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A test of the hierarchical model of litter decomposition

Bradford, M.A.; Veen, G.F.; Bonis, A.; Bradford, E.M.; Classen, A. T.; Cornelissen, J.H.C.; Crowther, Thomas W.; De Long, J.R.; Freschet, G.T.; Kardol, P.; Manrubia, Marta; Maynard, Daniel S.; Newman, G.S.; Van Logtestijn, R.; Viketoft, Maria; Wardle, David A.; Wieder, W.R.; Wood, S.A.; van der Putten, W.H.

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E-mail address:

pure@knaaw.nl

1 **Testing the hierarchical model of litter decomposition**

2

3 Mark A. Bradford,^{1,2*} G. F. (Ciska) Veen,² Anne Bonis,³ Ella M. Bradford,² Aimee T.
4 Classen,^{4,5} J. Hans C. Cornelissen,⁶ Thomas. W. Crowther,⁷ Jonathan R. De Long,⁸ Gregoire T.
5 Freschet,⁹ Paul Kardol,¹⁰ Marta Manrubia-Freixa,² Daniel S. Maynard,¹ Gregory S. Newman,^{4,5}
6 Richard S.P. van Logtestijn,⁶ Maria Viketoft,¹¹ David A. Wardle,^{10,12} William R. Wieder,¹³
7 Stephen A. Wood,¹⁴ and Wim H. van der Putten^{2,15}

8

9 ¹School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

10 ²Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6700 AB
11 Wageningen, The Netherlands

12 ³UMR 6553 ECOBIO – OSUR, University Rennes I – CNRS, Campus Beaulieu, Avenue du Gl
13 Leclerc, 35042 Rennes cedex, France

14 ⁴The Rubenstein School, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA

15 ⁵The Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
16 University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

17 ⁶Systems Ecology, Department of Ecological Science, Vrije Universiteit, De Boelelaan 1085,
18 1081 HV Amsterdam, The Netherlands

19 ⁷Institute of Integrative Biology, ETH Zurich, Univeritätstrasse 16, 8006, Zürich, Switzerland

20 ⁸School of Earth and Environmental Sciences, The University of Manchester, Manchester M13
21 9PT, UK

22 ⁹Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 (CNRS – Université de Montpellier –
23 Université Paul-Valéry Montpellier – EPHE), 1919 route de Mende, Montpellier 34293, France

24 ¹⁰Department of Forest Ecology and Management, Swedish University of Agricultural Sciences,
25 901-83 Umeå, Sweden

26 ¹¹Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, 750 07
27 Uppsala, Sweden

28 ¹²Asian School of the Environment, Nanyang Technological University, 50 Nanyang Avenue,
29 Singapore 639798

30 ¹³Climate and Global Dynamics Laboratory, National Center for Atmospheric Research,
31 Boulder, CO 80307, USA

32 ¹⁵The Nature Conservancy, Arlington VA, USA

33 ¹⁵Laboratory of Nematology, Wageningen University, P.O. Box 8123, 6700 ES Wageningen,

34 The Netherlands

35

36 *Correspondence e-mail: mark.bradford@yale.edu

37 **Our basic understanding of plant litter decomposition informs the assumptions underlying**
38 **widely applied soil biogeochemical models, including those embedded in Earth system**
39 **models. Confidence in projected carbon cycle-climate feedbacks therefore depends on**
40 **accurate knowledge about the controls regulating the rate at which plant biomass is**
41 **decomposed into products such as CO₂. Here, we test underlying assumptions of the**
42 **dominant conceptual model of litter decomposition. The model posits that a primary**
43 **control on the rate of decomposition at regional to global scales is climate (temperature and**
44 **moisture), with the controlling effects of decomposers negligible at such broad spatial**
45 **scales. Using a regional-scale litter decomposition experiment at six sites spanning from**
46 **northern Sweden to southern France – and capturing both within and among site variation**
47 **in putative controls – we find that contrary to predictions from the hierarchical model,**
48 **decomposer (microbial) biomass strongly regulates decomposition at regional scales.**
49 **Further, the size of the microbial biomass dictates the absolute change in decomposition**
50 **rates with changing climate variables. Our findings suggest the need for revision of the**
51 **hierarchical model, with decomposers acting as both local- and broad-scale controls on**
52 **litter decomposition rates, necessitating their explicit consideration in global**
53 **biogeochemical models.**

54
55 The dominant conceptual model of litter decomposition posits that the primary controls on the
56 rate of decomposition are climate, litter quality and decomposer organisms¹. These controls are
57 hypothesized to operate hierarchically in space, with climate and litter quality co-dominant at
58 regional to global scales²⁻⁴, and decomposers operating only as an additional local control whose
59 effect is negligible at broader scales⁵. Consequently decomposers have been omitted as controls

60 from biogeochemical models, whereas a recent surge of interest in their inclusion has shown that
61 carbon-cycle projections depend strongly on whether and how microbial decomposers are
62 represented⁶⁻⁹. Yet evidence that microbial decomposers regulate decomposition rates at
63 regional- to global-scales, independent of climate variables such as temperature and moisture, is
64 generally lacking. One possibility for this lack of evidence is suggested by scaling theory, where
65 the influence of mechanisms that act locally can be obscured in emergent, broad-scale patterns¹⁰.

66 Pattern and scale has been described as the central issue in ecology, where the inherent
67 challenge to prediction and understanding lies in the elucidation of mechanisms, which
68 commonly operate at different scales to those on which the patterns are observed¹⁰. This scale
69 mismatch appears true for at least some ecosystem processes, such as plant productivity^{10,11}.
70 Decomposition processes, also, are controlled by variables operating at finer scales than those at
71 which the variables are typically measured and evaluated¹. For example, extensive empirical
72 support for the hierarchical model of litter decomposition has been provided through multi-site
73 climate gradient studies¹²⁻¹⁵. These multi-site studies have some common characteristics, which
74 include collecting few observations (typically 2 to 4 per site per litter species per collection) –
75 from which a mean decomposition rate is determined – and also use of site-mean data to estimate
76 climatic controls¹. Yet the hierarchical model, and its representation in the structure of
77 biogeochemical models, is based on the assumption that controls act at the microsite level, by
78 regulating the activities of decomposer organisms^{5,16}. That is, the hierarchical model is
79 conceptually grounded in local (i.e. microsite) dynamics, but has been developed and
80 substantiated with site-mean data that represents climate control of decomposition as an among-
81 site relationship.

82 Understanding controls on litter decomposition across regional scales is then necessarily
83 intertwined with scaling theory. This body of theory¹⁰ suggests that broad-scale patterns might
84 emerge from distinct, local-scale causative relationships, which contrasts with the assumption of
85 the hierarchical model that among-site patterns in decomposition approximate patterns operating
86 at the microsite (Fig. 1). We refer to this as the “assumption of scale invariance” (Fig. 2a). Two
87 lines of evidence question the validity of the assumption of scale invariance for litter
88 decomposition. The first is that the activities of decomposer communities are shaped by
89 environmental selection for a subset of functional traits, which then uniquely dictate how
90 decomposition rates respond to changing climatic controls¹⁷⁻²⁰. The second is that microclimate
91 can vary widely within a site^{21,22}. As such, site-mean climate data are likely a poor surrogate for
92 the range in microclimate experienced by decomposer organisms within a site²¹. Both lines of
93 evidence support the possibility that among-site patterns in decomposition rates emerge from
94 distinct microsite-level relationships (the “assumption of scale dependence”, Fig. 2b).

95 We use a multi-site, litter decomposition study to test between the competing
96 assumptions of scale invariance and dependence (Figs. 1,2). We worked across a climate
97 gradient in Europe at six grassland sites spanning boreal climate in northern Sweden to
98 Mediterranean climate in southern France. We predicted two specific patterns would emerge if
99 the assumption of scale invariance were to be falsified. Prediction 1 was that relationships
100 between climate and decomposition rates should differ when site-mean versus microsite-level
101 climate data are analysed. That is, the emergent regional-scale pattern from microclimate data
102 should differ from the pattern observed with site-mean climate data. Prediction 2 was that any
103 variable expected to be an important control at the microsite-level (e.g. microbial biomass),
104 should have a strong effect when regional-scale patterns are analysed using microsite-level data.

105 Litter quality was included in our experimental design, by using two grass species with
106 contrasting litter functional traits, but was not under test. Instead, standardizing known
107 controlling variables can improve estimated effects of other controls under study. In addition,
108 litter traits are expected to interact with controls such as temperature²³ and so including this
109 variable allowed us to test this possibility. In total, we measured four controls (temperature,
110 moisture, microbial biomass and soil nitrogen availability) that naturally varied among
111 microsites. All four variables are expected to act as strong local and, in the case of the climate
112 variables, broad-scale controls on decomposition^{1,5,24,25}. We then built a set of regression models,
113 structured to represent and test between assumptions of scale invariance versus dependence in
114 controls (see Methods), to compare the estimated effect sizes of these different variables on litter
115 decomposition rates.

116

117 **Results and discussion**

118 Decomposition rates varied within and among sites and between the two litter types (Fig. 3a,b).
119 As expected, mass carbon (C) loss over the 3-month field incubations was approximately twice
120 as great for the higher quality *Holcus* litter ($33.8 \pm 11.62\%$; mean \pm SD) than for the *Festuca* litter
121 ($16.8 \pm 7.15\%$). However, there was considerable variation, with loss rates for *Holcus* ranging
122 from 7.72 to 53.7%, and for *Festuca* from 0.50 to 35.3%. Similarly there was marked variation in
123 the values of the climate controls, temperature and moisture, although they had contrasting
124 within versus among site distributions. Soil temperatures clustered within sites, meaning that
125 variation was much greater among sites (Fig. 3c), ranging from 10.0 to 25.3°C for the most
126 northern to southern site means. In contrast, microsite litter moisture only clustered around the
127 site mean at the two most southern sites, where mean site moisture was lowest (11.7 and 7.5%).

128 At the most northern site the mean moisture was 51.6% but varied among microsites from 12.8
129 to 81.3% (Fig. 3d). Microsite soil nitrogen (N) availability and microbial biomass were more
130 clustered than moisture but within- versus among-site variation was still large (Figs. 3e,f). Soil N
131 varied among sites from means of 9.0 to 32.8 $\mu\text{g N g soil}^{-1}$ but within the most northern site
132 alone from 2.3 to 70.6 $\mu\text{g N g soil}^{-1}$. Equally, microbial biomass site means varied ~2-times from
133 0.96 to 2.03 $\mu\text{g CO}_2 \text{ g soil}^{-1} \text{ h}^{-1}$, but within sites from about 1.6-times (most northern) to about
134 2.75-times (most southern).

135 Prediction 1 was that emergent patterns between mean-site climate and decomposition
136 might fail to capture relationships occurring at the microsite scale. We found no support for this
137 prediction for temperature, with the “Microclimate” and “Site-mean climate” models (see
138 Methods) giving similar temperature coefficients (Table 1) and effect sizes (Fig. 4a). That is, the
139 temperature-decomposition relationship was scale invariant (Fig. 1). This perhaps is not
140 surprising given that microsite soil temperature clustered around the site mean (Fig. 3c).
141 Consequently the regional temperature-decomposition relationship should be, and was,
142 approximately equivalent whether microsite or site-mean values were explored (Fig. 4a). There
143 is evidence that microsite temperature can differ markedly to the site mean in some
144 environmental contexts²². However across 60 sites spanning a broad range in eco-climatic
145 conditions, Loescher *et al.*²¹ found that microsite soil temperatures were representative of the site
146 mean, suggesting that our finding that the temperature-decomposition relationship is scale
147 invariant might generalize to numerous ecosystem types.

148 In contrast, the moisture-decomposition relationship was strongly scale dependent: there
149 was a pronounced moisture-decomposition relationship for the Microsite model but a weak one
150 for the emergent pattern estimated from the Site-mean model (Table 1, Fig. 4b). Specifically,

151 across the large observed range of microsite moisture availability (5.7 to 83.2%), the Site-mean
152 model projected mass loss values ranging from a low of 27.4% to a high of 28.7%. In contrast,
153 the Microclimate model estimated a shift in decomposition across the same range in moisture
154 from 23.9 to 33.2% mass loss (Fig. 4b). Site means therefore poorly captured regional
155 heterogeneity in microsite moisture availability, generating a scale mismatch between local
156 mechanism and broad-scale pattern. Our data (Fig. 4b) consequently suggest that patterns
157 emerging from among-site comparisons of site-mean moisture may fail to represent causative
158 relationships operating at the much finer spatial scales at which decomposer organisms respond
159 to the environment. These findings raise questions about the use of site-mean (or coarser
160 resolution) hydroclimatic data to parameterise ecosystem models. Overall, our data suggest that
161 assumptions of the hierarchical model about scale invariance in climatic control are variable
162 dependent, cautioning against its general application as a conceptual and numerical
163 representation of controls on decomposition.

164 Using the “Microsite interactions” model (see Methods), we evaluated Prediction 2 that
165 variables considered locally important should retain a strong influence at broad spatial scales.
166 Following this prediction, the effect size of microbial biomass on decomposition rates was of
167 similar magnitude to those for the climatic variables (Fig. 5a). Specifically, estimated
168 decomposition rates varied by ~16% mass C loss with temperature change, ~11% with moisture
169 change, and ~12% with microbial biomass change (Fig. 5a). Not surprisingly, given that we
170 experimentally generated marked differences in litter quality, estimated mass loss increased
171 ~24% (from 17 to 41%) with increasing initial litter N (Fig. 5a). The soil N effect size was by
172 contrast small, leading to about a 2% positive change in estimated mass C loss but, as with all the
173 other variables, the main effect coefficient was significant ($P < 0.05$; Table 1, Fig. 5a). Although

174 some 2-way interaction coefficients were of comparable or greater magnitude to the main effects
175 for temperature, moisture and microbial biomass (Table 1), qualitatively the estimated effect
176 sizes of these variables from the Microsite interactions and Microsite main effects models were
177 similar (Figs. 4, 5b). That is, when interactions were removed, litter quality, temperature,
178 moisture and microbial biomass all retained strong control on decomposition at the regional scale
179 of our study (Table 1, Supplementary Fig. 1).

180 Exclusion of soil animal decomposers does alter litter decomposition rates in at least
181 some biomes^{15,24,26-28} but microbial effects were not explicitly examined. However, the
182 representation of microbial biomass or growth in biogeochemical models can improve predictive
183 power^{9,29} and such variables are argued to relate most directly to spatial and temporal variation in
184 biogeochemical process rates^{7,8,30}. In support of these arguments, the absolute size of our
185 estimated effects of microclimate on decomposition depended strongly on microbial biomass.
186 Specifically, using the Microsite interactions model we set microbial biomass at five values
187 representing the observed range of microsite variation, and then varied temperature and moisture
188 (Fig. 5c,d). Higher microbial biomass values generated a much greater absolute change in
189 decomposition rates with increasing temperature or moisture (Fig. 5c,d). For example, estimated
190 mass loss rates across the microsite moisture range only varied by ~5% in absolute terms when
191 microbial biomass was low, to as much as ~25% (from 28.5 to 54.2% mass loss) when it was
192 high. This influence of microbial biomass was primarily additive given that, when it was dropped
193 from the modelling (giving the Microclimate model), there was minimal influence on the relative
194 effect sizes of litter quality, temperature and moisture (Fig. 4, Table 1). An outstanding question
195 is whether the microbial traits selected by a site's climatic context^{17,18} in turn influence the
196 magnitude of microclimate effects on decomposition, as is similarly observed through climate

197 selection of plant functional traits^{23,31}. Nevertheless, our data do support emerging numerical
198 frameworks showing that explicit representation of microbes as controlling variables can
199 dramatically change expected effects of climate on broad-scale decomposition dynamics^{6,8,32}.

200 We found positive but relatively weak effects of soil N availability on decomposition
201 (Supplementary Fig. 1), despite the fact stoichiometry is considered a key control on microbial
202 growth efficiencies and hence biogeochemical process rates³³⁻³⁶. The effects might have been
203 stronger had the litter been of lower quality (e.g. <1% initial N), requiring microbes to source N
204 from the environment for growth and enzyme production³⁵. Such possibilities emphasize the fact
205 that the effect sizes we report are specific to the spatial and temporal scale of our study. For
206 example, the relative effect size of controls changes with how progressed litter decay is³⁷⁻³⁹.
207 Future work will need to test whether the hierarchical model can approximate controls on later
208 decomposition stages, in other biomes and at even broader spatial scales^{37,38}, when challenged
209 with microsite data. Where the model cannot approximate controls (i.e. where broad-scale
210 emergent patterns do not reflect microsite relationships), new microsite-level studies will be
211 needed to re-estimate parameter values for important controls. Such studies should test whether
212 measuring fine-scale temporal as well as spatial variation might also necessitate a re-evaluation
213 of how decomposition rates are controlled. Notably, our study leaves unresolved how microsite
214 variation in litter quality might influence the nature of this co-dominant control. Further, it
215 suggests a need to re-design multi-site litter decomposition studies but does not address the
216 challenge of making these studies practical given the very large number of observations
217 apparently required to test when and to what extent emergent broad-scale patterns fail to capture
218 microsite-level mechanisms¹.

219 We acknowledge that three aspects of our design may have influenced our findings:
220 enclosing litter in mesh can alter the microclimate⁴⁰; the litter species do not occur at every site;
221 and the microsite scale we measured may also be mismatched with the litterbag scale of the
222 response variable⁴¹. However, these caveats also apply to the multi-site litter decomposition
223 experiments that have helped build and reinforce the hierarchical model¹²⁻¹⁵. The important
224 caveat that we remove from these previous studies is the assumption that aggregate (i.e. site-
225 mean) data accurately capture the relationships between decomposition and the variables
226 regulating it that operate at local (microsite) scales. Notably, there is growing evidence that C-
227 and N-cycling processes in soil are driven to a large extent by microsite variation in controlling
228 variables across landscape to regional scales⁴²⁻⁴⁴. Those working in population and community
229 ecology have wrestled with the insight that aggregate data may not represent local behaviour and
230 hence lead to false conclusions and projections⁴⁵; it seems the same insight may need to be
231 grappled with in ecosystem ecology.

232

233 **Conclusions**

234 Scaling theory in ecology describes how emergent patterns can arise from distinct and causative
235 relationships operating at finer-scales¹⁰. However, the issue is nested within a broader inferential
236 challenge traditionally debated in the social sciences and increasingly so in the natural
237 sciences^{42,46-48}. Although apparently named without reference to the field of ecology, the issue is
238 termed “ecological inference” and refers to the process of using aggregate data to draw
239 conclusions about individual-level behaviour⁴⁸. Causative relationships inferred from aggregate
240 data often fail to represent the variables that control how individuals respond to and act on the
241 environment⁴⁹. By comparison, relationships inferred from site-mean data in regional- to global-

242 scale litter decomposition experiments may operate locally, or instead emerge from a set of
243 distinct local-scale relationships and controlling variables. We have referred to these two
244 possibilities as the assumption of scale invariance versus scale dependence (Fig. 2). Although we
245 find temperature control scale invariant, our findings for moisture and microbial biomass control
246 suggest that the hierarchical model may be the product of a logical inference fallacy. That is, it
247 arises because aggregate data are falsely assumed to represent finer-scale causative
248 relationships^{42,48,49}. Encouragingly, the rich body of work on scaling theory and the ecological
249 inference fallacy⁵⁰ provides a platform for ecosystem ecology to test and potentially reformulate
250 its conceptual and numerical models used to explain and predict how biogeochemical processes
251 respond to a changing environment. Our findings help reinforce calls to test and reconsider
252 which environmental variables predominantly regulate biogeochemical process rates at regional-
253 to global-scales, and when doing so emphasize the need to work at the microsite scales at which
254 organisms perceive the environment.

255

256 **Methods**

257 **Experimental design. *Site layout.*** Our research was conducted in grasslands spanning ~20°
258 latitude in Western Europe (Fig. 1). At each of six study sites, we established four 30-m linear
259 transects between 50 m and up to 2 km apart. Transects were chosen to capture within-site
260 heterogeneity in microclimate and land-use intensity (e.g. with or without grazing). Along each
261 transect we established 20×20 cm quadrats at 5-m intervals, resulting in 7 quadrats per transect.
262 In the context of this study, ‘quadrat’ serves as the ‘microsite scale’. Between 28 April and 16
263 May 2015, we placed two nylon mesh bags (5×10 cm; mesh size 0.9×1 mm) at each quadrat, ~10
264 cm apart. The mesh size presumably minimized the effect of larger soil fauna (e.g. earthworms)

265 on decomposition rates, and so our decomposition rates were likely primarily the product of
266 microbes and micro- and mesofauna^{24,40}. Each mesh bag contained 1 g air-dried grass foliar litter
267 of either *Holcus lanatus* L. or *Festuca rubra* L., which differ in their litter chemical properties
268 (see below). This resulted in a total of 6 locations × 4 transects × 7 quadrats × 2 litter types = 336
269 litterbags. Litterbags were placed flush with the soil surface, within the existing litter layer and
270 were retrieved after ~3 months. Of the 336 bags placed, 32 were lost in the field to such events
271 as consumption by cows and accidental site mowing. The litter used to fill the litterbags was
272 collected as freshly senesced material in grasslands local to the Dutch site.

273
274 *Leaf litter.* Mean litter properties for *H. lanatus* versus *F. rubra* were pH of 6.12 vs. 5.61, %N of
275 1.78 vs. 1.03, C:N of 24.7 vs. 43.7, and lignin, calcium, magnesium and potassium contents of
276 157 vs. 175, 3.72 vs. 2.75, 1.31 vs. 0.79, and 6.55 vs. 1.50 mg g⁻¹, respectively. That is,
277 regardless of the chemical property measured, *H. lanatus* was always less recalcitrant. By
278 including the two contrasting litter types at every site, we generated equal within and among site
279 variation in this variable. Doing so provided a statistical control whereby the strong within-site
280 litter type effect should be approximated by the among site effect, and so generate a scale
281 invariant pattern (Fig. 2a). Second, standardizing known controlling variables can improve
282 estimated effects of the controls under study (e.g. microclimate). Third, litter traits are expected
283 to interact with other variables, such as temperature²³, and so including this variable allowed us
284 to test this possibility.

285
286 **Measurements.** *Field.* At each quadrat we determined microclimate at the start, after ~6 weeks
287 and at the end of the field incubation period. We collected three measures per quadrat and time

288 point of soil temperature at 5-cm depth using a hand-held thermometer. Such repeated spot
289 measurements are effective at characterizing relative variation in microclimate⁴², and so our
290 measures are not indicative of absolute values experienced by the decomposing litters but instead
291 capture generally warmer vs. cooler microsites, or drier vs. wetter, across the course of the study.
292 At the mid and end time point, soil moisture content was determined gravimetrically in three soil
293 cores (5 cm depth, 2 cm diam.) from each quadrat; cores were pooled and dried at 105°C until
294 constant mass. We had intended to use these measures (plus initial soil moisture) to estimate
295 microsite moisture conditions, but marked differences in soil texture from clay (Umeå) to loamy
296 sand (Wageningen) meant that soil gravimetric moisture was a poor surrogate for litter layer
297 moisture conditions. Instead, we used litter moisture values (see *Testing Prediction 1* below).
298 Additionally, at the start point of the field incubations, 8-10 soil cores of the same size were
299 taken and pooled per quadrat and were used to determine soil gravimetric moisture, microbial
300 biomass and N availability. Initial soil samples and retrieved litterbags were shipped to the
301 Netherlands Institute of Ecology to ensure common processing. Collectively these measures
302 were intended to give estimates of four variables identified as important controls of
303 decomposition either at broad-scales (i.e. temperature and moisture), or at local-scales (i.e.
304 microbial biomass and N availability)^{32,35,51,52}. For soil microbial biomass, it is probably fairer to
305 consider this an estimate of the spatial variation in soil community activity, which includes
306 invertebrate decomposers, many of which will have been able to access the litter^{24,40}, and
307 potentially also microbes not involved in litter decomposition.

308

309 *Laboratory*. Retrieved litter was cleaned of roots, fauna and soil, before mass was determined
310 fresh and after drying at 65°C. It was next milled to a fine powder and analysed for total C
311 content through elemental analysis (Flash 2000, Thermo Fisher Scientific, Bremen, Germany).

312 The initial 168 soils (6 locations × 4 transects × 7 quadrats) were passed through a 4-mm
313 sieve and sub-sampled for gravimetric moisture, microbial biomass and N availability. We used
314 the substrate-induced respiration (SIR) method to estimate active microbial biomass⁵³, modified
315 per Fierer *et al.*⁵⁴. We estimated soil N availability by determining potential net N mineralization
316 rates as the difference between salt-extractable N-NO₃⁻ and N-NH₄⁺ at time zero and after 14 d of
317 incubation at 20°C and 65% water holding capacity⁵⁵. Soils were extracted with 1M KCl and
318 extracts measured using an auto-analyser (QuAatro Segmented Flow Analyser; SEAL
319 Analytical; Norderstedt, Germany).

320 Initial litter properties were estimated using seven randomly collected samples per
321 species, matching the sub-sampling for the litterbags. Total C and N content were measured as
322 described above, lignin after a chloroform/methanol extraction and hydrolysis with HCl,
323 following Poorter & Villar⁵⁶. Mineral nutrient concentrations and pH were measured following
324 methods described in Hendry and Grime⁵⁷ and Cornelissen *et al.*⁵⁸, respectively.

325

326 **Data and inferential analysis.** *Overview of approach.* We built a set of regression models,
327 structured to represent and test between assumptions of scale invariance versus dependence in
328 controls on litter decomposition (Fig. 2), to compare estimated effect sizes on decomposition of
329 the four controlling variables under study. Specifically, we estimated the relative effect size for
330 temperature, moisture, soil N availability and microbial biomass, across the range of observed
331 values within and among our six sites. The relative effect size depends on the slope coefficient

332 for the specific variable, the slope coefficient for any interaction it is involved in, and the range
333 of observed values of the variable. We generated the coefficients by fitting linear mixed-effect
334 models (LMMs). The effect size of a variable on mass C loss was estimated using these
335 regression parameters, while holding all other variables constant (i.e. the mean of all
336 observations for each variable), and systematically varying the variable of interest across its
337 measured range of values. That is, we plotted the regression equation for a model using the
338 coefficients from the respective LMM, the mean value across all 168 quadrats for the controls
339 not under test, and then for the control under test we estimated decomposition rates by
340 systematically increasing the value of the control from the lowest to highest observed values
341 across the 168 quadrats.

342 The choice of variables to measure and then include in our statistical models (described
343 next) was based on the approach of Hobbs *et al.*⁵⁹, which rejects model selection on
344 philosophical and operational grounds. Philosophically, we investigated only variables where
345 biological mechanism as to their influence on decomposition is firmly established. Operationally,
346 there is subjectivity and lack of agreement in statistical model selection approaches, with
347 different decisions leading to markedly different conclusions as to effect sizes. Instead,
348 coefficients and hence effect sizes are generally most robust when all terms are retained,
349 assuming that each is included with well-established biological foundation.

350

351 *Testing Prediction 1.* Prediction 1 was that relationships between climate and decomposition
352 rates should differ when site-mean versus microsite-level climate data are analysed. This
353 prediction was evaluated by comparing whether temperature and moisture effects on mass C loss
354 differed when the slope coefficients were estimated from microsite versus site-mean data. We

355 established a single model structure to test Prediction 1. It included only recognized broad-scale
356 controls as variables (i.e. temperature, moisture and litter type), but involved different data
357 aggregation. The “Microclimate” model was tested with observations of mass C loss for each
358 litterbag and quadrat-level microclimate. The “Site-mean climate” model was also run with all
359 litterbag observations – to minimize changes in predictive power associated with changing
360 values of n – but the values of the climate variables were the mean per site of the microclimate
361 (i.e. quadrat) observations. Hence in the Microclimate model the dataset had 168 unique
362 temperature and moisture observations, whereas in the Site-mean climate model there were only
363 six possible values (one per site) of temperature and moisture. Specifically, microsite control
364 values were determined from the quadrat-level measures, and site mean values determined from
365 the mean of the 28 quadrat-measures within a site (i.e. they were based on the exact same set of
366 measurements). To account for potential spatial auto-correlation among the quadrats within a
367 site, we fit a random error structure accounting for the spatial hierarchy in the design (quadrat
368 nested within transect, with transect nested within site), assuming a common slope but spatially-
369 dependent intercept^{50,60}.

370 Similarly, litter type was included as the litterbag-level %N value, or as the mean %N per
371 litter type, respectively (note that climate effect sizes were independent of how litter type was
372 included). To determine a litterbag-level initial %N value, we randomly assigned to each
373 litterbag a %N value (to the nearest 0.1%) drawn from the measured range of initial %N values
374 from seven additional litterbag samples (Fig. 3b). We did this to acknowledge that there was
375 variation among litterbags in initial %N and so using the mean initial %N would give a false
376 account of the among-bag variation. For quadrat-level temperature, we calculated the mean soil
377 temperature across the three field measurement periods. For quadrat-level moisture, given that

378 soil gravimetric moisture was not useful given soil texture differences among sites, we calculated
379 quadrat-level moisture as the mean of the *Holcus* and *Festuca* litterbag moisture values on
380 collection. We acknowledge that litters were probably drier at collection than at earlier points of
381 the field incubations, given increasing temperatures and declining precipitation across the
382 incubations, and so these values provide an estimate of relative spatial differences in moisture
383 only. We used the mean across the two litter types, given that species-specific moisture values
384 are often a product of leaf litter traits and are thus correlated with litter quality⁴.

385

386 *Testing Prediction 2.* Prediction 2 was that any variable expected to be an important control at
387 the microsite-level, should have a strong effect when regional-scale patterns are analysed using
388 microsite data. Specifically, we evaluated whether effect sizes of the soil microbial biomass and
389 N availability variables had effect sizes comparable to recognized broad-scale controls
390 (specifically temperature and moisture). We developed three model structures. The “Microsite
391 interactions” model included all variables (i.e. temperature, moisture, microbial biomass, N
392 availability) and their 2-way interactions. We included two-way interactions among the main
393 effects given expectations that the relative effects of our variables should depend on one another.
394 For example, the decomposition rate of more recalcitrant litters is expected to be more
395 temperature sensitive^{61,62}. The “Microsite main effects” model removed the 2-way interactions to
396 determine whether the effect sizes of the variables were primarily additive. The “Microclimate”
397 model was used again but to evaluate whether dropping the soil microbial biomass and N
398 availability terms altered inferences about temperature and moisture controls on mass C loss.
399 Litter type (as initial %N) was again included in all models.

400

401 *Statistical model specifics.* The LMMs were fit with a Gaussian error distribution in the “lme4”
402 package for the “R” statistical program (version 3.1.3), using the “lmer” function.
403 Decomposition was calculated as the proportional mass C loss from the litterbags. Site, transect
404 and quadrat were fit as random variables to the LMMs, with the finer scale variables nested
405 within the broader scale variables, given the potential for autocorrelation caused by spatially
406 clustering the litterbags⁶⁰. Before we tested the model structures described above, we tested the
407 data distributions. A single and highly influential observation (based on Cook’s *D*) was dropped
408 from the dataset; it had a mass C loss value of 69.9%, far higher than any other observation (Fig.
409 3a), and markedly affected residual fits. The remaining data conformed to assumptions of
410 normality, and a second-order temperature term was included given the observed unimodal
411 relationship between temperature and mass loss. Also, initial extractable N was a better choice
412 (i.e. higher standardized coefficient) than potential N mineralization for soil N availability, and
413 litter moisture (mean per quadrat) performed better than gravimetric soil moisture. Litter initial
414 %N was used to represent litter quality given that it is a strong predictor of early-stage
415 decomposition in grasses such as *H. lanatus*^{39,63}.

416 The square-root variance inflation factors (vif) were <2 for the main effects, indicating
417 low collinearity. As would be expected, there was a strong correlation between temperature and
418 its second-order term, and where the effect of one variable strongly interacted with another. We
419 reduced these ‘vif’ values by standardizing the observed value of each variable by subtracting the
420 mean and dividing by two standard deviations⁶⁴. The resulting standardized coefficients also
421 permit coefficients to be directly compared for variables measured on different unit scales.
422 Confirming the validity of our inferences in spite of introduced collinearity when second-order
423 terms and interactions were permitted, variables with large effect sizes calculated on the basis of

424 the unstandardized coefficients also had large standardized coefficients. In addition, in the
425 ‘Microsite main effects’ model all 2-way interactions were dropped, removing collinearity and
426 concerns about over-fitting, and the relative magnitude of the coefficients were largely
427 unchanged (Table 1).

428 All reported *P*-values are quasi-Bayesian but retain the same interpretation as frequentist
429 *P*-values⁶⁵. We considered coefficients with *P*<0.05 to be significant and coefficients with
430 *P*<0.10 marginally significant. We calculated the r^2 values for each model following Nakagawa
431 and Schielzeth⁶⁶. Calculation of r^2 values is common practice when modelling decomposition
432 and a high value associated with a specific explanatory variable is often associated with that
433 variable having a strong effect size. This reasoning makes no sense within the context of our
434 study because litter type was experimentally controlled and accurately measured within and
435 among sites, whereas the other variables relied on observed variation and measurements that
436 represented – but likely did not fully characterize – the conditions that acted on decomposer
437 activity. The latter conditions make data more “noisy”, lowering r^2 values, but in the absence of
438 systematic bias will not change the coefficient estimates and hence effect sizes¹. We therefore
439 only report the r^2 value for each model, to verify they had the potential to explain a substantive
440 degree of the variance in decomposition rate.

441

442 **Data availability**

443 Experimental data in the support of these findings and the R code for the statistical models are
444 available via the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.c44h0>).

445

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595

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605

606 **Authorship**

607 MAB and GFV contributed equally to this work. They designed the study, co-wrote the
608 manuscript, constructed litterbags and carried out the lab analyses. All authors established,
609 maintained and collected data from the field sites. MAB, GFV, DSM and SAW analysed data.
610 All authors contributed to data interpretation and paper writing.

611

612 **Additional information**

613 **Supplementary information** is available for this paper.

614 **Correspondence and requests for materials** should be addressed to M.A.B.

615

616 **Competing interests**

617 The authors declare no competing financial interests.

618

619 **Figure 1 | Study design and site characteristics.** Spatial organisation and operational
620 definitions of the study extent and observational grain are given in the hierarchical figure (site to
621 microsite). Sites are named for the closest city and their climate data are from climatedata.eu for
622 the months (May-June) of litterbag incubation, giving the range across months in the average
623 high and low temperature and precipitation. Soil data are the mean soil temperature and litter

624 moisture data measured across the study period. Latitude and longitude data are for one transect
625 in each site.

626 **Figure 2 | Competing assumptions for how decomposer communities affect relationships**
627 **between climate and decomposition rates at regional to global scales.** Ecosystem theory
628 holds that soil decomposer communities influence functional relationships between controls and
629 decomposition rates in a spatially invariant manner. For example, broad-scale patterns among
630 site-mean climate conditions are representative of a common relationship operating at finer
631 spatial scales (a): the assumption of *scale invariance*. Increasingly there is empirical evidence
632 that decomposer communities can be functionally distinct, meaning that broad-scale patterns
633 may instead emerge from distinct fine-scale (in this case within-site) relationships (b): the
634 assumption of *scale dependence*.

635 **Figure 3 | Measured variation in decomposition rates and controlling variables within and**
636 **among sites.** The response variable (decomposition) is shown in (a), litter quality in (b), climate
637 variables in (c) and (d), soil nitrogen availability in (e) and an estimate of the active decomposer
638 biomass in (f). Points represent individual observations ($n=303$) and are jiggered around the site
639 number to help prevent similar observations obscuring one another. Sites are described in Fig. 1.

640 **Figure 4 | Estimated effects of temperature and moisture controls on decomposition rates.**
641 Effect sizes are estimated for temperature (a) and moisture (b) using the coefficients from the
642 models presented in Table 1. Specifically, these coefficients were used in a regression equation,
643 along with the mean value across all 168 quadrats for the controls not under test, and then for the
644 control under test by systematically increasing the control from the lowest to highest observed
645 values across the 168 quadrats. Comparisons of effect sizes between the Microclimate versus
646 Site-mean climate models test whether patterns between site-mean climate and decomposition

647 rates (effect sizes from the Site-mean climate model) approximate those operating at the
648 microsite scales at which decomposer organisms perceive the environment (effect sizes from the
649 Microclimate model). The temperature-decomposition relationship appears scale invariant
650 whereas the moisture-decomposition relationship is scale dependent (Fig. 2). The two Microsite
651 models ask whether inclusion of microbial biomass and N availability as additional variables
652 alters the estimated effects of temperature and moisture. Their inclusion does not appear to
653 strongly affect the climate-decomposition relationships.

654 **Figure 5 | Estimated effects of controls on decomposition rates.** Effect sizes are estimated
655 from the Microsite interactions model presented in Table 1, and in (b) also from the Microsite
656 main effects model, following the procedure described in the legend of Fig. 4. In (a), plots for
657 each variable are generated using unstandardized coefficients from the “Microsite interactions”
658 model and the measured range in microsite conditions. The levels of each variable are
659 relativized, ranging from the minimum (0%) to maximum (100%) measured value, revealing that
660 microbial biomass (Microbe) has an effect size approximately equivalent to both temperature and
661 moisture. In (b), comparison of the two models asks whether the effect size of the microbial
662 biomass is additive or non-additively dependent on the other controlling variables. Its effect
663 seems primarily additive, given the similarity in the two plots. However, the effect sizes plotted
664 in (c) and (d) reveal that this additive effect of microbial biomass can still strongly determine
665 temperature and moisture effects on decomposition rates. The level of microbial biomass is
666 relativized, with five values shown ranging from the minimum (0%) to maximum (100%)
667 observed value. There are much stronger absolute decomposition responses to temperature and
668 moisture when microbial biomass values are greater.

669

670 **Table 1** | Coefficients, significance and r^2 values for the linear mixed models used to evaluate
671 controls on litter decomposition rates.

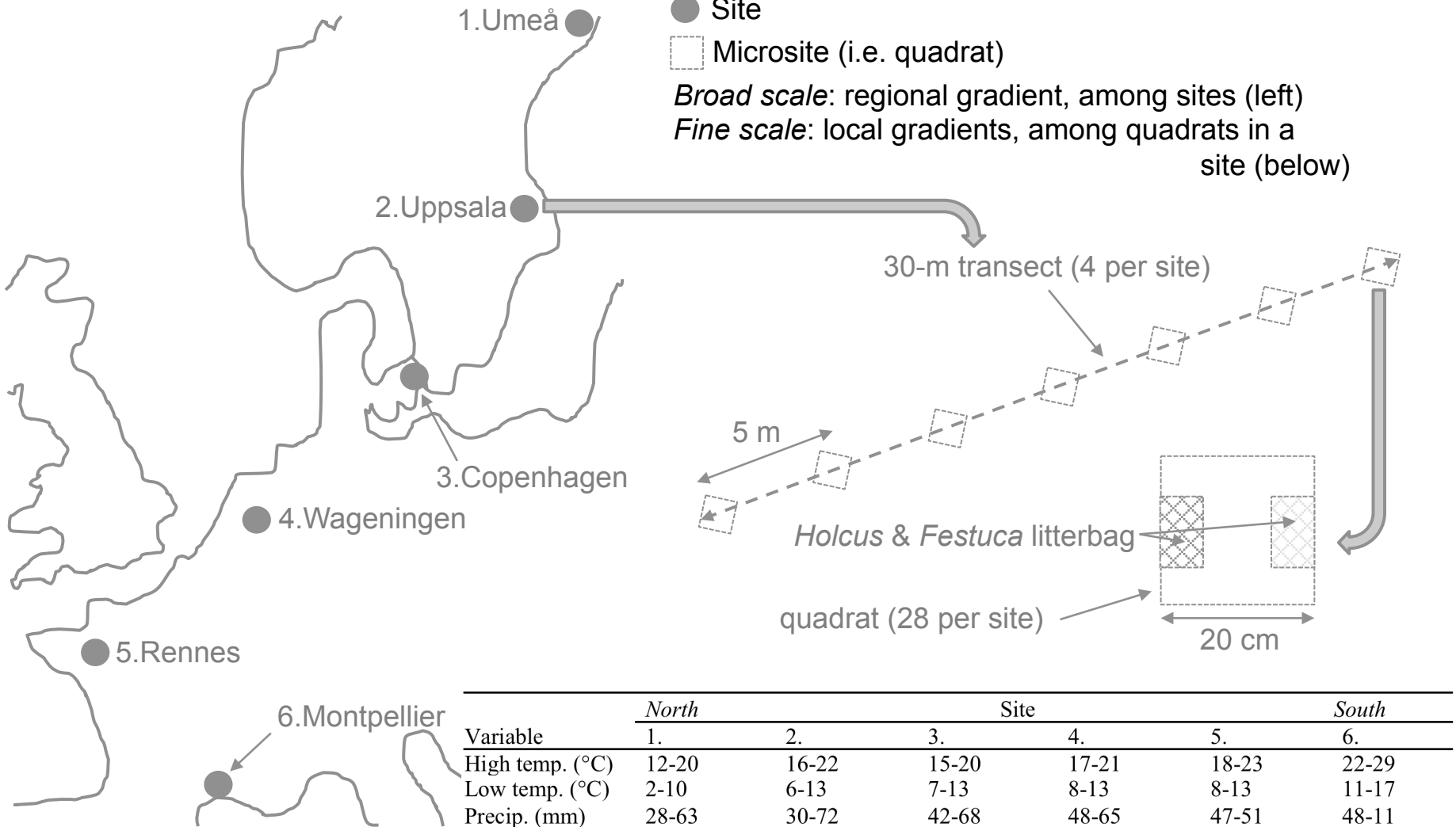
Operational definitions of scale and variance

● Site

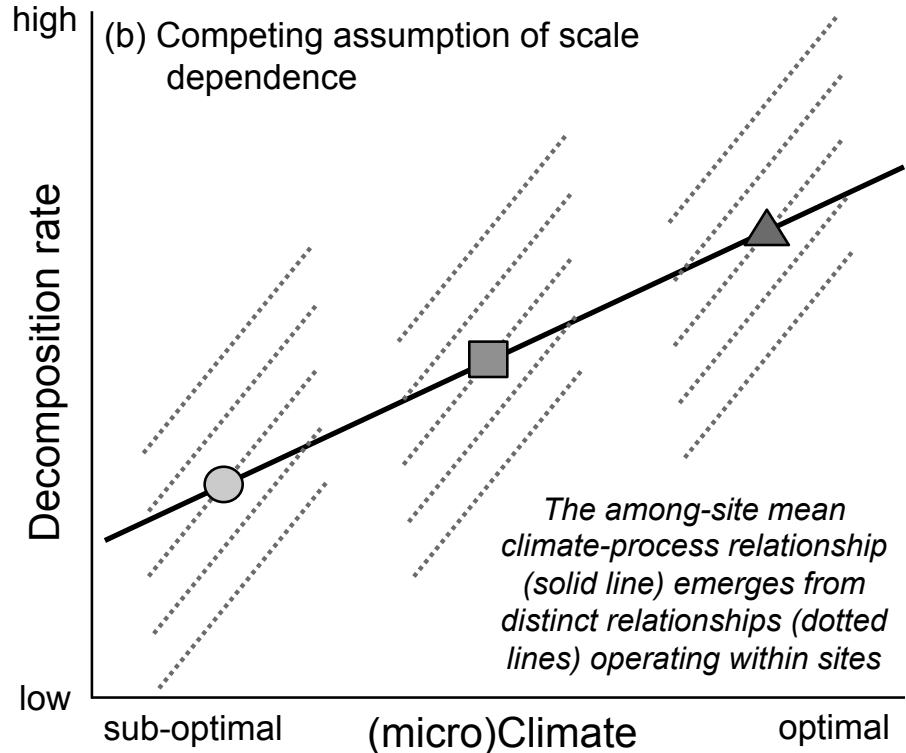
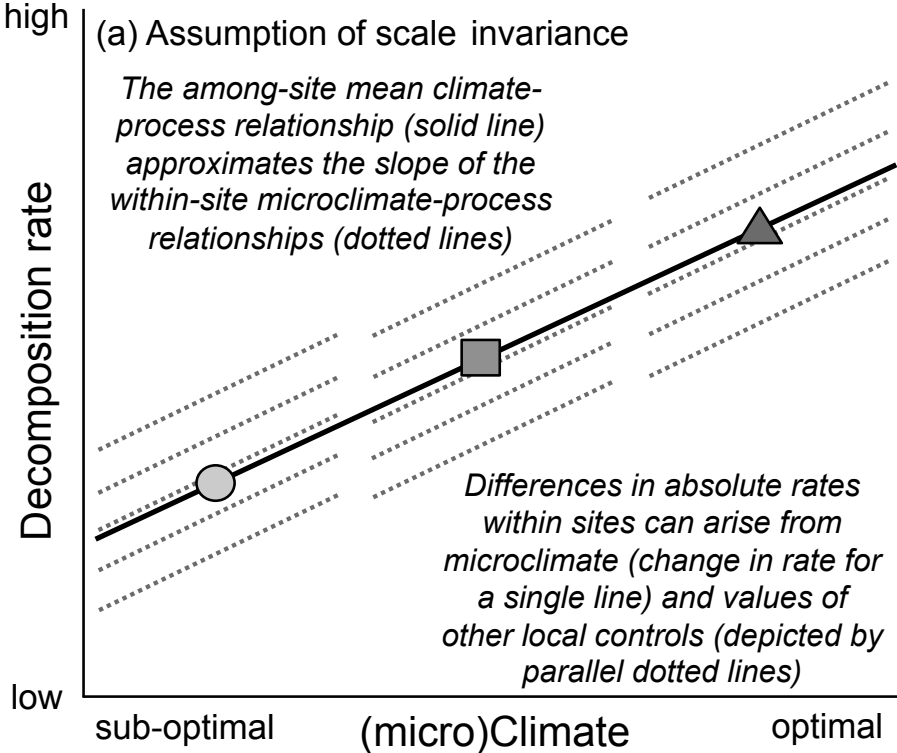
□ Microsite (i.e. quadrat)

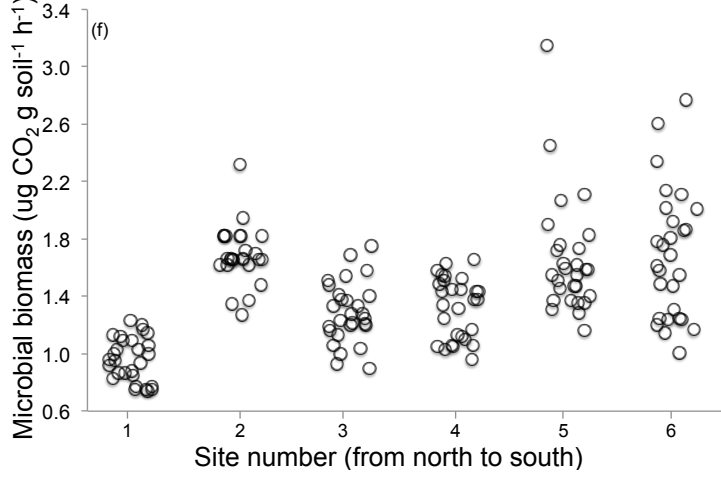
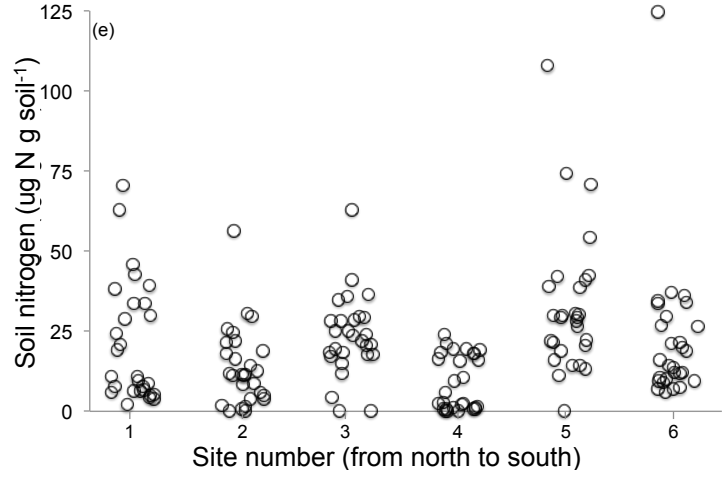
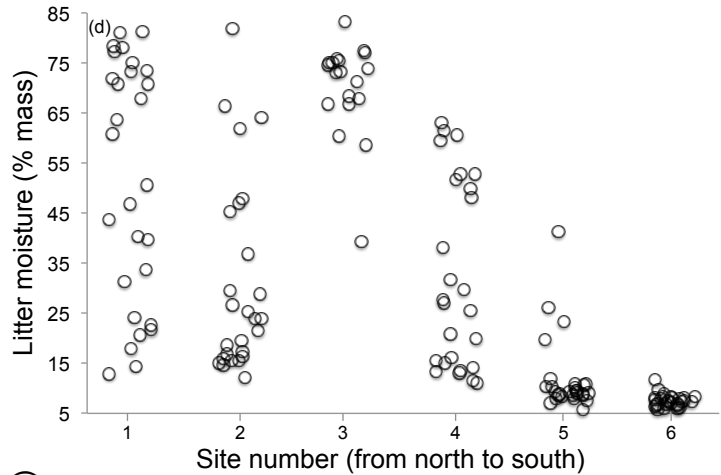
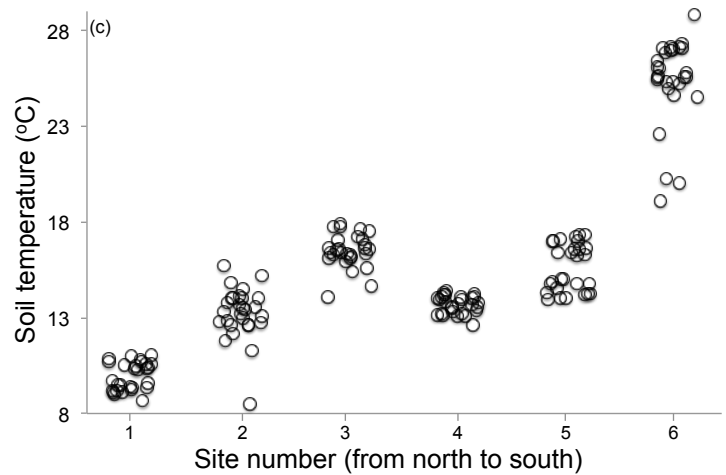
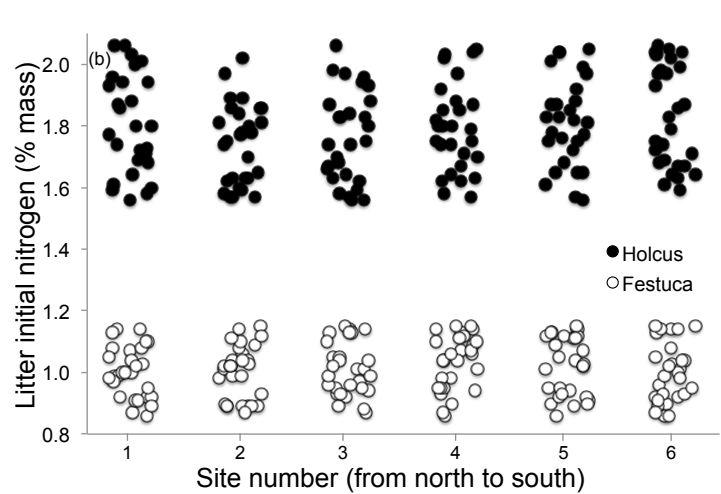
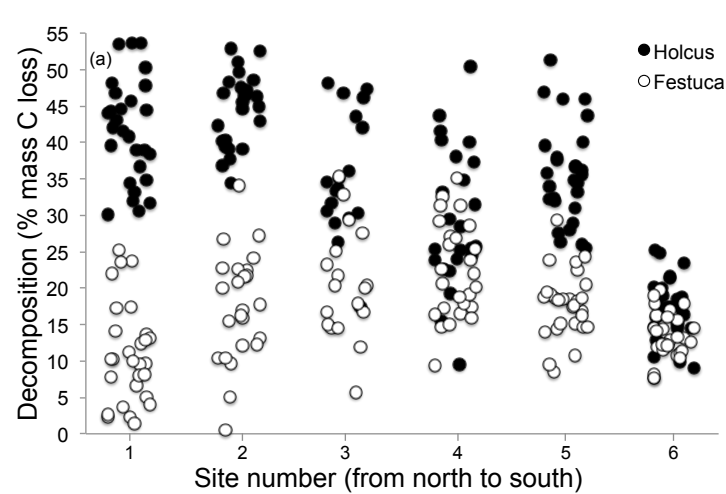
Broad scale: regional gradient, among sites (left)

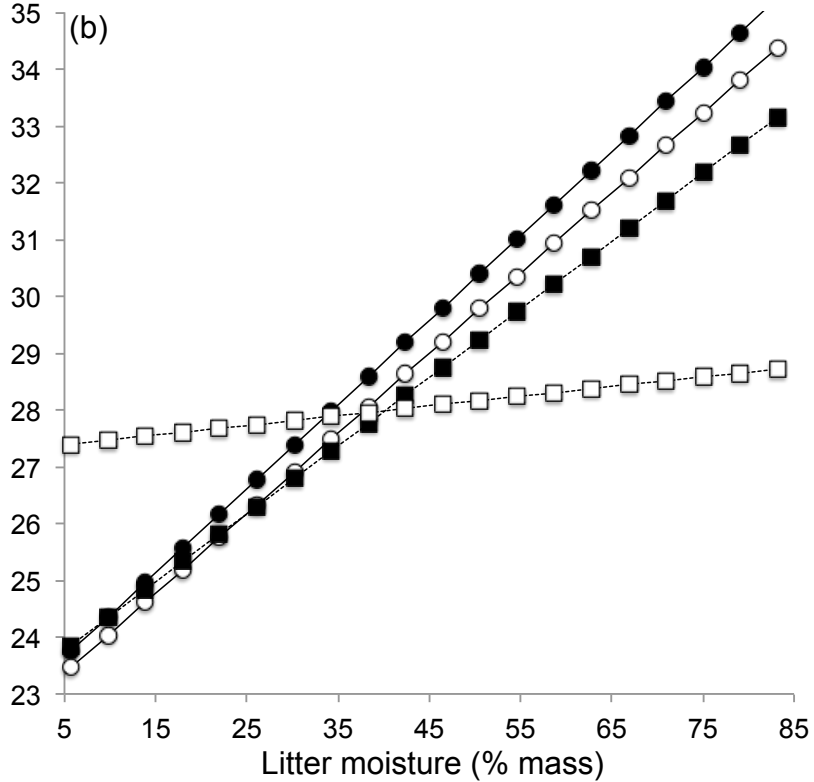
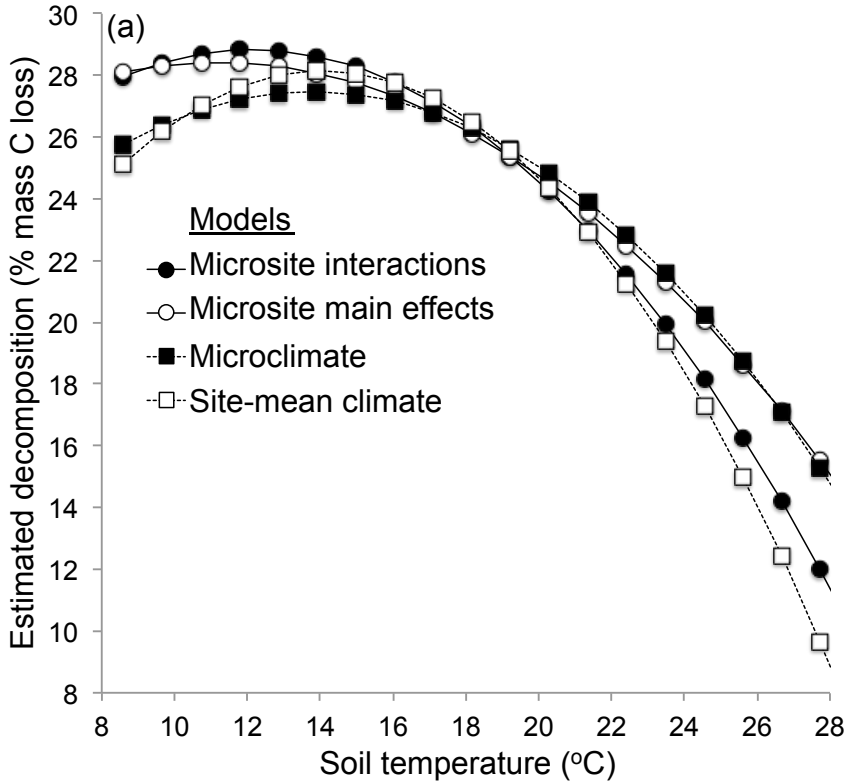
Fine scale: local gradients, among quadrats in a site (below)



Variable	Site						
	<i>North</i>	1.	2.	3.	4.	5.	<i>South</i>
High temp. (°C)		12-20	16-22	15-20	17-21	18-23	22-29
Low temp. (°C)		2-10	6-13	7-13	8-13	8-13	11-17
Precip. (mm)		28-63	30-72	42-68	48-65	47-51	48-11
Soil temp. (°C)		10.0	13.5	16.6	13.7	15.6	25.3
Litter moist. (%)		51.5	29.3	70.5	31.8	13.2	7.2
Latitude (N)		63°48'	59°46'	55°22'	52°04'	48°11'	43°55'
Longitude (E)		020°14'	017°34'	011°34'	005°45'	-001°46'	003°05'







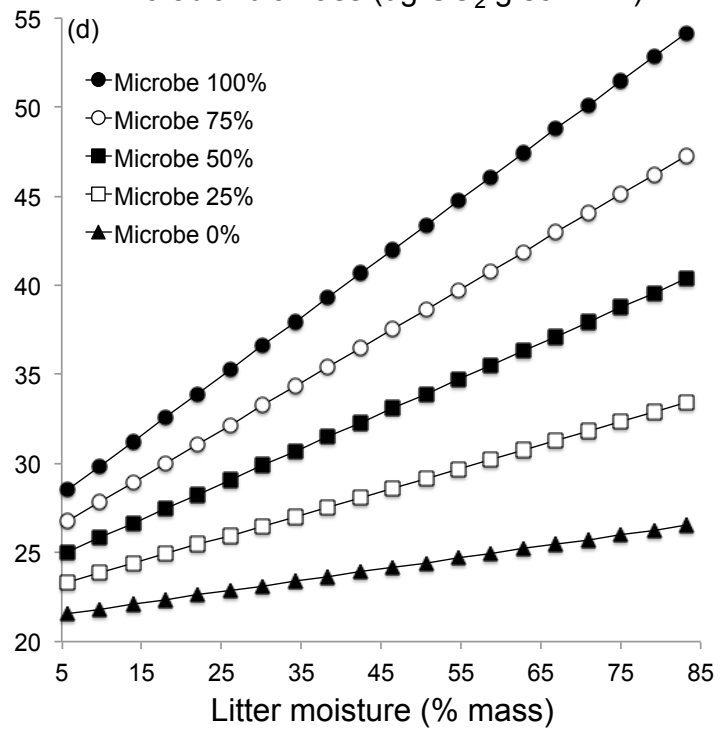
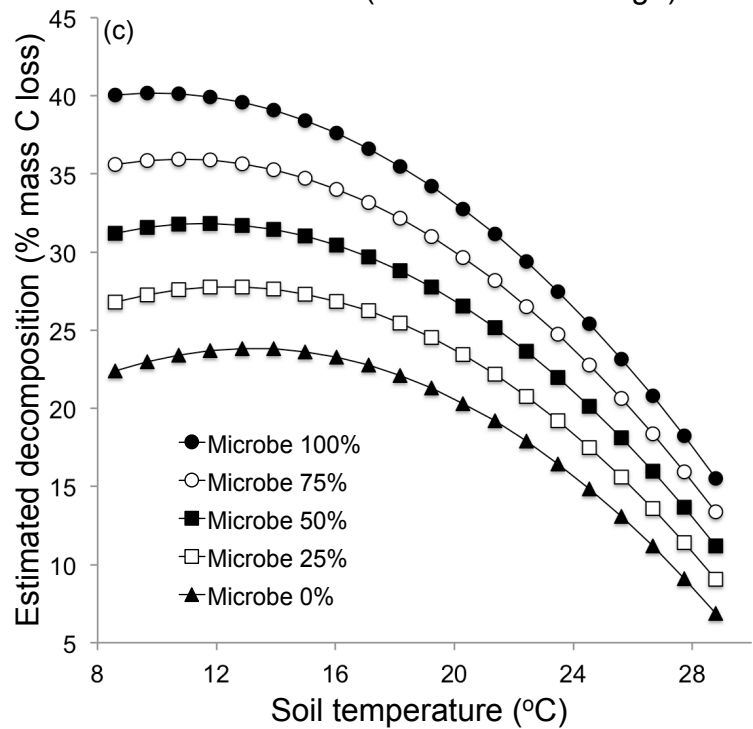
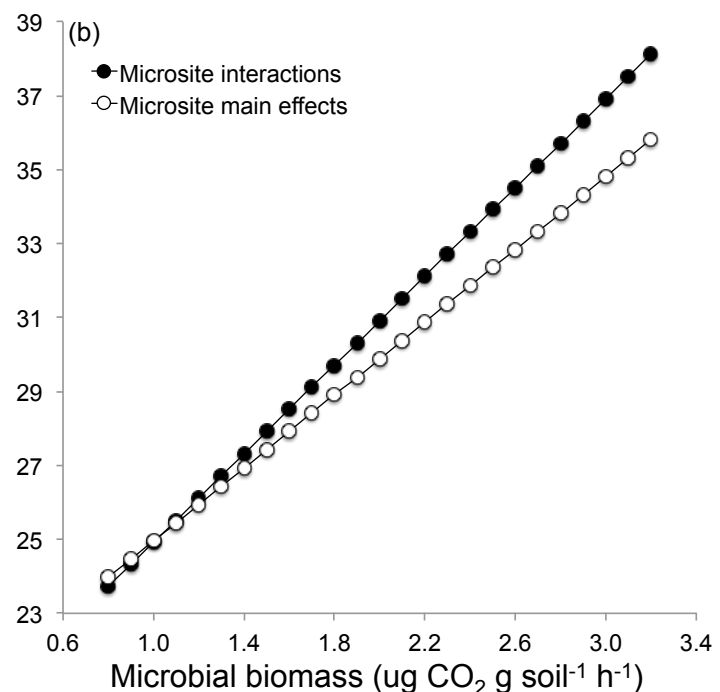
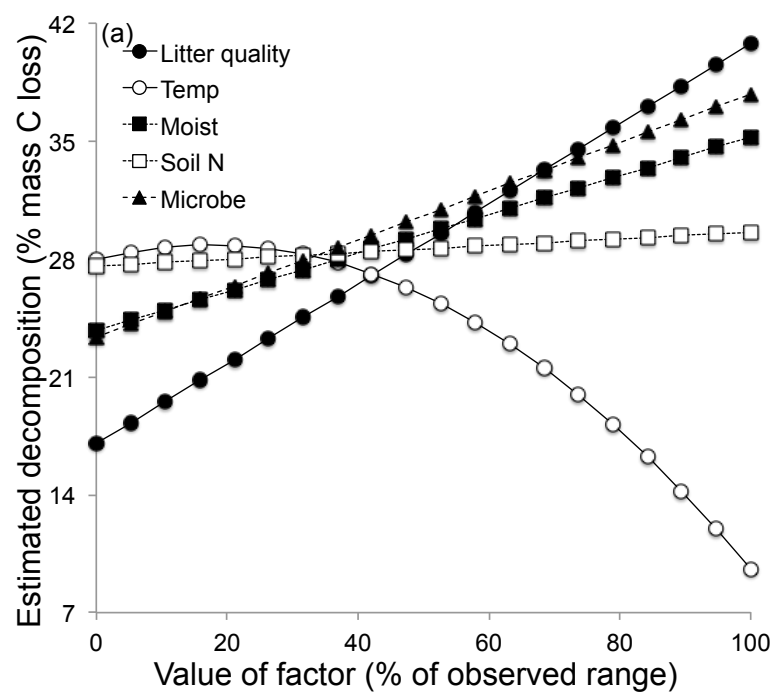


Table 1 Coefficients, significance and r^2 values for the linear mixed models used to evaluate controls on litter decomposition rates¹. Shown in the second column are standardized coefficients for the full model, where “Microsite” refers to the level at which the variables were observed, and “interactions” to the inclusion of all 2-way interactions among the predictors.

Unstandardized coefficients were used when plotting Figs. 4, 5 and Supplementary Fig. 1. The consequence of aggregating microsite variation to generate “Site means” for the predictor variables was examined, but microsite variation in the response variable was retained to maintain the number of observations ($n=303$). Significant ($P<0.05$) and marginally-significant ($P<0.1$) coefficients are shown in bold and italic fonts, respectively.

Variables	Model				
	Microsite interactions	<i>Unstandardized coefficients</i>			
		Microsite interactions	Microsite main effects	Microclimate	Site-mean climate
Intercept	27.0±0.689	-70.0±14.629	-17.1±6.264	-15.6±6.365	-24.1±6.960
Litter N	16.1±0.856	45.3±5.998	19.3±1.173	19.2±1.198	22.6±1.283
Temperature	-4.49±1.600	5.03±1.344	1.05±0.702	1.73±0.681	2.81±0.759
Temp ²	-6.84±3.285	-0.069±0.033	-0.047±0.018	-0.063±0.018	-0.100±0.021
Moisture	7.23±1.256	0.240±0.156	0.141±0.023	0.120±0.022	0.017±0.028
Soil N	0.732±1.075	0.151±0.158	<i>0.014±0.028</i>	na	na
Microbe	4.59±1.165	4.70±7.575	4.93±1.477	na	na
Lit × Temp	-13.9±1.888	-1.72±0.233	na	na	na
Lit × Moist	-0.275±2.057	-0.007±0.049	na	na	na
Lit × soilN	1.58±1.666	0.053±0.056	na	na	na
Lit × Mic	0.347±1.997	0.535±3.077	na	na	na
Temp × Moist	<i>-7.03±4.157</i>	<i>-0.014±0.008</i>	na	na	na
Temp × soilN	<i>-3.09±2.035</i>	<i>-0.009±0.006</i>	na	na	na
Temp × Mic	<i>-1.46±2.172</i>	<i>-0.185±0.276</i>	na	na	na
Moist × soilN	-3.02±2.536	-0.002±0.001	na	na	na
Moist × Mic	4.55±2.923	0.111±0.071	na	na	na
soil N × Mic	-0.409±1.226	-0.014±0.042	na	na	na
model r^2	66.3	66.3	57.1	55.2	57.6

¹Mean coefficients, their SD and significance are estimated using an MCMC sampling approach, and model r^2 values using a method that retains the random effects structure (see Methods).

Model r^2 values were identical for the fixed and full (i.e. fixed + random) effects.

Note: In the standardized Microsite interactions model, all sqrt VIFs were <2 except Temperature² which was 2.98 and Temperature \times Moisture which was 2.30. In the unstandardized Microsite interactions model, all sqrt VIFs were <10 except Temperature which was 16.0 and Temperature² which was 14.8.

In the unstandardized Microsite main effects model, all sqrt VIFs were <2 except Temperature and Temperature²; and the same was observed with the Microclimate model, and the Site-mean climate model.

na = not applicable