilization factor $S$ , indicating the	<20% GWC), moist (20–80% GWC) and wet (GWC >	209
165	amount of labile material that becomes recalcitrant (i.e.	80%).	210
166	the potential carbon storage).	Standard material and sampling design	211
167	In particular, the aims of the present study were: (i) to	Tea-bags were incubated and processed following the	212
168	assess the relative importance of litter quality and soil	Keuskamp et al. (2013) protocol. In each site, 3 to 5 sets	213
169	temperature and moisture in determining early-stage	of tea-bags, each set consisting of one green and one	214
170	mass loss of litter; (ii) to disentangle the effects of	rooibos tea type, were buried in the soil at 8 cm depth at	215
171	vegetation type and soil temperature and moisture on	the beginning of the summer 2016 or 2017, depending	216
172	decomposition parameters; and (iii) to compare the var-	on the site, and retrieved after approx. 3 months	217
173	iation in decomposition rate among types of vegetation	(Table 1). Lipton green tea (EAN: 87 22,700 05552 5)	218
174	and among group of sites characterised by different	and Lipton rooibos tea (EAN: 87 22,700 18,843 8) were	219
175	climatic conditions.	used, composed of nylon bags with a mesh size of	220
176	<b>Materials and methods</b>	0.25 mm. Each bag contained approx. 2 g of tea. The	221
177	Study sites and environmental data	two varieties of tea differ in the type of plant material	222
178	The study was carried out in 79 sites distributed all over	used, C:N ratio and percentage of water soluble fraction.	223
179	Italy (Fig. 1). Given the position of the Italian peninsula,	Whereas green tea consists of leaves, has a C:N ratio of	224
180	laying in the temperate zone of the Northern Hemi-	approx. 12 and a high water soluble fraction (ca. 50%),	225
181	sphere but located in the middle of the Mediterranean	rooibos tea consists of a mixture of mainly needle-like	226
182	basin, together with its orographic features, Italy	litter and stem tissue, with a C:N ratio of approx. 43 and	227
		contains half the amount of soluble compounds of green	228
		tea (Keuskamp et al. 2013). Because of their chemical	229

**Fig. 1** Location of the study sites, with vegetation type and soil moisture class. Tea-bag silhouette has the sole purpose of graphically representing the position and the number of the study sites occurring in neighbouring locations (small size <6, medium size = 6 to 10, large size >10)



230 properties, the two types of tea were used as surrogates  
 231 of higher and lower quality litter, respectively. After the  
 232 exclusion of damaged material, the data set included a  
 233 total of 464 tea-bags, for each of which the initial air-  
 234 dried mass and the final oven-dry mass was measured.  
 235 An independent set of tea-bags consisting of 26 green  
 236 and 26 rooibos tea-bags, was used to estimate the initial  
 237 oven-dry mass by calculating the ratio between air- and  
 238 oven-dry masses.

239 Estimation of litter mass loss and decomposition  
 240 parameters (*k* and *S*)

241 Litter mass loss was calculated for both green and  
 242 rooibos tea as:

$$\text{Mass loss} = (M_0 - M_1) / M_0 \quad (1)$$

243 where  $M_0$  and  $M_1$  are the initial and final oven-dry mass  
 244 of the tea, respectively.

245 In addition, two decomposition parameters were esti-  
 246 mated following the TBI approach (Keuskamp et al.  
 247 2013): the decomposition rate constant of the labile  
 248

fraction (*k*) and the stabilization factor (*S*). The TBI  
 249 approach is based on the assumption that the mass loss  
 250 of the recalcitrant fraction of plant material is negligible  
 251 during short incubation periods (i.e. ca. 3 months). There-  
 252 fore, the double exponential model was expressed as:  
 253

$$X = a * e^{-kt} + (1-a) \quad (2)$$

254 where *X* is the fraction of remaining mass at time *t*, *a* is  
 255 the labile fraction, (1 - *a*) is the recalcitrant fraction of  
 256 the material and *k* is the decomposition rate constant of  
 257 the labile fraction. The latter was estimated as:  
 258

$$k = -\ln((X_r - (1-a_r)) / a_r) / t \quad (3)$$

259 where  $X_r$  is the fraction of remaining rooibos tea (i.e.  $M_1$   
 260 /  $M_0$ ),  $a_r$  is the predicted labile fraction of rooibos tea and  
 261 *t* is the incubation time, expressed in days. The rooibos  
 262 tea labile fraction was calculated as:  
 263

$$a_r = H_r * (1-S) \quad (4)$$

264 where  $H_r$  is the hydrolysable fraction of rooibos tea and  
 265 *S* is the stabilization factor, which is assumed to be the  
 266 same for both tea types and can be interpreted as the  
 267

**Table 1** Site location and relative environmental features

Site (No.)	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Vegetation type	Soil temperature (°C)	Soil moisture (class)	T (°C)	P (mm)	CC (No.)	Incubation time (days)
s01	44.2445	10.4066	2005	SB	12.3	Moist	11.4	170	c11	86
s02	46.3410	10.4981	2681	SB	8.2	Moist	4.7	125	c17	80
s03	46.3409	10.4982	2681	SB	8.3	Moist	4.7	125	c17	80
s04	46.3400	10.4985	2681	SB	8.4	Moist	4.7	125	c17	80
s05	46.3405	10.4986	2681	SB	8.3	Moist	4.7	125	c17	80
s06	44.3709	10.0682	1716	WL	15.2	Wet	13.0	216	c03	84
s07	44.3628	10.1086	1357	WL	14.2	Wet	14.8	250	c01	85
s08	44.3580	10.1409	1123	WL	17.6	Wet	15.5	259	c01	85
s09	43.8363	10.3519	0	WL	24.0	Wet	23.0	130	c15	95
s10	44.2183	10.3808	1458	WL	15.9	Wet	14.3	253	c01	89
s11	46.3432	10.4996	2658	WL	10.1	Wet	5.6	109	c16	80
s12	46.2997	10.5042	1594	WL	11.3	Wet	11.7	42	c04	84
s13	39.4302	8.4396	96	GL	30.6	Dry	23.4	31	c05	95
s14	45.1919	9.0807	56	GL	28.2	Dry	22.1	156	c10	103
s15	45.1916	9.0815	51	GL	28.1	Dry	22.1	156	c10	87
s16	45.1696	9.1629	76	GL	22.9	Wet	22.2	157	c10	93
s17	45.1864	9.1629	76	GL	23.4	Wet	22.2	158	c10	93
s18	45.1746	9.1926	65	GL	30.3	Dry	22.2	157	c10	89
s19	40.0157	9.3031	1824	GL	18.8	Dry	15.9	78	c09	99
s20	40.0170	9.3061	1743	GL	16.3	Dry	16.1	75	c09	99
s21	40.2429	9.4318	1445	GL	18.2	Dry	19.1	66	c06	96
s22	44.3610	10.2026	1054	GL	19.4	Moist	16.6	261	c01	95
s23	44.3312	10.2073	1933	GL	10.5	Moist	12.3	197	c02	85
s24	44.2685	10.2530	1759	GL	12.3	Moist	12.8	210	c03	86
s25	44.7683	10.3147	80	GL	26.6	Moist	22.9	155	c10	90
s26	43.7339	10.3416	3	GL	21.9	Moist	23.1	121	c14	95
s27	44.2498	10.4060	2001	GL	12.5	Moist	11.4	170	c11	95
s28	46.3183	10.4967	2219	GL	13.7	Moist	7.8	67	c08	84
s29	46.3429	10.4993	2654	GL	8.6	Moist	5.6	109	c16	80
s30	44.1182	10.6108	1687	GL	12.0	Moist	13.2	219	c03	101
s31	44.2020	10.6922	1785	GL	12.4	Moist	12.7	196	c02	103
s32	44.5141	10.8253	206	GL	29.1	Dry	22.4	162	c10	93
s33	43.8094	11.8156	1074	GL	19.5	Moist	16.9	259	c01	95
s34	42.9561	13.0174	1130	GL	18.6	Moist	17.3	176	c12	90
s35	43.1369	13.0711	625	GL	25.1	Moist	21.4	174	c12	86
s36	42.9001	13.9093	0	GL	24.8	Dry	22.8	136	c15	86
s37	42.9001	13.9097	0	GL	26.2	Dry	22.8	136	c15	86
s38	42.8960	13.9137	0	GL	28.2	Dry	22.8	136	c15	84
s39	42.8960	13.9139	0	GL	26.2	Dry	22.8	136	c15	84
s40	38.6318	15.8529	158	GL	29.5	Dry	23.7	60	c07	90
s41	39.8076	16.0425	1302	GL	18.4	Moist	16.4	95	c13	90
s42	39.8480	16.0932	1395	GL	21.0	Dry	17.8	94	c13	90
s43	39.9126	16.1313	1610	GL	14.5	Dry	15.4	97	c13	87
s44	39.9104	16.1321	1614	GL	13.0	Moist	15.4	97	c13	87

t1.47

**Table 1** (continued)

Site (No.)	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Vegetation type	Soil temperature (°C)	Soil moisture (class)	T (°C)	P (mm)	CC (No.)	Incubation time (days)
s45	39.9214	16.2089	1936	GL	13.7	Moist	12.7	101	c13	87
s46	39.9236	16.2100	1954	GL	15.4	Dry	12.7	101	c13	87
s47	39.1851	9.1571	56	SL	31.0	Dry	24.2	24	c05	98
s48	40.0224	9.3076	1484	SL	13.1	Dry	16.1	75	c09	99
s49	40.2588	9.4247	1135	SL	23.1	Dry	21.0	58	c07	96
s50	40.2530	9.4303	1137	SL	18.8	Dry	19.5	64	c06	96
s51	44.5288	10.1424	493	SL	24.2	Dry	20.0	217	c03	85
s52	44.2499	10.4064	2002	SL	12.1	Moist	11.4	170	c11	95
s53	46.3203	10.4938	2259	SL	10.0	Moist	7.8	67	c08	84
s54	43.1369	13.0712	625	SL	20.0	Moist	21.4	174	c12	86
s55	42.8998	13.9101	0	SL	24.3	Dry	22.8	136	c15	86
s56	39.4419	8.4317	32	BF	22.9	Dry	24.0	28	c05	95
s57	40.1184	8.5724	724	BF	19.0	Moist	21.1	59	c07	97
s58	40.1641	8.6252	890	BF	17.2	Dry	19.8	64	c06	97
s59	40.1309	8.6437	465	BF	19.4	Moist	21.9	52	c07	97
s60	44.8071	8.9046	308	BF	20.6	Moist	21.7	163	c10	97
s61	40.0720	9.2824	1286	BF	15.5	Moist	18.0	69	c06	99
s62	40.0220	9.3048	1565	BF	14.3	Wet	16.1	75	c09	99
s63	44.3824	10.0551	1514	BF	11.8	Moist	13.4	220	c03	90
s64	44.3871	10.1973	708	BF	16.4	Moist	17.6	229	c03	95
s65	44.3598	10.2185	1222	BF	12.6	Moist	15.4	254	c01	95
s66	44.7685	10.3153	80	BF	23.1	Moist	22.9	155	c10	90
s67	43.7339	10.3419	3	BF	20.8	Moist	23.0	122	c14	95
s68	44.2183	10.3821	1481	BF	12.7	Moist	14.3	253	c01	89
s69	43.8132	11.8300	1253	BF	13.5	Moist	16.2	252	c01	95
s70	42.9558	13.0173	1130	BF	15.2	Moist	17.3	176	c12	90
s71	42.9566	13.0179	1130	BF	15.3	Moist	17.3	176	c12	90
s72	38.5265	16.1211	270	BF	21.6	Dry	23.5	64	c06	85
s73	38.5252	16.1261	248	BF	20.8	Dry	23.3	66	c06	85
s74	39.9104	16.1321	1620	BF	10.2	Moist	15.4	97	c13	87
s75	39.1877	9.1580	91	CF	22.8	Dry	24.2	24	c05	98
s76	40.2485	9.4263	1258	CF	15.8	Moist	19.1	66	c06	96
s77	44.3645	10.2206	1261	CF	12.5	Moist	15.4	254	c01	95
s78	46.2987	10.5087	1681	CF	10.9	Moist	11.7	42	c04	84
s79	39.9282	16.2117	1970	CF	12.0	Dry	12.9	99	c13	87

Abbreviations: *SB* snowbed; *WL* wetland; *GL* grassland; *SL* shrubland; *BF* broad-leaved forest; *CF* coniferous forest. Soil temperature refers to the average temperature of the soil measured at the same depth of the tea-bags during the incubation period, whereas T and P stand, respectively, for the mean air temperature and cumulative precipitation of the warmest quarter of the year extracted from the WorldClim dataset (Fick and Hijmans 2017). CC indicates the climatic cluster

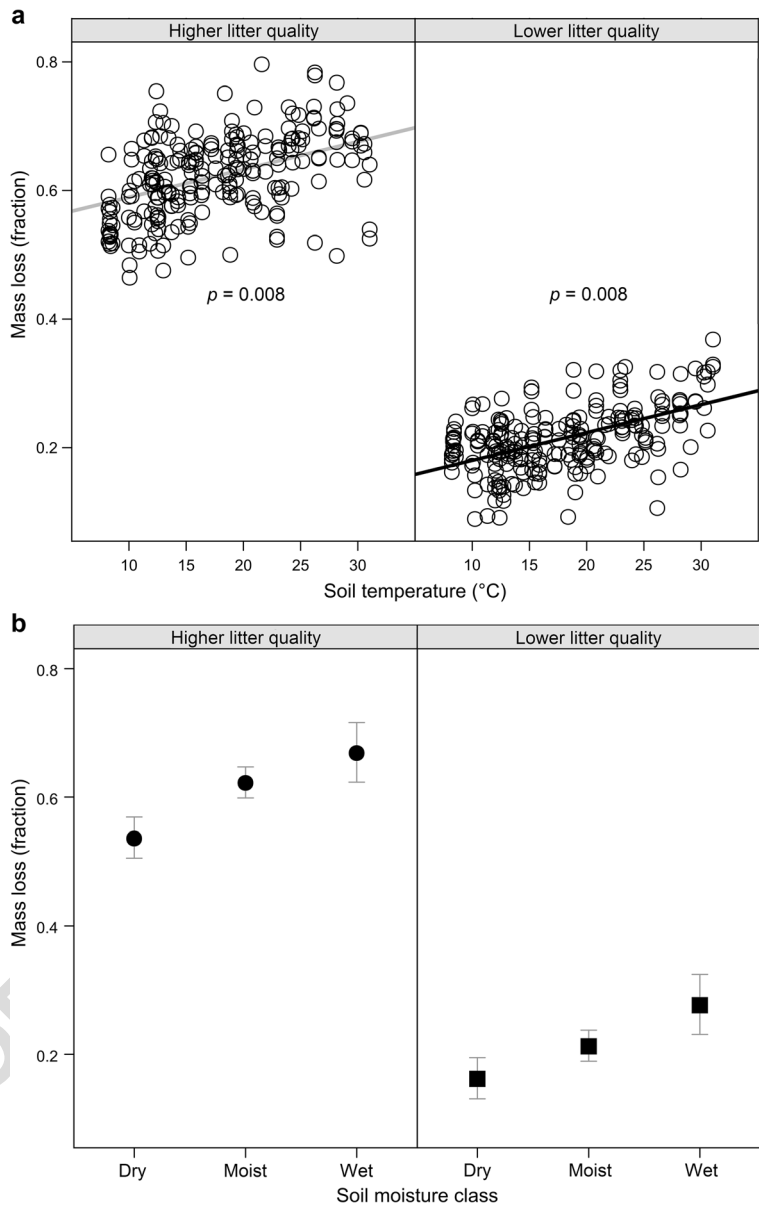
268 inhibiting effect of environment on the decomposition  
 269 of the labile fraction of litter (Keuskamp et al. 2013).  
 270 The stabilization factor, which indicates the amount of  
 271 labile materials that tends to stabilize becoming recalci-  
 272 trant, was calculated as:

$$S = 1 - a_g / H_g \quad (5)$$

where  $a_g$  and  $H_g$  are respectively the decomposable 274  
 fraction and hydrolysable fraction of green tea. 275

276	Statistical analyses		
277	A linear mixed-effect model (LMM) was performed to		
278	assess the effects of litter quality and soil temperature and		
279	moisture on initial (3-month period) mass loss. The pro-		
280	portion of mass loss was set as the response variable,		
281	whereas the tea type (2-level factor: green and rooibos		
282	tea, for higher and lower quality litter, respectively), the		
283	average soil temperature during the incubation period		
284	(continuous variable, in °C), the soil moisture class (3-		
285	level factor: dry, moist and wet) and their 2-way interac-		
286	tions were considered as predictors. Since we buried		
287	multiple sets of teabags in each site, site identity was		
288	included in the model as a random factor. For this and the		
289	following analyses, minimal adequate models were obta-		
290	ined by means of model selection following Crawley		
291	(2013), and model assumptions were checked through		
292	visual inspection of residual patterns (Zuur et al. 2009).		
293	LMMs were then fitted to $k$ and $S$ , considered as		
294	response variables, to investigate whether the decompo-		
295	sition parameters differ among vegetation types and		
296	how these are influenced by soil temperature and mois-		
297	ture. In both models, the vegetation type (6-level factor:		
298	snowbed, wetland, grassland, shrubland, broad-leaved		
299	forest and coniferous forest), soil temperature and mois-		
300	ture class and their 2-way interactions were set as the		
301	fixed effects, whereas the site was set as the random		
302	effect. To meet linear model assumptions, $k$ values were		
303	square root transformed prior to analysis.		
304	Finally, differences in the coefficient of variation		
305	(CV) of $k$ among climatic clusters and among vegetation		
306	types were analysed using the asymptotic test of Feltz		
307	and Miller (1996). Climatic clusters were defined		
308	through a cluster analysis on mean air temperature and		
309	cumulative precipitation data of the warmest quarter of		
310	the year during the period 1970–2000; climatic variables		
311	were extracted from WorldClim version 2 (Fick and		
312	Hijmans 2017) at a 30 s (~1 km <sup>2</sup> ) spatial resolution.		
313	Cluster analysis was performed with the Ward (mini-		
314	imum variance) clustering method and the Euclidean		
315	dissimilarity index. Finally, the optimal number of clus-		
316	ters was identified following the silhouette width crite-		
317	rium (Rousseeuw 1987).		
318	Statistical analyses were carried out in R version 3.4.3		
319	(R Core Team 2017) with the following packages: lme4		
320	(Bates et al. 2015) for model fitting, car (Fox and		
321	Weisberg 2011) for model selection, multcomp (Hothorn		
322	et al. 2008) for post-hoc comparisons, vegan (Oksanen		
323	et al. 2017) for cluster analysis, cvequality (Marwick and		
	Krishnamoorthy 2018) for comparison of CVs and visreg	324	
	(Breheny and Burchett 2017) for graphs of regressions.	325	
	<b>Results</b>	326	
	Mass loss	327	
	Results illustrated the following hierarchy regarding the	328	
	drivers which determine mass loss: litter quality	329	
	( $F_{1,382} = 6110.30$ , $P < 0.001$ ) >>> soil moisture	330	
	( $F_{1,75} = 10.49$ , $P < 0.001$ ) > soil temperature ( $F_{1,74} =$	331	
	$7.54$ , $P = 0.008$ ). Thus, variation due to different litter	332	
	quality was significantly greater than that due to soil	333	
	temperature (Fig. 2a) and moisture (Fig. 2b) variation.	334	
	The interaction between litter type and soil moisture was	335	
	also significant ( $F_{2,382} = 4.75$ , $P = 0.009$ ), with wetter	336	
	soil conditions promoting the mass loss of higher litter	337	
	quality to a greater extent compared to the mass loss of	338	
	lower litter quality. Overall, mass loss was higher in wet	339	
	and moist soils compared to dry ones ( $Z = 4.445$ ,	340	
	$P < 0.001$ and $Z = 3.183$ , $P < 0.001$ , respectively), while	341	
	the difference between wet and moist soils was margin-	342	
	ally significant ( $Z = 2.204$ , $P = 0.069$ ).	343	
	Decomposition parameters	344	
	The analysis did not evidence an overall effect of soil	345	
	temperature on the decomposition constant $k$ ( $F_{1,72} =$	346	
	$1.93$ , $P = 0.169$ ), which, on the other hand, exhibited a	347	
	significant response to both soil moisture ( $F_{2,73} = 6.36$ ,	348	
	$P = 0.003$ ) and the interaction between soil moisture and	349	
	temperature ( $F_{2,73} = 8.39$ , $P < 0.001$ ) (Fig. 3a). Hence, the	350	
	effects of soil temperature and moisture were not additive	351	
	and increasing temperatures were associated to higher $k$	352	
	values only in dry and wet soils. On average, $k$ values	353	
	were higher in wet soils than in dry ( $Z = 4.338$ , $P < 0.001$ )	354	
	and moist soils ( $Z = 3.914$ , $P < 0.001$ ), whereas dry and	355	
	moist soils did not differ between each other ( $Z = 1.122$ ,	356	
	$P = 0.497$ ). The vegetation type did not exhibit a signifi-	357	
	cant influence on $k$ (variable excluded from the model).	358	
	The stabilization factor $S$ was significantly affected	359	
	by both soil temperature ( $F_{1,65} = 8.16$ , $P = 0.006$ ) and	360	
	moisture ( $F_{1,67} = 4.73$ , $P = 0.012$ ) (Fig. 3b), while dif-	361	
	ferences among vegetation types were marginally	362	
	significant ( $F_{1,65} = 2.07$ , $P = 0.080$ ). Overall, dry	363	
	sites exhibited a higher $S$ than moist ones ( $Z =$	364	
	$-2.894$ , $P = 0.010$ ). Moreover, the effects of tem-	365	
	perature and moisture were additive (interaction	366	

**Fig. 2** Mass loss of higher and lower quality litter in relation to (a) temperature variation and (b) soil moisture classes



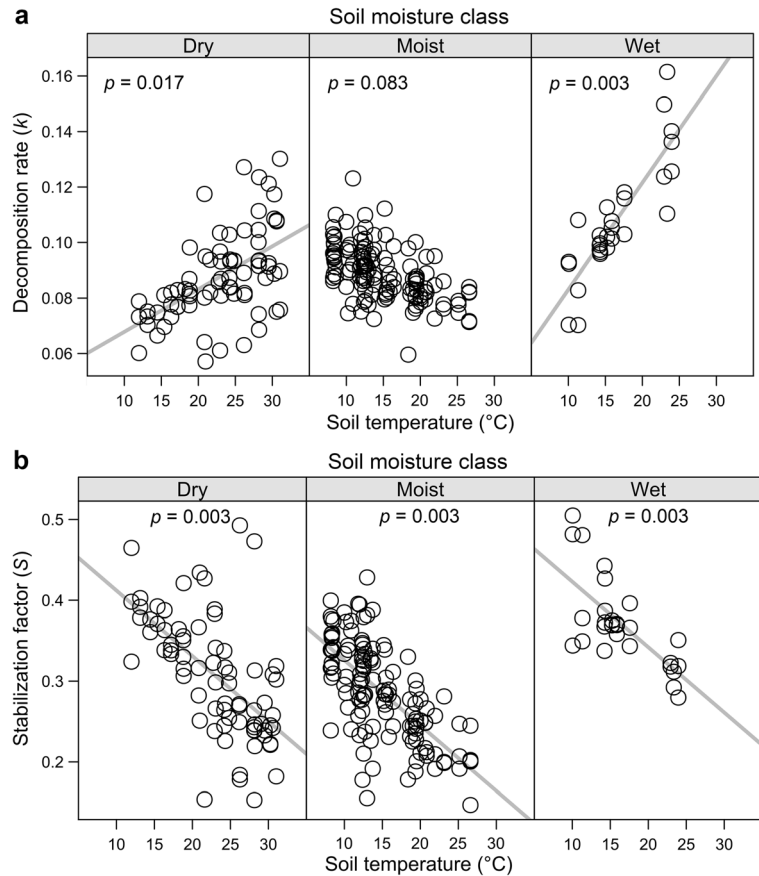
367 excluded from the model), unlike those of temper- 377  
 368 ature and vegetation type ( $F_{1,67} = 5.22$ ,  $P < 0.001$ ) 378  
 369 (Fig. 4). In particular, a significant decrease of  $S$  379  
 370 occurred with increasing temperatures in 380  
 371 snowbeds, wetlands and grasslands, whereas in 381  
 372 vegetation dominated by shrubs or trees  $S$  did 382  
 373 not vary at different temperatures. 383

374 Variation in decomposition rate

375 The coefficient of variation (CV) showed signifi- 384  
 376 cant differences both among the 17 climatic 385

377 clusters and among the six vegetation types 378  
 379 ( $D'AD = 57.5$ ,  $P < 0.001$  and  $D'AD = 23.8$ ,  $P <$  380  
 381  $0.001$ , respectively). Despite substantial variation 382  
 383 occurring in almost all the clusters (Fig. S1 in 384  
 385 Supplementary Material), the CV seemed to follow 386  
 387 a trend towards lower values at colder tempera- 388  
 388 tures (Fig. 5a) and higher values at high tempera- 389  
 389 tures and low precipitation. Finally, among the 390  
 390 vegetation types investigated, the lowest CV of  $k$  391  
 391 was found in snowbed communities (Fig. 5b), 392  
 392 whereas grasslands and coniferous forests showed 393  
 393 the highest variation in the decomposition rate. 394

**Fig. 3** Relationships between (a) the decomposition constant and (b) the stabilization factor with temperatures and moisture classes of the soil



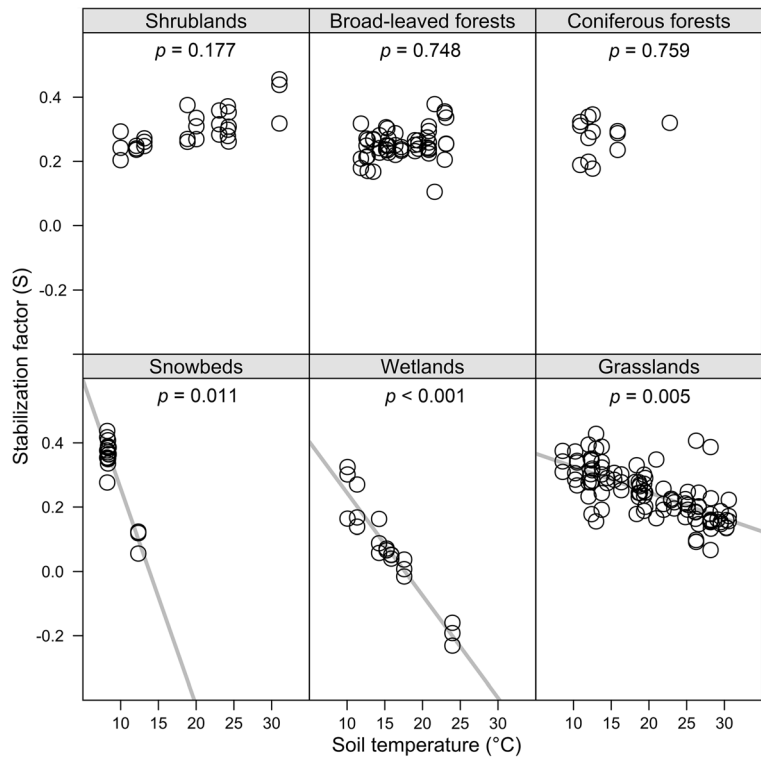
## 389 Discussion

390 Studies on decomposition processes based on stan-  
 391 dard litter allow the investigation of environmental  
 392 drivers without being conditioned by marginal effects  
 393 such as the “home-field advantage” (Gholz et al.  
 394 2000). Based on incubations performed in a wide  
 395 range of environmental conditions, the present study  
 396 demonstrated that litter quality exerts a stronger ef-  
 397 fect on early-stage mass loss than variation of soil  
 398 temperature and moisture, supporting the conclusions  
 399 of previous studies (Carbognani et al. 2014;  
 400 Cornwell et al. 2008; Djukic et al. 2018; Shaw and  
 401 Harte 2001; Zhang et al. 2008). Furthermore, the  
 402 results suggested that the differences in chemical  
 403 and physical properties of litter are more important  
 404 in determining mass loss compared to the variation  
 405 in biological processes, such as microbial respiration  
 406 induced by increasing temperature (Fig. 2a) and the  
 407 variation of abiotic processes, such as leaching in-  
 408 duced by soil water availability (Fig. 2b).

409 The analysis of the interplay of controlling factors  
 410 revealed the occurrence of three significant interactions:  
 411 (i) between litter quality and soil moisture, affecting  
 412 mass loss (Fig. 2b); (ii) between soil temperature and  
 413 moisture, influencing the decomposition constant  $k$  (Fig.  
 414 3a); and (iii) between soil temperature and vegetation  
 415 type, acting on the stabilization factor  $S$  (Fig. 4).

416 With regard to the first interaction, although res-  
 417 sponses of mass loss to temperature in green and rooibos  
 418 tea were similar, the two litter types did not decompose  
 419 equally in soils with different moisture content: the  
 420 difference in mass loss of high quality litter in sites with  
 421 different soil moisture (i.e. dry vs moist and wet sites)  
 422 was higher compared to the mass loss of low quality  
 423 litter (Fig. 2b). This result is consistent with the conclu-  
 424 sions of Yajun et al. (2016), indicating that the magni-  
 425 tude of synergistic interactions between soil water  
 426 content and litter type increases with increasing water  
 427 availability. Liu et al. (2005) also showed that water  
 428 addition favours mass loss in high quality litter. The  
 429 greater sensitivity of high quality litter in the leaching

**Fig. 4** Effects of soil temperatures on the stabilisation factor in different vegetation types

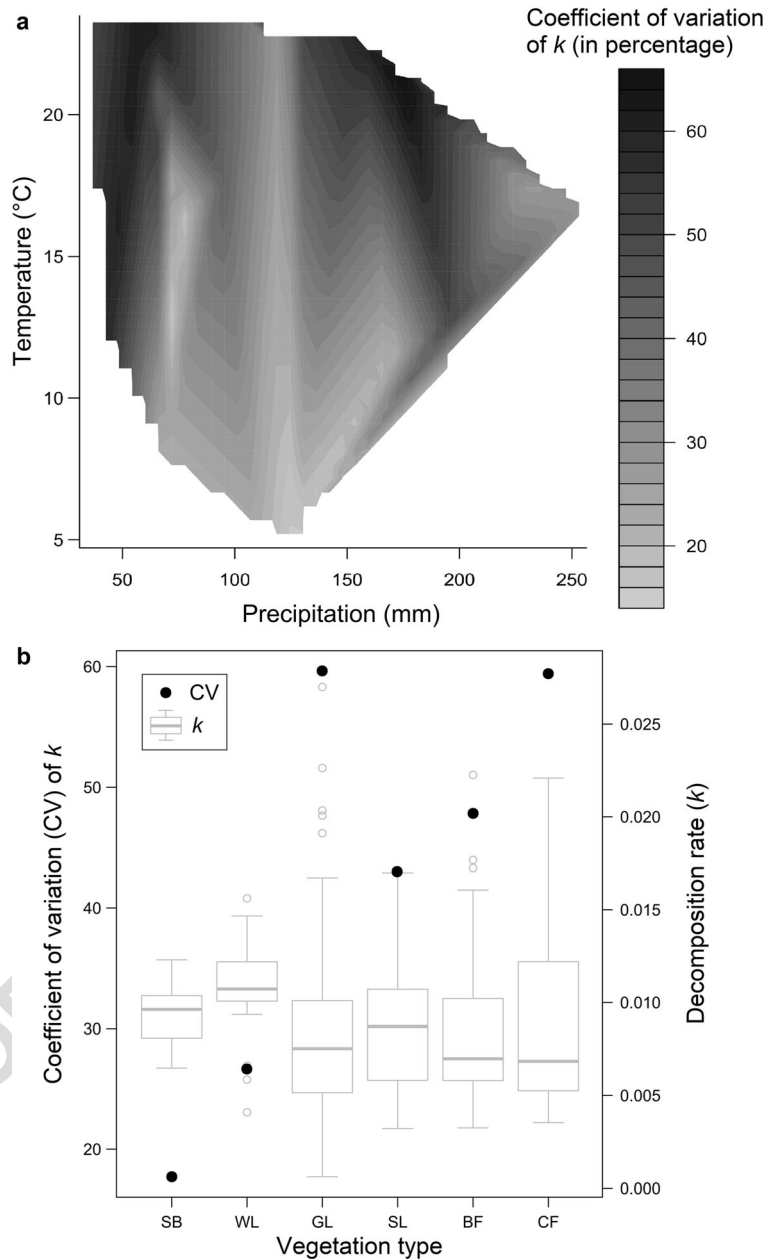


430 phase could explain the higher responsiveness of mass  
 431 loss to increasing soil water content in this type of litter  
 432 compared to low quality litter. Indeed, a substantial part  
 433 of litter mass loss during the early stages of litter decom-  
 434 position occurs during the leaching phase, when both  
 435 inorganic elements and simple organic compounds are  
 436 removed (MacLean and Wein 1978). Given the impor-  
 437 tance of the water-driven phase on litter decomposition  
 438 and its dependence on both the quantity and quality of  
 439 water-soluble compounds (Ibrahima et al. 2008), it could  
 440 be asserted that high soil water content can potentially  
 441 determine a stronger mass loss in litter types rich in  
 442 carbohydrates, these being easily leached during the first  
 443 decomposition stages (Cotrufo et al. 2015; Mansfield and  
 444 Bärlocher 2005). Liu et al. (2005) suggested that the  
 445 different responses of the two litter types to soil water  
 446 content could also be related to their different physical  
 447 structures: while, in the case of rooibos tea coriaceous  
 448 and lignified leaves are present, green tea is composed of  
 449 softer and more fragile leaves, which could be more  
 450 prone to physical fragmentation and leaching.

451 The litter decomposition rate, driven mainly by mi-  
 452 crobial activity, is largely temperature-dependent  
 453 (Davidson and Janssens 2006; Kirschbaum 2006). The  
 454 results revealed, however, that a significant increment in

455 *k* was determined by warmer soil temperatures only in 455  
 456 dry and wet sites, whereas in moist soils the decompo- 456  
 457 sition rate did not exhibit any significant response to 457  
 458 temperature variation (Fig. 3a). The impact of tempera- 458  
 459 ture on *k* is, therefore, not consistent in soils with dif- 459  
 460 ferent moisture levels. Results from both green and 460  
 461 rooibos tea (Fig. 2b) showed that dry soils are charac- 461  
 462 terized by a lower mass loss than moist and wet soils. It 462  
 463 seems, therefore, that the reduction of the decomposi- 463  
 464 tion rate associated with drier conditions counteracts the 464  
 465 enhancing effect of temperature on microbial activity 465  
 466 (Fig. 2a), resulting in no significant increase of decom- 466  
 467 position rates with increasing temperatures in moist 467  
 468 conditions (Fig. 3a). A possible explanation of these 468  
 469 results could be that, although a temperature increase 469  
 470 enhances the activity of decomposers, it also reduces the 470  
 471 moisture of the soil. It is likely that in intermediate soil 471  
 472 moisture conditions (i.e. GWC ranging from 20 to 80%) 472  
 473 warmer temperatures may cause larger differences in 473  
 474 soil moisture compared to those occurring in dry and 474  
 475 wet soils. Similarly, Christiansen et al. (2016) reported a 475  
 476 negative relation between litter decomposition rates and 476  
 477 temperature increase in both xeric and wet tundra sites, 477  
 478 due to evaporative drying associated with warmer 478  
 479 temperatures, which counteracted the enhancing effect 479

**Fig. 5** Values of the coefficient of variation in relation to site-specific temperature and precipitation extracted from the WorldClim dataset (Fick and Hijmans 2017) and in the six vegetation types



480 of temperature on microbial activity. Alternatively, the  
 481 vegetation type could also explain the lack of response  
 482 of  $k$  to temperature variation in soils with intermediate  
 483 water content, since most of the sites with soil classified  
 484 as moist were grasslands, a vegetation type that has  
 485 already been found to exhibit unexpected responses to  
 486 warming. In the study by Bontti et al. (2009) litter  
 487 decomposition in grasslands was not shown to be af-  
 488 fected by any of the climatic variables under  
 489 consideration.

In contrast to the decomposition constant  $k$ , the sta- 490  
 bilization factor  $S$  was significantly reduced by both 491  
 increasing soil temperature and moisture, with the ef- 492  
 fects of the two variables resulting as additive - i.e. 493  
 temperature has the same effect in soils belonging to 494  
 different moisture classes. These results are consistent 495  
 with those reported by Mueller et al. (2018) for tidal 496  
 wetlands, indicating that the stabilization of organic 497  
 material is higher in colder and drier soils. In the 498  
 present research, the vegetation type did not seem to 499

exhibit any direct control on early decomposition rates, confirming the results of Djukic et al. (2018) on land use categories. The absence of a direct effect with regard to the vegetation type on litter decomposition dynamics could be explained by the greater influence of climatic factors, with values of temperature and moisture varying greatly among vegetation types. However, the effect of the interaction between vegetation type and temperature on the stabilization factor  $S$  was highly significant (Fig. 4). This suggests that warming-induced effects on the potential storage of organic carbon in the soil could differ among vegetation types: although  $S$  consistently decreased with increasing temperature in all soil moisture categories (Fig. 3b), consistent patterns across all the considered vegetation types were not observed (Fig. 4). Whereas soil temperature in shrublands and forests did not affect  $S$ , the stabilization factor was significantly reduced by warmer temperatures in snowbeds, wetlands and grasslands, which may suggest a lower stability of the soil carbon stocks of these vegetation types under warmer climatic conditions. More specifically, the lack of temperature sensitivity of  $S$  in shrublands and forests is not consistent with the well-known warming-induced increase in decomposition of soil organic carbon (SOC) that can strongly affect the ecosystem carbon storage (e.g. Ding et al. 2014; Melillo et al. 2011; Trumbore et al. 1996). Furthermore, in a study on the drivers of SOC stability in temperate forests, Tian et al. (2016) reported that MAT only influences the labile carbon pool size but does not affect the SOC stability. Another study by Crowther et al. (2016) showed that the sensitivity of soil carbon stock to warming strictly depends on its initial size. Our results seems consistent with those reported by this last study since wetlands, snowbeds and mountain grasslands generally hold a large amount of SOC (e.g. Garcia-Pausas et al. 2017). Our findings could also help in predicting in which ecosystems the SOC might be more sensitive to the current warming trend: in particular, peatlands (i.e. wetlands) and alpine tundra (i.e. snowbeds) communities seem to be the most sensitive to warming-induced changes in carbon fluxes, confirming the long-held concern about possible positive feedbacks on climate warming (Conant et al. 2011; Davidosn and Janssens 2006; Kirschbaum 2006). Considering that significant influences of warmer temperatures were found in vegetation types characterised by small-size plants (i.e. snowbeds, wetlands and grasslands), it is likely that the effects of climate warming on decomposition could be especially pronounced in sites with reduced vegetation

cover or small plant size, where solar radiation can warm the soil without being screened by the canopy. The results lead to the conclusion that the vegetation type could effectively modulate the impact of temperature increase on ecosystem carbon stocks and should, therefore, be taken into consideration when modelling future scenarios of carbon cycle responses to climate change.

It is also important to note that local microclimatic conditions are also influenced by further environmental factors other than temperature and precipitation characterising regional climate regimes. Topography and evapotranspiration can, in fact, determine a substantial variation in the decomposition rate  $k$ , as suggested by the analysis along the climatic gradients investigated in the present study (Fig. 5a). The variation in  $k$  was generally high both among sites characterised by similar climatic conditions and among similar vegetation types. Low variation of  $k$  was found in the coldest sites, characterised by alpine tundra vegetation (i.e. snowbeds) and in vegetation types associated with high level of soil moisture (i.e. wetlands) (Fig. 5b). Among the investigated vegetation types, grasslands and coniferous forests had the highest variation in decomposition rate, probably due to the high range of climatic conditions where these types of vegetation can develop, with grasslands being present along a wide elevation gradient (from 0 to 2654 m a.s.l.) and coniferous forests covering a broad latitudinal range (from 39.2° to 46.3° N).

## Conclusions

The Tea-Bag Index, allowing the testing of litter decomposition with a replicable standard over a wide range of environments, has proved to be an effective method for studying the drivers of litter decomposition. The present study provides evidence that litter quality not only exerts the strongest influence on early litter decomposition dynamics, but also modulates the effect of soil moisture on mass loss. Moreover, while the temperature effect on the decomposition constant  $k$  depends on soil moisture, the warming-induced decrease of the amount of organic material accumulated in the soil is constant at varying levels of moisture. The temperature effect appears, however, to be related to the vegetation type, with the stabilization factor in colder and wetter ecosystems, such as snowbeds and wetlands, being potentially more sensitive to current climate change. In addition, when gridded climatic factors were used as predictors,

substantial variation in the decomposition rate was revealed, as well as in types of vegetation occurring over wide environmental gradients. In the light of these results, the variability in the response of carbon stock to climatic drivers as a function of climatic conditions and vegetation types should be taken into consideration when modelling future scenarios of carbon fluxes across terrestrial ecosystems.

**Acknowledgements** We thank T'ai Gladys Whittingham Forte for proof reading, and the Handling Editor and three anonymous reviewers for their comments on an earlier version of the manuscript. Fieldwork of DG was financially supported by Ente Parco Nazionale del Pollino as part of the research program "Un laboratorio di campo permanente nel Parco Nazionale del Pollino". SC was supported by Nature State Reserve "Montagna di Torricchio" (LTER\_EU\_IT\_033) and by Sentina Nature Reserve.

## References

Q613  
614

615 Aerts R (1997) Climate, leaf litter chemistry and leaf litter decom-  
616 position in terrestrial ecosystems: a triangular relationship.  
Q617 *Oikos* 79:439–449 <http://www.jstor.org/stable/3546886>  
618 Austin AT, Vitousek PM (2000) Precipitation, decomposition and  
619 litter decomposability of *Metrosideros polymorpha* in native  
620 forests on Hawai'i. *J Ecol* 88:129–138. <https://doi.org/10.1046/j.1365-2745.2000.00437.x>  
621  
622 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear  
623 mixed-effects models using lme4. *J Stat Softw* 67:1–48.  
624 <https://doi.org/10.18637/jss.v067.i01>  
625 Bockock KL, Gilbert OJW (1957) The disappearance of leaf litter  
626 under different woodland conditions. *Plant Soil* 9:179–185.  
627 <https://doi.org/10.1007/BF01398924>  
628 Bontti EE, Decant JP, Munson SM, Gathany MA, Przeszlowska A,  
629 Haddix ML, Owens S, Burke IC, Parton WJ, Harmons ME  
630 (2009) Litter decomposition in grasslands of Central North  
631 America (US Great Plains). *Glob Change Biol* 15:1356–1363.  
632 <https://doi.org/10.1111/j.1365-2486.2008.01815.x>  
633 Breheny P, Burchett W (2017) Visualization of regression models  
634 using visreg. *The R Journal* 9:56–71  
635 Carbognani M, Petraglia A, Tomaselli M (2014) Warming effects  
636 and plant trait control on the early-decomposition in alpine  
637 snowbeds. *Plant Soil* 376:277–290. <https://doi.org/10.1007/s11104-013-1982-8>  
638  
639 Christiansen CT, Haugwitz MS, Priem A, Nielsen CS, Elberling B,  
640 Michelsen A, Grogan P, Blok D (2016) Enhanced summer  
641 warming reduces fungal decomposer diversity and litter mass  
642 loss more strongly in dry than in wet tundra. *Glob Change*  
643 *Biol* 23:406–420. <https://doi.org/10.1111/gcb.13362>  
644 Conant RT, Ryan MG, Agren GI et al (2011) Temperature and soil  
645 organic matter decomposition rates – synthesis of current  
646 knowledge and a way forward. *Glob Change Biol* 17:3392–  
647 3404. <https://doi.org/10.1111/j.1365-2486.2011.02496.x>  
648 Cornelissen JHC, van Bodegom PM, Aerts R et al (2007) Global  
649 negative vegetation feedback to climate warming responses

of leaf litter decomposition rates in cold biomes. *Ecol Lett* 10: 650  
619–627. <https://doi.org/10.1111/j.1461-0248.2007.01051.x> 651  
Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, 652  
Eviner VT, Godoy O, Hobbie SE (2008) Plant species traits 653  
are the predominant control on litter decomposition rates 654  
within biomes worldwide. *Ecol Lett* 11:1065–1071. 655  
<https://doi.org/10.1111/j.1461-0248.2008.01219.x> 656  
Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, 657  
Wall DH, Parton WJ (2015) Formation of soil organic matter 658  
via biochemical and physical pathways of litter mass loss. 659  
*Nat Geosci* 8:776–779. <https://doi.org/10.1038/ngeo2520> 660  
Crawley MJ (2013) *The R book*. Wiley, Chichester. <https://doi.org/10.1002/9781118448908> 661  
Crowther TW, Todd-Brown KEO, Rowe CW et al (2016) 662  
Quantifying global soil carbon losses in response to 663  
warming. *Nature* 540:104–110. <https://doi.org/10.1038/nature20150> 664  
665  
Davidson EA, Janssens IA (2006) Temperature sensitivity of soil 666  
carbon decomposition and feedbacks to climate change. 667  
*Nature* 440:165–173. <https://doi.org/10.1038/nature04514> 668  
669  
Ding F, Huang Y, Sun W, Jiang G, Chen Y (2014) Decomposition 670  
of organic carbon in fine soil particles is likely more sensitive 671  
to warming than in coarse particles: an incubation study with 672  
temperate grassland and forest soils in northern China. *PLoS* 673  
*One* 9:e95348. <https://doi.org/10.1371/journal.pone.0095348> 674  
675  
Djukic I, Kepfer-Rojas S, Schmidt IK et al (2018) Early stage litter 676  
decomposition across biomes. *Sci Total Environ* 628–629: 677  
1369–1394. <https://doi.org/10.1016/j.scitotenv.2018.01.012> 678  
679  
Feltz CJ, Miller GE (1996) An asymptotic test for the equality of 679  
coefficients of variation from k populations. *Stat Med* 15: 680  
647–658 <https://www.ncbi.nlm.nih.gov/pubmed/8731006> 681  
682  
Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial 682  
resolution climate surfaces for global land areas. *Int J* 683  
*Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086> 684  
685  
Fox J, Weisberg S (2011) *An {R} companion to applied regres-* 685  
*sion*. Sage, Thousand Oaks 686  
687  
García-Palacios P, Maestre FT, Kattge J, Wall DH (2013) Climate 687  
and litter quality differently modulate the effects of soil fauna 688  
on litter decomposition across biomes. *Ecol Lett* 16:1045– 689  
1053. <https://doi.org/10.1111/ele.12137> 690  
691  
García-Palacios P, McKie BG, Handa IT, Frainer A, 691  
Hättenschwiler S (2016) The importance of litter traits and 692  
decomposers for litter decomposition: a comparison of aquatic 693  
and terrestrial ecosystems within and across biomes. *Funct* 694  
*Ecol* 30:819–829. <https://doi.org/10.1111/1365-2435.12589> 695  
696  
García-Pausas J, Montané F, Rios AI, Tauli M, Rovira P, Casals P 696  
(2017) Are soil carbon stocks in mountain grasslands com- 697  
promised by land-use changes? In: Catalan J, Ninot JM, Aniz 698  
M (eds) *High mountain conservation in a changing world*. 699  
Springer Nature, Cham, pp 207–230. [https://doi.org/10.1007/978-3-319-55982-7\\_9](https://doi.org/10.1007/978-3-319-55982-7_9) 700  
701  
Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ 702  
(2000) Long-term dynamics of pine and hardwood litter in 703  
contrasting environments: toward a global model of decom- 704  
position. *Glob Change Biol* 6:751–765. <https://doi.org/10.1046/j.1365-2486.2000.00349.x> 705  
706  
Graham EA, Rundel PW, Kaiser W, Lam Y, Stealey M, Yuen EM 707  
(2012) Fine-scale patterns of soil and plant surface tempera- 708  
tures in an alpine fellfield habitat, White Mountains, 709

- California. *Arct Antarct Alp Res* 44:288–295. <https://doi.org/10.1657/1938-4246-44.3.288>
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363. <https://doi.org/10.1002/bimj.200810425>
- Ibrahima A, Biyanzi P, Halima M (2008) Changes in organic compounds during leaf litter leaching: laboratory experiment on eight plant species of the Sudano-Guinea savannas of Ngaoundere, Cameroon. *iForest* 1:27–33. <https://doi.org/10.3832/ifer0450-0010027>
- Jagadamma S, Mayes MA, Steinweg JM, Schaeffer SM (2014) Substrate quality alters the microbial mineralization of added substrate and soil organic carbon. *Biogeosciences* 11:4665–4678. <https://doi.org/10.5194/bg-11-4665-2014>
- Kane ES, Valentine DW, Schuur EAG, Dutta K (2005) Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska. *Can J For Res* 35:2118–2129. <https://doi.org/10.1139/x05-093>
- Keuskamp JA, Dingemans BJJ, Lehtinen T, Sameel JM, Heffing MM (2013) Tea bag index: a novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol Evol* 4:1070–1075. <https://doi.org/10.1111/2041-210X.12097>
- Kirschbaum MUF (2006) The temperature dependence of organic-matter decomposition – still a topic of debate. *Soil Biol Biochem* 38:2510–2518. <https://doi.org/10.1016/j.soilbio.2006.01.030>
- Liu P, Huang J, Han X, Sun OJ, Zhou Z (2005) Differential responses of litter decomposition to increased soil nutrients and water between two contrasting grassland plant species of Inner Mongolia. *China Appl Soil Ecol* 34:266–275. <https://doi.org/10.1016/j.apsoil.2005.12.009>
- MacLean DA, Wein RW (1978) Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. *Can J Botany* 56:2730–2749. <https://doi.org/10.1139/b78-326>
- Mansfield SD, Bärlocher F (2005) Determination of soluble carbohydrates. In: Graça MAS, Bärlocher F, Gessner MO (eds) *Methods to study litter decomposition*. Springer, Dordrecht, pp 85–90. [https://doi.org/10.1007/1-4020-3466-0\\_12](https://doi.org/10.1007/1-4020-3466-0_12)
- Marwick B, Krishnamoorthy K (2018) cvequality: tests for the equality of coefficients of variation from multiple groups. R software package version 01.3. <https://github.com/benmarwick/cvequality>
- Melillo JM, Butler S, Johnson J et al (2011) Soil warming, carbon–nitrogen interactions, and forest carbon budgets. *P Natl Acad Sci USA* 108:9508–9512. <https://doi.org/10.1073/pnas.1018189108>
- Mueller P, Schile-Beers LM, Mozdzer TJ et al (2018) Global-change effects on early-stage decomposition processes in tidal wetlands – implications for a global survey using standardized litter. *Biogeosciences* 15:3189–3202. <https://doi.org/10.5194/bg-15-3189-2018>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Stevens MHH, Szoecs E, Wagner H (2017) *Vegan: community ecology package*. R package version 2.4–4. <https://CRAN.R-project.org/package=vegan>
- Parton W, Silver WL, Burke IC et al (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* 315:361–364. <https://doi.org/10.1126/science.1134853>
- R Core Team (2017) *R: a language and environment for statistical computing*. The R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Rousseeuw PJ (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *J Comput Appl Math* 20:53–65. [https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)
- Shaw MR, Harte J (2001) Control of litter decomposition in a subalpine meadow–sagebrush steppe ecotone under climate change. *Ecol Appl* 11:1206–1223. <https://doi.org/10.2307/3061022>
- Sierra CA, Malghani S, Loescher HW (2017) Interactions among temperature, moisture, and oxygen concentrations in controlling decomposition rates in a boreal forest soil. *Biogeosciences* 14:703–710. <https://doi.org/10.5194/bg-14-703-2017>
- Taylor PG, Cleveland CC, Wieder WR, Sullivan BW, Doughty CE, Doughty SZ, Townsend AR (2017) Temperature and rainfall interact to control carbon cycling in tropical forests. *Ecol Lett* 20:779–788. <https://doi.org/10.1111/ele.12765>
- Tian Q, He H, Cheng W, Bai Z, Wang Y, Zhang X (2016) Factors controlling soil organic carbon stability along a temperate forest altitudinal gradient. *Sci Rep-UK* 6:18783. <https://doi.org/10.1038/srep18783>
- Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272:393–396. <https://doi.org/10.1126/science.272.5260.393>
- Tucker C, Reed SC (2016) Low soil moisture during hot periods drives apparent negative temperature sensitivity of soil respiration in a dryland ecosystem: a multi-model comparison. *Biogeochemistry* 128:155–169. <https://doi.org/10.1007/s10533-016-0200-1>
- Wang D, He N, Wang Q, Lü Y, Wang Q, Xu Z, Zhu J (2016) Effects of temperature and moisture on soil organic matter decomposition along elevation gradients on the Changbai Mountains, Northeast China. *Pedosphere* 26:399–407. [https://doi.org/10.1016/S1002-0160\(15\)60052-2](https://doi.org/10.1016/S1002-0160(15)60052-2)
- Wu Z, Dijkstra P, Koch GW Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob Change Biol* 17:927–942. <https://doi.org/10.1111/j.1365-2486.2010.02302.x>
- Wundram D, Pape R, Löffler J (2010) Alpine soil temperature variability at multiple scales. *Arct Antarct Alp Res* 42:117–128. <https://doi.org/10.1657/1938-4246-42.1.117>
- Yajun X, Yonghong X, Xinsheng C, Feng L, Zhiyong H, Xu L (2016) Non-additive effects of water availability and litter quality on decomposition of litter mixtures. *J Freshw Ecol* 31:153–168. <https://doi.org/10.1080/02705060.2015.1079559>
- Zhang D, Hui D, Luo Y, Zhou G (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol* 1:85–93. <https://doi.org/10.1093/jpe/rtn002>
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York. <https://doi.org/10.1007/978-0-387-87458-6>

## AUTHOR QUERIES

### **AUTHOR PLEASE ANSWER ALL QUERIES.**

- Q1. A table caption must have a descriptive title which must only be one sentence in length; however, Table 1 contains more than one. In this regard, please be informed that the second and succeeding sentences were presented as a table footnote to comply with journal requirements. Please check if appropriate. Otherwise, kindly advise us on how to proceed.
- Q2. The citation “Davidson and Janssens 2006” has been changed to “Davidosn and Janssens, 2006” to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.
- Q3. Reference [Kane et al, 2005] was provided in the reference list; however, this was not mentioned or cited in the manuscript. As a rule, all references given in the list of references should be cited in the main body. Please provide its citation in the body text.
- Q4. If applicable, please provide the access dates of references [Aerts R (1997), Feltz CJ, Miller GE (1996), Marwick B, Krishnamoorthy K (2018), Oksanen J et al 2017, R Core Team (2017)].

UNCORRECTED PROOF