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

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Abstract	We examined t	he 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
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Electronic supplementary material

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REGULAR ARTICLE

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

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15 Abstract

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Aims We examined the importance of litter quality and
 microclimate on early-stage litter mass loss,
 analysed the importance of interactions among en vironmental factors in determining key decomposi tion parameters and compared the variation in de composition 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.

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

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Results Litter type exerted a stronger control on mass 27loss compared to climatic factors. The effects of soil 28moisture were not the same for high and lower quality 29litter. In addition, the effects of temperature on the 30 decomposition rate depended on soil moisture. The 31stabilization factor was strongly temperature-dependent, 32 but the influence of temperature differed among vege-33 tation types: those dominated by small-size plants 34showed a strong decrease in the potential amount of 35plant material entering into the soil stock under warmer 36 temperatures. The lowest variation in decomposition 37 rate was found in sites characterised by low 38

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- temperatures, and, among the vegetation types, in alpinesnowbeds.
- 41 *Conclusions* The role of litter quality and of the inter-
- 42 actions among environmental conditions can potentially
- 43 determine significant shifts in the expected patterns of
- 44 ecosystem carbon fluxes.

45 Keywords Tea-bag index · Litter quality · Microclimate ·
 46 Vegetation type · Decomposition constant · Stabilization
 47 factor

48 Abbreviations

GWC Gravimetric water content 5053 LMM Linear mixed-effect model MAP Mean annual cumulative precipitation 54Mean annual air temperature MAT 56 59 SOC Soil Organic Carbon TBI Tea-Bag Index 60 62

63 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 71century, but it was the introduction of the litter bags 72technique (Bocock and Gilbert 1957) that triggered the 73proliferation of a wide range of systematic studies, 74which were also motivated by the growing concern 75about global climate change (e.g. Cornwell et al. 76 2008). Research undertaken in recent decades has tried 7778 to identify the main drivers of litter decomposition as well as highlighting the importance of such factors 7980 across a wide range of environmental conditions at different spatial scales (e.g. Gholz et al. 2000; 81 Cornelissen et al. 2007; García-Palacios et al. 2013, 82 2016; Parton et al. 2007; Zhang et al. 2008). This 83 research identifies climatic factors and litter quality as 84 key drivers of litter decomposition on both a regional 85 and global scale (Aerts 1997; Austin and Vitousek 2000; 86 Cornwell et al. 2008; García-Palacios et al. 2013; Zhang 87 et al. 2008). 88

Climate can affect litter decomposition directly, by 89 regulating the activity of decomposers, and indirectly 90through changes in plant species composition and abun-91dance and, as a result, in variation in litter quality and 92quantity. The decomposability of the litter depends also 93on the specific physical and chemical properties of plant 94tissues (i.e. their quality as a resource for decomposers) 95due to their responsiveness to microbial mineralization 96 (Jagadamma et al. 2014). However, the lack of a wide-97 spread implementation of an easy-to-use and well-98standardized method for estimating litter decomposition 99 has hampered investigations aimed at understanding the 100 relative importance of climatic factors and litter quality. 101 In order to overcome the conceptual and practical 102setbacks involved in the use of local litter, Keuskamp 103 et al. (2013) have recently proposed the use of the Tea-104 Bag Index (TBI), a method based on commercially 105available tea as a standard plant material. The TBI can 106 be a useful tool to increase understanding of decompo-107sition processes through an assessment of the relative 108 importance of different drivers and through pinpointing 109the role of the interactions among environmental factors. 110

The function of the principal climatic factors (i.e. 111 temperature and precipitation) and litter quality has been 112investigated independently in the past. The potential 113interactions among these agents is poorly known, de-114spite their potential importance in the carbon balance of 115terrestrial ecosystems (Wu et al. 2011), in particular 116under changing climatic conditions and vegetation dy-117namics. Although the importance of the interactions 118between temperature and soil moisture on soil respira-119tion rates has recently been demonstrated (Sierra et al. 1202017; Tucker and Reed 2016; Wang et al. 2016), re-121search on the role of the interactions among drivers of 122litter decomposition processes (i.e. litter quality, vegeta-123tion properties and climatic features) remains limited. 124The few available studies on the influence of interac-125tions among environmental factors on litter decomposi-126tion are based on the interaction between mean annual 127air temperature (MAT) and mean annual cumulative 128precipitation (MAP) (Taylor et al. 2017) and on the 129interactions between litter quality and MAT, MAP, 130land-use and biome (Djukic et al. 2018). Furthermore, 131in most studies on litter decomposition, the main climat-132ic variables tested were treated as constant across large 133areas and within biomes (e.g. Cornelissen et al. 2007; 134Cornwell et al. 2008). Topographic variability and veg-135etation cover, however, should be taken into consider-136 ation as these factors can potentially influence local 137

microclimatic conditions (e.g. Wundram et al. 2010; 138Graham et al. 2012) and their spatial variation occurs 139at finer scales compared to the ones provided by high-140 resolution gridded climatic datasets. Variations in soil 141 slope and aspect coupled with plant shading and tran-142spiration are able to determine detailed patterns of soil 143temperature and moisture conditions on a very small 144 spatial scale. In addition, historical land-use coupled 145with the occurrence of azonal vegetation types such as 146147 those associated with specific site conditions (e.g. waterlogging, high salt content, long-lasting snow-cov-148 er, frequent disturbance) contribute to a substantial plant 149150cover differentiation of the landscape. It is, therefore, unknown how much variation in litter decomposition 151occurs at a local level, such as in sites characterised by 152153similar climate but with different vegetation types.

We measured early-stage mass loss and decomposi-154tion parameters following the TBI approach (Keuskamp 155et al. 2013) in order to investigate the effects of litter 156quality, microclimatic conditions, vegetation types and 157their interactions on litter decomposition and also to 158estimate the variation occurring in sites with similar 159climate and among different vegetation types. This 160was achieved by calculating the decomposition rate 161constant k, representing the turnover time of the labile 162fraction of material (i.e. the short-term dynamics of new 163inputs) and the stabilization factor S, indicating the 164amount of labile material that becomes recalcitrant (i.e. 165the potential carbon storage). 166

In particular, the aims of the present study were: (i) to 167assess the relative importance of litter quality and soil 168temperature and moisture in determining early-stage 169mass loss of litter; (ii) to disentangle the effects of 170vegetation type and soil temperature and moisture on 171decomposition parameters; and (iii) to compare the var-172iation in decomposition rate among types of vegetation 173and among group of sites characterised by different 174175climatic conditions.

176 Materials and methods

177 Study sites and environmental data

The study was carried out in 79 sites distributed all over
Italy (Fig. 1). Given the position of the Italian peninsula,
laying in the temperate zone of the Northern Hemisphere but located in the middle of the Mediterranean
basin, together with its orographic features, Italy

provides a wide range of contrasting climatic regimes 183within relatively small areas. Moreover, the historical 184 influence of human land-use offers a variety of natural 185 and semi-natural habitats within short distances and, 186consequently, experiencing the same climatic regime. 187 The study sites were located at an elevation ranging 188 from 0 to 2681 m a.s.l. and comprised different zones, 189 ranging from the coastal areas of the southern peninsular 190 regions and Sardinia, characterised by a typical Medi-191terranean climate, to the alpine tundra environment in 192the Rhaetian Alps (Table 1). 193

Each site was assigned one of six vegetation types - 194 snowbed, wetland, grassland, shrubland, broad-leaved 195 forest, coniferous forest – on the basis of the composition and structure of its plant communities. 197

Soil temperature was recorded hourly at each site by 198a Pendant sensor (Onset, Cape Cod, MA, USA) placed 199in the soil at a depth of 8 cm, while soil water content 200 was estimated through direct observations of the phys-201ical features of the soil - i.e. friability, ductility, 202 waterlogging - carried out during the burying of the 203tea-bags in the soil and their subsequent retrieval. An 204 estimate of the percentage of gravimetric water content 205(GWC) of the soil was undertaken in order to assign a 206 categorical class of soil moisture to each site. Three 207 categories of soil moisture were identified: dry (roughly 208 <20% GWC), moist (20-80% GWC) and wet (GWC > 20980%). 210

Standard material and sampling design

Tea-bags were incubated and processed following the 212Keuskamp et al. (2013) protocol. In each site, 3 to 5 sets 213of tea-bags, each set consisting of one green and one 214rooibos tea type, were buried in the soil at 8 cm depth at 215the beginning of the summer 2016 or 2017, depending 216on the site, and retrieved after approx. 3 months 217(Table 1). Lipton green tea (EAN: 87 22,700 05552 5) 218and Lipton rooibos tea (EAN: 87 22,700 18,843 8) were 219used, composed of nylon bags with a mesh size of 2200.25 mm. Each bag contained approx. 2 g of tea. The 221two varieties of tea differ in the type of plant material 222used, C:N ratio and percentage of water soluble fraction. 223Whereas green tea consists of leaves, has a C:N ratio of 224approx. 12 and a high water soluble fraction (ca. 50%), 225rooibos tea consists of a mixture of mainly needle-like 226litter and stem tissue, with a C:N ratio of approx. 43 and 227 contains half the amount of soluble compounds of green 228tea (Keuskamp et al. 2013). Because of their chemical 229

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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)



properties, the two types of tea were used as surrogates 230of higher and lower quality litter, respectively. After the 231232exclusion of damaged material, the data set included a 233 total of 464 tea-bags, for each of which the initial air-234dried mass and the final oven-dry mass was measured. An independent set of tea-bags consisting of 26 green 235and 26 rooibos tea-bags, was used to estimate the initial 236 237oven-dry mass by calculating the ratio between air- and oven-dry masses. 238

- Estimation of litter mass loss and decompositionparameters (k and S)
- Litter mass loss was calculated for both green androoibos tea as:

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

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

In addition, two decomposition parameters were estimated following the TBI approach (Keuskamp et al.
2013): the decomposition rate constant of the labile

fraction (k) and the stabilization factor (S). The TBI249approach is based on the assumption that the mass loss250of the recalcitrant fraction of plant material is negligible251during short incubation periods (i.e. ca. 3 months). There-252fore, the double exponential model was expressed as:253

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

where X is the fraction of remaining mass at time t, a is 254 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

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

where X_r is the fraction of remaining rooibos tea (i.e. M_1 269 / 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

$$\mathbf{a}_{\mathrm{r}} = \mathbf{H}_{\mathrm{r}}^{*} (1 - \mathbf{S}) \tag{4}$$

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

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 Table 1
 Site location and relative environmental features

Site (No.)	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Vegetation type	Soil temperatue (°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 temperatue (°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-

trant, was calculated as:

$$S = 1 - a_g / H_g \tag{5}$$

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

276 Statistical analyses

277A linear mixed-effect model (LMM) was performed to assess the effects of litter quality and soil temperature and 278moisture on initial (3-month period) mass loss. The pro-279280portion of mass loss was set as the response variable. whereas the tea type (2-level factor: green and rooibos 281tea, for higher and lower quality litter, respectively), the 282283average soil temperature during the incubation period (continuous variable, in °C), the soil moisture class (3-284level factor: dry, moist and wet) and their 2-way interac-285tions were considered as predictors. Since we buried 286multiple sets of teabags in each site, site identity was 287included in the model as a random factor. For this and the 288following analyses, minimal adequate models were ob-289tained by means of model selection following Crawley 290(2013), and model assumptions were checked through 291visual inspection of residual patterns (Zuur et al. 2009). 292

293LMMs were then fitted to k and S, considered as response variables, to investigate whether the decompo-294295sition parameters differ among vegetation types and 296how these are influenced by soil temperature and moisture. In both models, the vegetation type (6-level factor: 297 298snowbed, wetland, grassland, shrubland, broad-leaved 299forest and coniferous forest), soil temperature and moisture class and their 2-way interactions were set as the 300fixed effects, whereas the site was set as the random 301302 effect. To meet linear model assumptions, k values were square root transformed prior to analysis. 303

Finally, differences in the coefficient of variation 304 (CV) of k among climatic clusters and among vegetation 305 types were analysed using the asymptotic test of Feltz 306and Miller (1996). Climatic clusters were defined 307 through a cluster analysis on mean air temperature and 308cumulative precipitation data of the warmest quarter of 309 310 the year during the period 1970–2000; climatic variables were extracted from WorldClim version 2 (Fick and 311Hijmans 2017) at a 30 s (~1 km²) spatial resolution. 312313Cluster analysis was performed with the Ward (minimum variance) clustering method and the Euclidean 314315dissimilarity index. Finally, the optimal number of clus-316ters was identified following the silhouette width criterion (Rousseeuw 1987). 317

Statistical analyses were carried out in R version 3.4.3
(R Core Team 2017) with the following packages: lme4
(Bates et al. 2015) for model fitting, car (Fox and
Weisberg 2011) for model selection, multcomp (Hothorn
et al. 2008) for post-hoc comparisons, vegan (Oksanen
et al. 2017) for cluster analysis, cvequality (Marwick and

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Krishnamoorthy 2018) for comparison of CVs and visreg 324 (Breheny and Burchett 2017) for graphs of regressions. 325

Results

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 $(F_{1,75} = 10.49, P < 0.001) > soil temperature (F_{1,74} =$ 3317.54, P = 0.008). Thus, variation due to different litter 332quality was significantly greater than that due to soil 333temperature (Fig. 2a) and moisture (Fig. 2b) variation. 334 The interaction between litter type and soil moisture was 335also 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 338lower litter quality. Overall, mass loss was higher in wet 339and moist soils compared to dry ones (Z = 4.445,340 P < 0.001 and Z = 3.183, P < 0.001, respectively), while 341the difference between wet and moist soils was margin-342ally significant (Z = 2.204, P = 0.069). 343

Decomposition parameters

The analysis did not evidence an overall effect of soil 345temperature 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 ($F_{2,73} = 6.36$, 348P = 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 351and increasing temperatures were associated to higher k352values only in dry and wet soils. On average, k values 353were higher in wet soils than in dry (Z = 4.338, P < 0.001) 354and moist soils (Z = 3.914, P < 0.001), whereas dry and 355moist soils did not differ between each other (Z = 1.122, 356 P = 0.497). The vegetation type did not exhibit a signifi-357cant influence on k (variable excluded from the model). 358

The stabilization factor S was significantly affected 359by 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-368 ature and vegetation type ($F_{1,67} = 5.22$, P < 0.001) 369 (Fig. 4). In particular, a significant decrease of *S* 370 occurred with increasing temperatures in 371 snowbeds, wetlands and grasslands, whereas in 372 vegetation dominated by shrubs or trees *S* did 373 not vary at different temperatures.

374 Variation in decomposition rate

The coefficient of variation (CV) showed significant differences both among the 17 climatic clusters and among the six vegetation types 377 (D'AD = 57.5, P < 0.001 and D'AD = 23.8, P < 0.0013780.001, respectively). Despite substantial variation 379 occurring in almost all the clusters (Fig. S1 in 380Supplementary Material), the CV seemed to follow 381a trend towards lower values at colder tempera-382 tures (Fig. 5a) and higher values at high tempera-383 tures and low precipitation. Finally, among the 384vegetation types investigated, the lowest CV of k385was found in snowbed communities (Fig. 5b), 386 whereas grasslands and coniferous forests showed 387 the highest variation in the decomposition rate. 388 Fig. 3 Relationships between (a) the decomposition constant and (b) the stabilization factor with temperatures and moisture classes of the soil



389 Discussion

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

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

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

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



phase could explain the higher responsiveness of mass 430 431loss to increasing soil water content in this type of litter compared to low quality litter. Indeed, a substantial part 432 of litter mass loss during the early stages of litter decom-433position occurs during the leaching phase, when both 434inorganic elements and simple organic compounds are 435removed (MacLean and Wein 1978). Given the impor-436tance of the water-driven phase on litter decomposition 437 and its dependence on both the quantity and quality of 438water-soluble compounds (Ibrahima et al. 2008), it could 439 be asserted that high soil water content can potentially 440 determine a stronger mass loss in litter types rich in 441 carbohydrates, these being easily leached during the first 442 decomposition stages (Cotrufo et al. 2015; Mansfield and 443Bärlocher 2005). Liu et al. (2005) suggested that the 444different responses of the two litter types to soil water 445content could also be related to their different physical 446 structures: while, in the case of rooibos tea coriaceous 447and lignified leaves are present, green tea is composed of 448 softer and more fragile leaves, which could be more 449450prone to physical fragmentation and leaching.

The litter decomposition rate, driven mainly by microbial activity, is largely temperature-dependent
(Davidosn and Janssens 2006; Kirschbaum 2006). The
results revealed, however, that a significant increment in

k was determined by warmer soil temperatures only in 455dry and wet sites, whereas in moist soils the decompo-456sition rate did not exhibit any significant response to 457temperature variation (Fig. 3a). The impact of tempera-458ture on k is, therefore, not consistent in soils with dif-459ferent moisture levels. Results from both green and 460 rooibos tea (Fig. 2b) showed that dry soils are charac-461 terized by a lower mass loss than moist and wet soils. It 462 seems, therefore, that the reduction of the decomposi-463tion rate associated with drier conditions counteracts the 464 enhancing effect of temperature on microbial activity 465 (Fig. 2a), resulting in no significant increase of decom-466 position rates with increasing temperatures in moist 467 conditions (Fig. 3a). A possible explanation of these 468results could be that, although a temperature increase 469 enhances the activity of decomposers, it also reduces the 470moisture of the soil. It is likely that in intermediate soil 471 moisture conditions (i.e. GWC ranging from 20 to 80%) 472warmer temperatures may cause larger differences in 473soil moisture compared to those occurring in dry and 474wet soils. Similarly, Christiansen et al. (2016) reported a 475negative relation between litter decomposition rates and 476 temperature increase in both xeric and wet tundra sites, 477 due to evaporative drying associated with warmer 478temperatures, which counteracted the enhancing effect 479 Fig. 5 Values of the coefficient of variation in relation to sitespecific temperature and precipitation extracted from the WorldClim dataset (Fick and Hijmans 2017) and in the six vegetation types



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

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-492fects of the two variables resulting as additive - i.e. 493temperature has the same effect in soils belonging to 494different moisture classes. These results are consistent 495with 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, 500confirming the results of Djukic et al. (2018) on land use 501categories. The absence of a direct effect with regard to 502 the vegetation type on litter decomposition dynamics 503could be explained by the greater influence of climatic 504factors, with values of temperature and moisture varying 505greatly among vegetation types. However, the effect of the 506 interaction between vegetation type and temperature on 507the stabilization factor S was highly significant (Fig. 4). 508 This suggests that warming-induced effects on the poten-509tial storage of organic carbon in the soil could differ 510among vegetation types: although S consistently de-511512creased with increasing temperature in all soil moisture categories (Fig. 3b), consistent patterns across all the 513considered vegetation types were not observed (Fig. 4). 514515Whereas soil temperature in shrublands and forests did not affect S, the stabilization factor was significantly 516reduced by warmer temperatures in snowbeds, wetlands 517518and grasslands, which may suggest a lower stability of the soil carbon stocks of these vegetation types under warmer 519climatic conditions. More specifically, the lack of temper-520ature sensitivity of S in shrublands and forests is not 521consistent with the well-known warming-induced in-522crease in decomposition of soil organic carbon (SOC) that 523524can strongly affect the ecosystem carbon storage (e.g. Ding et al. 2014; Melillo et al. 2011; Trumbore et al. 5251996). Furthermore, in a study on the drivers of SOC 526stability in temperate forests, Tian et al. (2016) reported 527 that MAT only influences the labile carbon pool size but 528does not affect the SOC stability. Another study by 529Crowther et al. (2016) showed that the sensitivity of soil 530carbon stock to warming strictly depends on its initial 531size. Our results seems consistent with those reported by 532this last study since wetlands, snowbeds and mountain 533grasslands generally hold a large amount of SOC (e.g. 534Garcia-Pausas et al. 2017). Our findings could also help 535in predicting in which ecosystems the SOC might be 536more sensitive to the current warming trend: in particular, 537538peatlands (i.e. wetlands) and alpine tundra (i.e. snowbeds) communities seem to be the most sensitive to warming-539540induced changes in carbon fluxes, confirming the longheld concern about possible positive feedbacks on climate 541warming (Conant et al. 2011; Davidosn and Janssens 5422006; Kirschbaum 2006). Considering that significant **Q2**543 influences of warmer temperatures were found in vegeta-544tion types characterised by small-size plants (i.e. 545546 snowbeds, wetlands and grasslands), it is likely that the effects of climate warming on decomposition could be 547especially pronounced in sites with reduced vegetation 548

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cover or small plant size, where solar radiation can warm549the soil without being screened by the canopy. The results550lead to the conclusion that the vegetation type could551effectively modulate the impact of temperature increase552on ecosystem carbon stocks and should, therefore, be553taken into consideration when modelling future scenarios554of carbon cycle responses to climate change.555

It is also important to note that local microclimatic 556conditions are also influenced by further environmental 557factors other than temperature and precipitation 558characterising regional climate regimes. Topography 559and evapotranspiration can, in fact, determine a substan-560tial variation in the decomposition rate k, as suggested 561by the analysis along the climatic gradients investigated 562in the present study (Fig. 5a). The variation in k was 563generally high both among sites characterised by similar 564climatic conditions and among similar vegetation types. 565Low variation of k was found in the coldest sites, 566characterised by alpine tundra vegetation (i.e. 567snowbeds) and in vegetation types associated with high 568level of soil moisture (i.e. wetlands) (Fig. 5b). Among 569the investigated vegetation types, grasslands and conif-570erous forests had the highest variation in decomposition 571rate, probably due to the high range of climatic condi-572tions where these types of vegetation can develop, with 573grasslands being present along a wide elevation gradient 574(from 0 to 2654 m a.s.l.) and coniferous forests covering 575a broad latitudinal range (from 39.2° to 46.3° N). 576

Conclusions

The Tea-Bag Index, allowing the testing of litter decom-578position with a replicable standard over a wide range of 579environments, has proved to be an effective method for 580studying the drivers of litter decomposition. The present 581study provides evidence that litter quality not only exerts 582the strongest influence on early litter decomposition 583dynamics, but also modulates the effect of soil moisture 584on mass loss. Moreover, while the temperature effect on 585the decomposition constant k depends on soil moisture, 586 the warming-induced decrease of the amount of organic 587 material accumulated in the soil is constant at varying 588levels of moisture. The temperature effect appears, how-589ever, to be related to the vegetation type, with the 590stabilization factor in colder and wetter ecosystems, 591such as snowbeds and wetlands, being potentially more 592sensitive to current climate change. In addition, when 593gridded climatic factors were used as predictors, 594

substantial variation in the decomposition rate was re-595vealed, as well as in types of vegetation occurring over 596597wide environmental gradients. In the light of these results, the variability in the response of carbon stock to 598climatic drivers as a function of climatic conditions and 599 600 vegetation types should be taken into consideration when modelling future scenarios of carbon fluxes across 601 602 terrestrial ecosystems.

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