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Relative Importance of Climate, Soil and Plant Functional Traits During the Early Decomposition Stage of Standardized Litter

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ABSTRACT

Climatic factors have long been considered predominant in controlling decomposition rates at large spatial scales. However, recent research suggests that edaphic factors and plant functional traits may play a more important role than previously expected. In this study, we investigated how biotic and abiotic factors interacted with litter quality by analyzing decomposition rates for two forms of standardized litter substitutes: green tea (high-quality litter) and red tea (low-quality litter). We placed 1188 teabags at two different positions (forest floor and 8 cm deep) across 99 forest sites in France and measured 46 potential drivers at each site. We found that high-quality litter decomposition was strongly related to climatic factors, whereas low-quality litter decomposition was strongly related to edaphic factors and the identity of the dominant tree species in the stand. This indicates that the relative importance of climate, soil and plant functional traits in the litter decomposition process depends on litter quality, which was the predominant factor controlling decomposition rate in this experiment. We also found that burying litter increased decomposition rates, and that this effect was more important for green tea in drier environments. This suggests that changes in position (surface vs. buried) at the plot scale may be as important as the role of macroclimate on decomposition rates because of varying water availability along the soil profile. Acknowledging that the effect of climate on decomposition depends on litter quality and that the macroclimate is not necessarily the predominant factor at large spatial scales is the first step toward identifying the factors regulating decomposition rates from the local scale to the global scale.

Key words: Carbon turnover; climate; decomposition; nutrient cycling; plant traits; tea bag index; soil depth; soil parent material; soil properties.

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Author's Contribution This study was conceived and designed by LA with the help of NF. LA and NF prepared the kits for the foresters. MN and SC supervised the RENECOFOR network. Laboratory data were obtained by SB with the help of NF and LA. NF analyzed the data and wrote the first draft of the manuscript in close consultation with LA and with significant help from JMS. All authors contributed to manuscript completion and revision.

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HIGHLIGHTS

- Decomposition of high-quality litter is strongly related to climatic factors.
- Decomposition of low-quality litter is strongly related to edaphic factors.
- Position (surface vs. buried) can be as important as macroclimate on decomposition rates.

INTRODUCTION

Decomposition is an important ecological process that influences nutrient mineralization and carbon sequestration both within and among ecosystems (Moorhead and Sinsabaugh 2006; Prescott 2010). Over the last decades, an increasing body of literature has shown that climate change may strongly alter decomposition rates at the global scale (Meentemeyer 1978; Raich and Schlesinger 1992; Davidson and Janssens 2006; Currie and others 2010). This stems from the paradigm in ecology where climate (for example, temperature and precipitation) is viewed as the predominant factor regulating decomposition rates (Gholz and others 2000; Trofymow and others 2002; Liski and others 2003; Zhou and others 2008; Powers and others 2009; Portillo-Estrada and others 2016). In addition, litter chemistry and edaphic factors (that is, physical and chemical soil properties) are thought to become more important drivers at smaller spatial scales, where differences in the range of climatic conditions become narrower and hence modulate microbial activity and soil biota less (Swift and others 1979; Coûteaux and others 1995). However, the interactions between climate, soil properties and litter quality on decomposition rates have rarely been investigated, and the interplay of these different factors is especially unclear at intermediate spatial scales (Bradford and others 2016; Augusto and others 2017; Bradford and others 2017). For instance, plant species and their resource-use strategies (that is, from acquisitive to conservative strategies) often shift along with climatic or resource conditions (Ordoñez and others 2009; Adler and others 2013; Augusto and others 2015; Guittar and others 2016). This means that the combination of plant functional traits, edaphic factors and climate may become simultaneously less favorable for decomposer communities as environmental conditions become harsher (Aerts 1997; Reich and others 2003), mainly because slow-growing plant species produce recalcitrant and well-defended foliage that reduce biological activity and impair litter decomposition rates (Freschet and others 2012; Wardle and others 2012; Reich 2014; Díaz and others 2016).

In this study, we assessed the relative importance of climate, edaphic factors and plant functional traits of the dominant tree species on the decomposition process and investigated how these biotic and abiotic factors interacted with litter quality. To do so, we used standardized litter substitutes in the form of green tea (that is, high-quality litter), rich in nutrients and soluble carbon compounds, and red tea (that is, low-quality litter), poor in nutrients and soluble carbon compounds but rich in lignin (Keuskamp and others 2013). We evaluated two non-mutually exclusive mechanisms (that is, climate control vs. plant and soil control) that could explain the variability in decomposition rates between green and red tea at a large spatial scale, namely all of France (Figure 1A). First, we hypothesized that the decomposition of high-quality litter (green tea) would mainly be limited by climatic factors rather than by edaphic factors (H_1). This is because when the soluble carbon compounds and nutrients (for example, nitrogen and phosphorus) available in the litter are sufficient to fulfill the stoichiometric and metabolic requirements of microbial decomposer communities (Fanin and others 2013; Mooshammer and others 2014), decomposition would be mainly limited by temperature and humidity (Liu and others 2006; Krishna and Mohan 2017). Second, we hypothesized that the decomposition of low-quality litter (red tea) would mainly be limited by the functional traits of green leaves of the dominant tree species (for example, leaf nutrient content) and edaphic factors (for example, soil fertility) rather than by climate (H_2). This is because even if the climatic conditions are ideal for the decomposition, the carbon and nutrients available in the litter would be insufficient to satisfy the stoichiometric and metabolic requirements of the microbial communities (Zechmeister-Boltenstern and others 2015; Fanin and others 2017). Although these two mechanisms can potentially work individually or in concert, we know little about how their relative contribution to decomposition rates changes with climate, soil properties and plant functional traits at large spatial scales.

The classic tea bag method implies burying the bags at a soil depth of 8 cm (Keuskamp and others 2013). At this depth, microclimatic conditions like humidity differ considerably from those on the soil surface (Beare and others 1992; Rovira and Vallejo 1997). Differences in water content are important for decomposer communities throughout the litter–

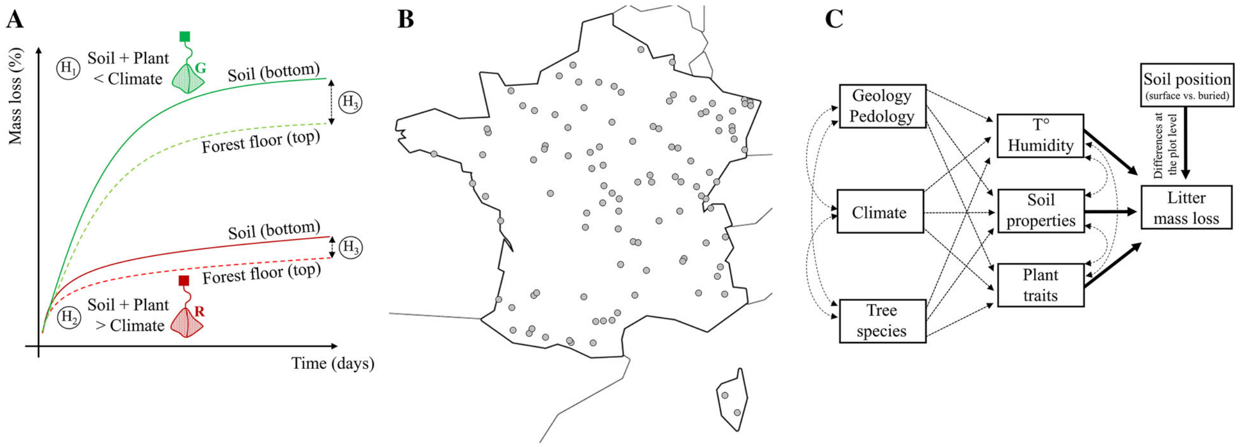


Figure 1. **A** Schematic diagram of decomposition rates for green tea (high-quality litter) and red tea (low-quality litter) at two different soil positions: forest floor (dashed lines) versus soil (solid lines). We hypothesize that climatic factors would be the main drivers of litter mass loss when litter quality was high (that is, green tea) (H_1), whereas edaphic factors and plant traits would be the main drivers of litter mass loss when litter quality was low (that is, red tea) (H_2). We also hypothesize that burying tea bags would favor decomposition for high-quality litter (that is, green tea) more than for low-quality litter (that is, red tea) because of interactions between microclimatic conditions and litter quality (H_3). **B** Distribution of the forest sites in the French RENECOFOR network. A list with location, species and site characteristics is provided in Table S1. **C** Simplified a priori conceptual structural equation model (SEM) depicting pathways by which the interactive effects of climate, geology–pedology and tree species may influence temperature and humidity, soil properties or plant traits and, ultimately, litter decomposition. We included soil position as a supplementary factor controlling litter mass loss to test our third hypothesis about the importance of microclimatic conditions at the plot level. Single-headed black arrows indicate a hypothesized causal influence of one variable upon another. Double-headed black arrows indicate a hypothesized co-variation between two variables.

soil continuum (Moorhead and Reynolds 1993; Manzoni and others 2012), and it has previously been shown that buried litter decomposed more rapidly than did litter placed on the soil surface (Vivanco and Austin 2006; Liu and others 2015; Coulis and others 2016). Nevertheless, the positive effect of soil position on decomposition rates may depend on litter quality, with labile, nutrient-rich litter being more sensitive to favorable microclimatic conditions than recalcitrant, nutrient-poor litter (Liu and others 2006; Austin and others 2009). Accordingly, we hypothesized that the decomposition of high-quality litter (green tea) would benefit more from being buried in the soil than low-quality litter (red tea) (H_3) (Figure 1A).

Our main objective was to evaluate the regulatory mechanisms that control decomposition rates at the national scale to improve our mechanistic understanding of the terrestrial carbon cycle. In practice, we monitored the decomposition of high-quality litter (green tea) and low-quality litter (red tea) at two different positions (forest floor and 8 cm in depth) at 99 forest sites in France (Figure 1B). These sites represent a wide range of climatic conditions, soil parent material, soil physicochemical properties and tree species. We measured 46 potential drivers at each site and addressed the relative importance of climate, soil and plant functional traits in relation with litter quality. Finally, we tested our hypotheses by using an *a priori* structural equation model (SEM), which enabled us to simultaneously test the effects of climate, soil properties and plant traits on tea bag mass loss (Figure 1C). We also tested whether the changing environmental conditions with increasing soil depth significantly influenced decomposition and whether local differences in position (at the plot level) controlled litter mass loss to a greater extent than large-scale differences.

MATERIALS AND METHODS

Study Sites

After the forest dieback crises of the 1980s, the French National Forest Office ('Office National des Forêts') set up a national monitoring network: the RENECOFOR network. Since 1992, the RENECOFOR's regular surveys and samplings have enabled researchers to identify symptoms of nutrition stress in trees (Jonard and others 2009) and to quantify important ecosystem processes which are difficult to measure in the short run, such as carbon sequestration in soils (Jonard and others 2017) or nutrient remobilization (Achat and others 2018). Composed of 102 different forest ecosystems (Figure 1B), this network covers a large gradient of climates (for example, mean annual temperature = 5.6–13.6°C, mean annual precipitation = 651–1987 mm year^{-1}), soil parent material (from acidic to calcareous) and soil physicochemical properties (for example, soil clay content = 0.1–59.7%, $\text{pH}_{\text{-H2O}}$ = 3.6–8.3 and P_{tot} = 18.5–1824.0 µg P g^{-1}). Tree species and plant functional groups (broadleaf vs. deciduous) also vary strongly among sites (see Table S1 for a brief description of each site). After eliminating three of the 102 sites for logistical reasons, we carried out our litter decomposition experiment on 99 distinct forest ecosystems in the network.

Decomposition Experiment

It is widely known that litter quality affects its decomposition dynamics (Aerts 1997; Fanin and others 2014; Augusto and others 2015; Djukic and others 2018). Consequently, we choose the tea bag method to standardize the initial litter quality among sites (Keuskamp and others 2013). The bags were made of non-woven PET fabric, thus allowing microorganisms and microfauna to access the contents. Because tea is functionally and phylogenetically distant from any of the main tree species in French forests, using it in standardized decomposition kits prevents any '*home field advantage,*' that is, when decomposer communities are specialized toward the litter they most frequently encounter (Gholz and others 2000; Vivanco and Austin 2008; Fanin and others 2016). We employed two types of tea that are commonly used in tea bag studies: green tea and rooibos tea (Keuskamp and others 2013). The former (green tea 'Sencha,' Lipton reference: EAN8722700055525; mean content weight = 1.82 ± 0.03 g) is representative of foliage litter, that is, it is nutrient-rich and high in water-soluble compounds. The latter (red tea 'Rooibos,' Lipton reference EAN8722700188438; mean content weight = 1.92 ± 0.02 g) is representative of woody litterfall, that is, it is nutrient poor and high in recalcitrant carbon compounds. We employed the terms 'green tea' and 'red tea' throughout the manuscript to simplify the nomenclature.

The tea bag protocol involves burying the bags 8 cm deep and retrieving them after 90 days (Keuskamp and others 2013). In this study, we placed tea bags at two different positions: at 8 cm in depth (according to the common protocol) and directly on the forest floor ('FF'). In total, 1188 tea bags were incubated in situ (99 sites × 2 tea types × 2 positions × 3 replicates); they were placed from 6 to 8 June, 2017 and retrieved 3 months later from 5 to 7 September, 2017. Because it was not possible for a single team to visit so many forests in such short periods, we relied on the hundreds of permanent correspondents in the RENECOFOR network (that is, two ONF agents per site). To limit the 'operator' effect, we wrote a documented protocol (16 pages with photos and diagrams) and tested it during the 2016 vegetation season. Briefly, in each site we selected an area of about 5 m × 1 m called the TBI (tea bag index) area protected by a fence. In each TBI area, 3 small areas of about 0.4 m in diameter were located. The distance between two small areas varied between 0.5 to 1.5 m maximum. In each small area, two plastic sticks (one per tea type) were planted and tea bags were attached to be retrieved after the incubation period. The kit of material (tea bags, plastic sticks, envelops) was sent to all operators in early 2017, and the field campaigns in June and September 2017 were followed closely to respond to questions and collect feedback.

Sampling, Data Management and General Information

After 3 months of incubation, the tea bags were collected at all the sites, soil and roots were cleaned off, the bags were oven-dried (70°C for 48 h), and the weight of the remaining tea was recorded. In total, 92.9% of the tea bags were retrieved (n = 1104), with a clear difference between those that were placed on the forest floor (87.5%) and those that were buried in the soil (98.3%). There was no difference between green tea and red tea. According to operators' reports, it seems that most of lost bags were removed by animals, even though the plots were protected by a high fence. It is likely that the lost bags were taken by rodents (except in one site where wild boars managed to intrude and destroy half of the bags on the forest floor).

We classified the 1104 recovered tea bags into four classes, based on the state of the bag: (1) intact (that is, no sign of damage on the bag; 76%); (2) slightly damaged (only one small hole [< 2 mm]; 10%); (3) moderately damaged (several small holes; 10%); and (4) severely damaged (at least one large hole; 4%). To assess the reliability of the remaining tea mass data values from the damaged bags, we compared damaged with intact bags. In practice, for a given 'site–tea type–position' combination, when there was at least one intact bag and at least one damaged bag among the three

Table 1. Mixed Models for Litter Mass Loss

	numDF	denDF	*F* value	*P* value
Soil position (SP)	1	275	74.0	< 0.001
Litter quality (LQ)	1	275	5370.9	< 0.001
SP/LQ	1	275	16.0	< 0.001

Results of the linear mixed effects models testing for the effects of soil position (that is, forest floor or soil), litter quality (that is, red or green tea) and their interaction on litter mass loss. Forest sites were considered as random factor.

replicates, we calculated a damaged-to-intact ratio for the remaining tea mass. A ratio value below 1.0 suggested that some tea had been lost through the bag's hole(s). The mean value of the ratio was not significantly different from 1.0 for the slightly damaged and the moderately damaged classes (mean ratio values $\approx$ 0.99 in both cases). Consequently, these two classes were considered reliable and the data were kept for our analyses. Conversely, the severely damaged bags produced unreliable data. However, because there were three replicates per site–tea–position combination, we ultimately had at least one reliable value for tea mass at, respectively, 91, 88, 99 and 99 sites for green tea on the forest floor, red tea on the forest floor, green tea in the soil and red tea in the soil. Only the average value per tea type (red vs. green) and per 'position' (surface vs. buried) of each forest was considered in our subsequent analyses.

Variables Selected to Explain Decomposition Rates

In all, data from 46 variables per site were collected to assess the importance of climate, edaphic factors and plant functional traits of the dominant tree species on decomposition rates. Climatic factors were determined at the site level for the 1961–1990 period. Edaphic factors and plant functional traits were determined at the site level and were representative of local conditions in which the tea bags were decomposed (Jonard and others 2009; Achat and others 2016; Achat and others 2018). Climate variables included actual evapotranspiration (AET), potential evapotranspiration (PET), mean annual precipitation (MAP), mean annual temperature (MAT), climatic water balance and climate factor (an index accounting for effects of temperature and water availability on decomposition). Plant functional traits of the dominant tree species included leaf life span, foliar N-P-S-Ca-K-Mg and foliar N/P ratio. Edaphic factors included clay, sand, silt, pH, Al oxides, Fe oxides, base saturation, cation exchange capacity (CEC), $CaCO_3$, mineralized N, N deposition, available P, exchangeable Al-Ca-Fe-H-K-Mg-Mn-Na, availability factor (an index assessing the proportion of biodegradable SOM), total N-P-Ca-K-Mg, organic C, C_{org}/N_{tot} ratio, C_{org}/P_{tot} ratio and N_{tot}/P_{tot} ratio. Elevation and forest age were not used to classify a site into a specific category as they may contribute to several of the factors above; elevation contributes to climate and edaphic factors, whereas forest age contributes to edaphic factors and plant traits. The methods and units of measurement are presented in Supporting Information (see Supplementary Methods and Table S2). Because the assessment of the microsite scales at which soil communities perform decomposition would require measuring each of the variables at the 'replicate level' (Bradford and others 2016; Bradford and others 2017), we caution that our measurements represent only the 'site level.' The use of aggregate data to draw conclusions about individual-level behavior may not represent finer-scale causative relationships, and more effort will be necessary to understand the factors that regulate biogeochemical process rates at small spatial scales. It is also important to note that biotic factors such as microbial biomass and soil biota that were not considered in this study and may also play an important role during litter decomposition (Bradford and others 2017; Lin and others 2019).

Data Analyses

We employed mixed linear models to assess the effect of tea type, soil position and their interaction on litter mass loss. Study site was a random factor in this model. We applied contrasts and performed post hoc tests (Tukey's HSD test, $\alpha = 0.05$) to assess significant differences in decomposition rates among tea types or among soil positions. We then employed variation partitioning analyses to determine the relative importance of climate, soil position, dominant tree species, geology (that is, soil parent material) or pedology (that is, soil classification) in mass loss for each tea type (green or red tea). Random forest analysis was employed to assess the best variables explaining litter mass loss for each combination tea type × soil position. We used principal component analysis (PCA) and a correlation matrix to visualize how the 46 variables were related. Litter mass loss for each tea type × soil position combination was then fitted as a supplementary variable (colored arrows in the PCA) to avoid affecting the relationships among the different variables. To visualize the differences among the different forest sites and the variables related to climate, edaphic factors and plant traits, we calculated the barycenter and the projection area between low versus high elevation, broadleaf versus evergreen and among soil parent materials or soil types. We then conducted structural equation modeling (SEM) to examine the direct and indirect effects of climate, geology–pedology and tree species on climatic factors, soil properties and plant traits, and their combined influence on litter mass loss. We selected variables that were not strongly correlated using variance inflation factors and a threshold of 3.3 to avoid multicollinearity issue in our models (Kock 2015). We also assessed whether litter mass loss varied with soil position due to differences in local conditions. A simplified version of the *a priori* model that we used is shown in Figure 1C. We also tested whether the difference in mass loss between green and red tea (Δmass loss) was affected by soil position. We then assessed the relationship between Δmass loss and climate variables and used contrasts to test whether the slopes of the regressions differed for the tea bags placed on the forest floor and for those buried in the soil. Finally, we calculated the tea bag index (TBI), based on the decomposition rate constant (*K*-TBI) and a stabilization factor (*S*-TBI). In short, the *K*-TBI value is calculated from mass loss *W* (Equation 1) after incubation time t, and *a* is the labile and $(1-a)$ is the recalcitrant fraction of the litter (Keuskamp and others 2013). The decomposition rate constant is described by *K*:

$$W(\mathrm{t}) = ae^{-Kt} + (1-a) \tag{1}$$

Environmental conditions can increase the stability of less recalcitrant compounds, reducing the mass loss of the hydrolysable fraction. This inhibiting effect is referred to as *S* (Equation 2), with *ag* being the decomposable fraction and *Hg* the hydrolysable fraction of green tea.

$$S = 1 - \frac{ag}{Hg} \tag{2}$$

We drew the relationship between *K*-TBI and *S*-TBI per soil type to verify whether soil position affected this relationship. All statistical analyses were done in R, version 3.4.3 (R Development Core Team 2014).

RESULTS

Effects of Litter Quality and Soil Position on Litter Mass Loss Across Sites

After 3 months of decomposition across the 99 forest sites, we found that litter mass loss varied significantly with litter quality (Table 1), averaging 25.8 and 65.4% for red tea and green tea, respectively (Figure 2A). Litter quality accounted for 89% of the variability in litter mass loss. Litter mass loss also varied significantly with soil position (Table 1), increasing on average by 4.7% when the tea bags were buried in the soil compared to when they were placed on the forest floor (Figure 2A). Furthermore, there was a significant interaction between litter quality and soil position (Table 1): burying tea bags increased average litter mass loss by 2.8 and 7.1% for red tea and green tea, respectively (Figure 2A).

Relative Importance of Climate, Soil Position, Dominant Tree Species, Geology and Pedology on Litter Mass Loss

The variation explained by soil position was almost threefold higher for green tea (18.7%) compared with red tea (7.5%) (Figure 2B). Similarly, the variation explained by climate was twice as important for green tea (25.5%) as for red tea (11.4%). Conversely, local factors (that is, tree species, geology and pedology) explained a smaller proportion of green tea variations in mass loss (8.6%) than they did red tea variations (15.0%). In particular, we found that the variation explained by tree species was lower for green tea (3.4%) than for red tea (10.0%). The effect of pedology (that is, soil classification) on litter mass loss was roughly similar for green tea and red tea, with about 5% of the variation explained (Figure 2B), while the effect of geology (that is, soil parent material) was relatively minor for both tea types (< 2% of the variation explained). The interactions between soil position × pedology and soil position × tree species explained on average about 4% of the variation in litter mass loss, while the interactions between soil position × climate and soil position × geology explained on average less than 2% of the variation (Figure 2B).

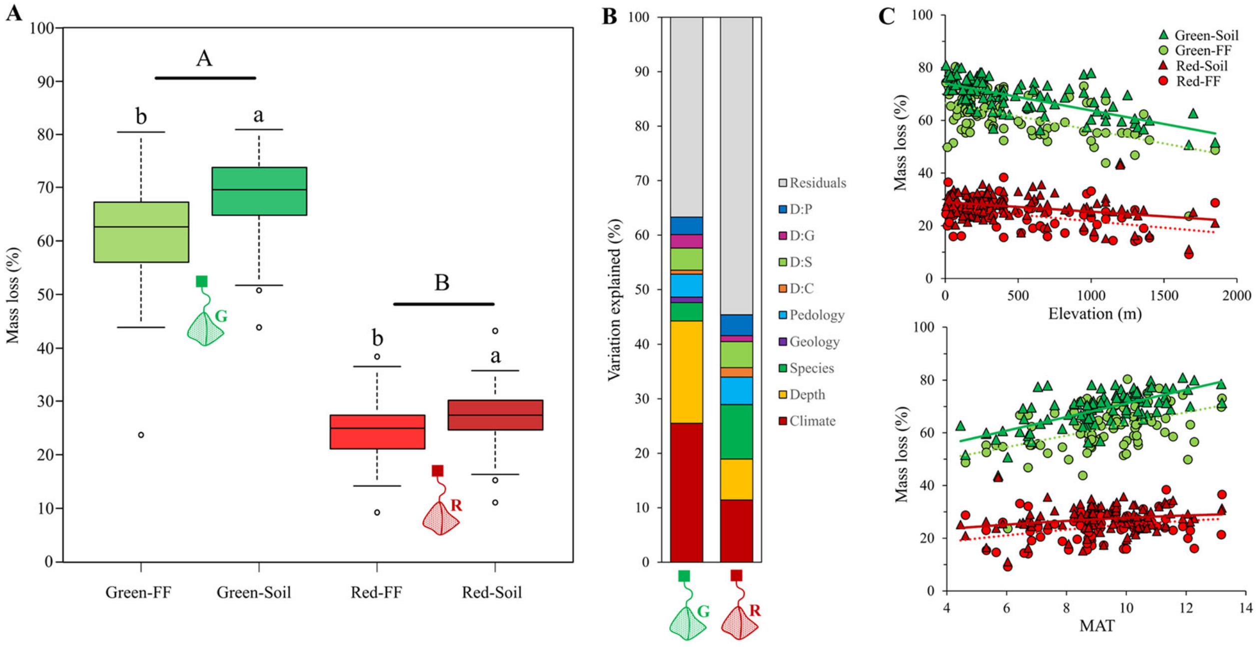
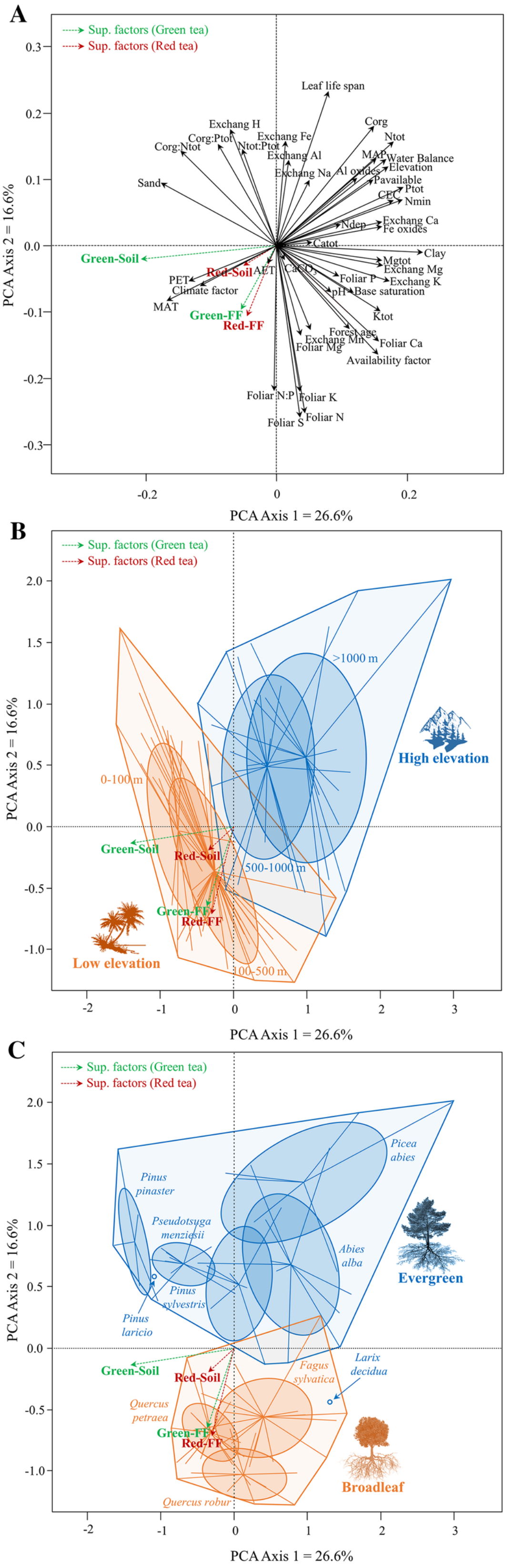


Figure 2. **A** Results of litter mass loss for green tea and red tea at different positions: on the forest floor (FF) or buried in the soil (8 cm). Boxplots characterize the lower, median and upper quartiles and interquartile range (upper quartile–lower quartile) for the central 50% of the data; whiskers represent 95% of the data. Different uppercase letters indicate significant differences between tea types and different lowercase letters indicate significant differences between soil positions for a given tea type ($P < 0.05$, Tukey HSD tests). **B** Percentage of overall variation explained by soil position (D; FF vs. soil), climate (C; climate factor), geology (G; soil parent material), pedology (P; soil classification), species (S; tree species identity) and their interactions on green and red tea mass loss. **C** Relationship between mean annual temperature (MAT) or elevation and green and red tea mass loss at different positions: on the forest floor (filled circle—dashed lines) or buried in the soil (filled triangle—solid lines). MAT and elevation were selected through random forest analysis; see Figure S1.

Identifying the Main Drivers Controlling Litter Mass Loss

Among 46 potential variables measured across the different forest sites (Table S2), elevation was always among the best three variables explaining variations in mass loss for both green and red tea (Figure S1): litter mass loss systematically decreased with increasing elevation (Figure 2C). This result was confirmed by the PCA analysis; elevation pointed in the opposite direction from the variables related to litter mass loss (Figure 3A). This is because climatic conditions in French forests depend strongly on elevation (Table S2). Elevation also represents relatively well shifts in soil properties, including soil texture (that is, from clay to sand), soil organic matter (C_{org} and N_{tot}) and CEC (that is, exchangeable K, Mg and Ca; Figure S2). Other than the effect of elevation, the most important explanatory variables for green tea were related to climate (for example, MAT), whatever the soil position considered (Figures 2C, 3A). For red tea, on the other hand, the most important variables explaining mass loss differed depending on position; for tea bags on the forest floor, variables were related to plant traits (for example, foliar N), whereas the most important variables for buried bags were related to soil properties (for example, clay and C_{org}/N_{tot}) (Figure S1, Figure 3A). The covariation among variables is shown in Table S3.

When observing the differences between soil positions (that is, forest floor vs. soil) for each tea type separately (that is, green vs. red) in the PCA analysis, we found that the variation in green tea mass loss was mainly linked to PC1, whereas for red tea, it was mainly linked to PC2 (Figure 3A). Elevation (low vs. high elevation) was the best factor explaining the variation along PC1 ($P < 0.001$, Figure 3B), whereas tree functional group (broadleaf vs. evergreen) was the best categorical factor explaining the variation along PC2 ($P < 0.001$, Figure 3C). Soil parent material was also significantly related to PC1, but no specific trend was observed for soil classification (Figure S3).



◀**Figure 3.** **A** Principal component analysis with loading vectors related to climate, edaphic factors and plant functional traits (black arrows) across the 99 experimental forest sites in the French RENECOFOR network. Green and red tea mass loss at different depths was afterward correlated with the PCA (green or red arrows) to avoid any influence during the calculation of the PCA axes and eigenvectors. The convex hulls and lines therein represent the distance of the experimental plots from the centroid for: **B** each elevation class (0–100; 100–500 in green; 500–1000: > 1000 in red); or **C** the different tree species grouped by plant functional types (broadleaf in green; coniferous in red) (Color figure online).

Building a General Model to Explain Litter Mass Loss Across Different Forest Sites

The SEM analysis of our a priori model showed that many variables were directly affected by MAT, MAP, geology classification and tree species (Figure 4). Among them, we found that the C_{org}/N_{tot} ratio, clay and foliar N were the best variables representing soil properties and plant traits, and contributed significantly to model quality (Figure 1C). Overall, the direct effect of MAT was important in explaining green tea and red tea mass loss (Figure 4A), whereas the soil C_{org}/N_{tot} ratio was important in explaining red tea mass loss (Figure 4B). Finally, we found that soil position (that is, forest floor vs. buried in the soil) participated significantly in explaining litter mass loss (Figure 4). The effects of soil position occurred in addition to those exerted by climate, soil properties or plant traits; the path coefficients for soil position were 0.45 and 0.28 for green and red tea, respectively.

Importance of Soil Position When Studying Differences Between Red Tea and Green Tea

The difference between green tea and red tea (Δmass loss) was affected by soil position (Figure 5A): Δmass loss was higher when tea bags were buried in the soil compared to when they were placed on the forest floor. When investigating the main drivers explaining these differences, we found that water-related variables (for example, MAP, AET, PET) were the main variables explaining Δmass loss. In particular, we found that the slope of the relationship between climatic water balance (that is, difference between MAP and PET) and Δmass loss varied according to soil position (AN-

COVA, $P < 0.001$): Δmass loss increased as climatic water balance decreased (that is, as the soil became drier) when the tea bags were buried in the soil but not when they were placed on the forest floor (Figure 5B). This had important consequences on the relationship between decomposition rates (*K*-TBI) and the stabilization factor (*S*-TBI). For instance, we found that, across different soil types, *S*-TBI varied with soil position for relatively similar levels of *K*-TBI (Figure S4).

DISCUSSION

Through a decomposition experiment set up across nearly one hundred forest sites, we investigated the relative importance of climate, edaphic factors and plant functional traits on litter mass loss. We specifically focused on three hypotheses (Figure 1): Climatic factors would be the main drivers of green tea mass loss (H_1) because high-quality litter alleviates energy and nutrient limitations on soil decomposer communities, meaning decomposition is mainly limited by temperature and soil moisture. Edaphic factors and plant traits would be the main drivers of red tea mass loss (H_2) because microbial decomposition of nutrient-poor, recalcitrant litter depends on nutrient availability for decomposer communities in their surrounding environment. Burying the litter would increase mass loss more for high-quality litter (H_3) due to its possibly higher sensitivity to microclimatic conditions than it would for low-quality litter. In line with our hypotheses, we found that litter mass loss did indeed depend on the interaction between litter quality and climatic or edaphic factors and plant traits, and that these effects varied with soil position (surface vs. buried). Our results have important implications for understanding the decomposition process at broad spatial scales, but they also challenge standardized protocols such as the tea bags index (TBI), since burying litter can lead to an overestimation of decomposition rates for high-quality litter in drier ecosystems.

Litter Quality as a Major Controller of Decomposition Rates

In accordance with other studies investigating mass loss with the tea bag method from local scale to global scale (Mayer and others 2017; Djukic and others 2018; Houben and others 2018; Poeplau and others 2018; Tresch and others 2018; Petraglia and others 2019), we found that green tea decomposed at faster rates (65.4% average mass loss) than did red tea (25.8%). This difference is likely due to the larger fraction of water-soluble compounds and higher nutrient content in green tea (Keuskamp and others 2013; Didion and others 2016), which favor abiotic processes such as leaching and biological processes such as microbial activity. Overall, the type of tea explained 89% of the variability in litter mass loss at the national scale, which supports the idea that litter quality is the main driver con-

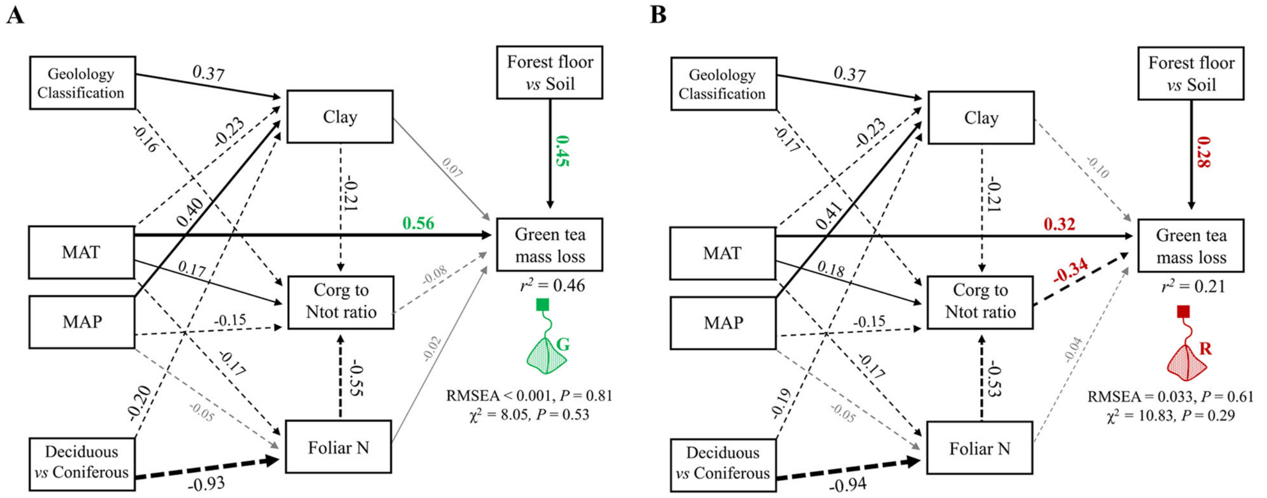


Figure 4. Structural equation model depicting the effects of climate, edaphic factors, plant functional types and soil position on mass loss of **A** green tea or **B** red tea. Because geology (that is, soil parent material) or pedology (that is, soil classification) did not explain litter mass loss, these parameters were replaced by elevation, which summarized edaphic factors relatively well (see Figure S3). Arrow width is proportional to the standardized path coefficient, indicated by a number next to the line. Solid and dashed arrows are used for positive and negative effects, respectively. The r^2 values represent the proportion of total variance explained for the dependent variable of interest.

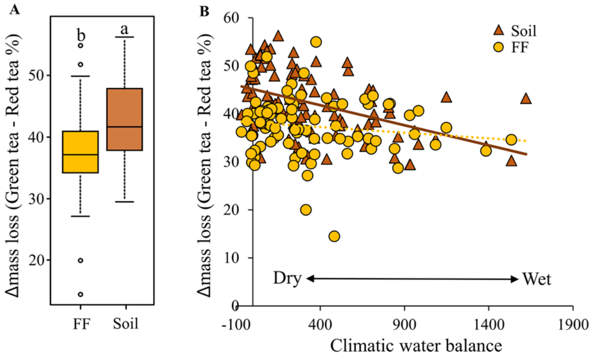


Figure 5. Δmass loss (% difference between green and red tea) at different positions: **A** boxplots depicting Δmass loss when tea bags decomposed on the forest floor (FF) or in the soil (8 cm), **B** relationships between Δmass loss and climatic water balance across forest sites. Boxplots characterize the lower, median, upper quartiles and the interquartile range (upper quartile–lower quartile) for the central 50% of the data; whiskers represent 95% of the data. Different letters indicate significant differences between soil positions ($P < 0.05$, Tukey HSD tests).

trolling litter decomposition rates within or across ecosystems (Cornwell and others 2008; Cleveland and others 2014; Fanin and others 2016; Djukic and others 2018; Petraglia and others 2019). Furthermore, this indicates that potential shifts in plant species and their relative abundance brought about by climatic changes and other environmental factors, or by changes in land use, may have an important impact on soil carbon stocks and nutrient recycling by altering decomposition rates through modifications in litter quality.

Climatic Factors Are the Main Factors Controlling the Decomposition of High-Quality Litter

In line with our first hypothesis (H_1), we found that the effect of climate was greater than that of edaphic factors or plant traits on green tea decomposition. This result confirms that climatic conditions can strongly constrain litter decomposition (Aerts 1997; Trofymow and others 2002; Davidson and Janssens 2006; Zhou and others 2008; Powers and others 2009), especially when litter quality is high (Gholz and others 2000; Liu and others 2006; Petraglia and others 2019). This is probably because when temperature and water content conditions are optimal, the decomposition process is not limited by energy or nutrients (Schimel and others 2007; Prescott 2010). In addition, greater leaching of soluble compounds could explain the higher green tea mass loss, especially when soil water content is high.

Among the main climatic factors controlling decomposition rates, MAT was the best explanatory variable for tea bag mass loss at the national scale in France. However, in the literature, the direct effects of temperature on tea bag decomposition appear to be strongly scale-dependent. For instance, Mayer and others (2017) found a positive relationship between temperature and tea bag mass loss in a temperate forest in the Austrian Alps at the local scale, whereas Djukic and others (2018) found no relationship across biomes (for example, from artic to arid subtropical) at the global scale. This is probably because the effect of temperature on decomposition rates depends on soil moisture levels, and these vary markedly at broad spatial scales, as recently shown across 79 sites in Italy (Petraglia and others 2019). To take another example, along a precipitation gradient in Norway, a positive relationship between temperature and decomposition rate was found within climate regimes, but not across different climate regimes (Althuizen and others 2018). These results underline that considering soil moisture and temperature together is important to accurately predict decomposition rates at large spatial scales (Gholz and others 2000; Aerts 2006). This further highlights that a climatic predictor such as temperature can have important consequences on overall functioning at one spatial scale and minimal impact at another.

Edaphic Factors Are the Main Factors Controlling the Decomposition of Low-Quality Litter

Partly in agreement with our second hypothesis (H_2), we found that the effect of edaphic factors and plant traits was slightly greater than that of climate on red tea decomposition. This indicates that, when the substrate is recalcitrant and poor in nutrients, increases in temperature and humidity have only a limited impact on litter decomposition. Instead, red tea decomposition was predominantly affected by the identity of the dominant tree species in the stand and soil type, thereby confirming previous studies showing that the identity of plants and their impact on soil physicochemical properties can markedly influence the decomposition process (Berg and others 1996; Prescott 2010). In particular, we observed that forest sites dominated by broadleaf deciduous species positively affected red tea decomposition rates, likely because broadleaf litter is richer in soluble compounds and nutrients (N, P, K, Ca, Mg, Mn) than evergreen coniferous litter (Berg and others 1996; Reich and others

2005; Augusto and others 2015). The long-term input of high-quality litter may create a favorable environment for microbial communities while reducing soil C/N ratios (Cools and others 2014; Fanin and others 2014), thereby promoting microbial biomass and enzymatic synthesis and ultimately quickening decomposition rates (Schimel and others 2007; Fanin and Bertrand 2016). This is in line with a recent study in agro-systems showing that red tea decomposition - but not green tea - was markedly affected by varying winter cover crops (Barel and others 2019), probably because residue amendments stimulate the turnover of organic matter *via* a knock-on effect on soil microbial communities.

The Unexpected Role of Elevation in Controlling Decomposition Rates

Interestingly, elevation was a central factor influencing the decomposition of both green and red tea (see also Becker and Kuzyakov 2018). Although temperature decreases and precipitation increases with altitude, elevation cannot be reduced to climatic factors alone. In particular, we found that elevation also represents shifts in important soil factors such as soil texture and cation exchange capacity (CEC), which vary strongly at broad spatial scales (Figure S3). In short, carbon and nitrogen content increased with elevation in our study network parallel to the increasing abundance of evergreen gymnosperms (Achat and others 2018). In addition, soil clay content increased with increasing elevation, probably because soils tend to be older, hence more weathered, in plains than in mountains (Houlton and others 2018). The coupled increase of clay and C_{org} positively affected CEC and the availability of key elements such as Mg, K or Ca, and this may strongly limit soil functioning and decomposition rates across contrasting ecosystems (Kaspari and others 2008; Makkonen and others 2012). Thus, although elevation is often thought to represent changes in climatic conditions only, it also reflects important changes in plant community composition and edaphic factors (Gerdol and others 2016), which have repercussions on nutrient availability, humus build-up and ultimately on decomposition rates (Nottingham and others 2015; Althuizen and others 2018).

Importance of Soil Position and Microclimatic Conditions in Explaining Decomposition Rates

In agreement with previous studies showing that litter decomposition depended on soil depth (Vivanco and Austin 2006; Liu and others 2015; Coulis and others 2016), we found that both green and red tea decomposed more slowly on the forest floor than when they were buried in the soil. At 8 cm in depth, microclimatic conditions such as humidity differ from those on the soil surface (Beare and others 1992; Moorhead and Reynolds 1993; Rovira and Vallejo 1997; Manzoni and others 2012), and may favor microbial activity, especially during the growing season when the climate is relatively dry. Furthermore, our data demonstrate that plot-level environmental conditions can explain more variation in litter mass loss than the macroclimate (Figure 4). This supports Joly and others (2017) recent results showing that differences in the local decomposition environment may control decomposition to a greater extent than large-scale differences. This challenges the paradigm where macroclimate is the predominant factor controlling decomposition rates at large spatial scales (Bradford and others 2016), and also underlines the necessity to consider the microsite scales at which soil communities perform decomposition (Bradford and others 2017).

In line with our third hypothesis (H_3), green tea was more influenced by soil position than red tea. This is in agreement with previous observations showing that the decomposition of high-quality litter is more likely to be limited by soil moisture regimes than for low-quality litter (Austin and others 2009; Petraglia and others 2019), which is more sensitive to nutrient availability and/or biotic interactions with microbial communities (Liu and others 2006; Fanin and others 2016). It resulted in greater differences between green tea and red tea (Δmass loss) in the soil than on the forest floor. Interestingly, Δmass loss was strongly related to climatic water balance (that is, difference between AET and precipitation), but the slope of the relationship changed with soil position (Figure 5). This means that although Δmass loss varies markedly between the forest floor and the underlying soil in dry ecosystems, Δmass loss changes little in wet ecosystems. This is in agreement with Mikola and others (2018) who showed that the decomposition of green tea strongly depended on the water regime on the soil surface, but varied less when tea bags were buried deeper in the soil.

The variability in litter mass loss along the soil profile has important implications for the interpretation of the tea bag index (TBI). Indeed, variations in green tea mass loss and Δmass loss with soil position may affect the relationships between the stabilization factor and the decomposition rate. For instance, when considering the different soil types in our study, we found that *S*-TBI strongly varied for a relatively similar *K*-TBI (Figure S4), with higher *S*-TBI values for the forest floor than in the underlying soil layer. This means that the inhibiting effect of environmental conditions on the decomposition of the labile fraction is higher in the surface litter layer (Keuskamp and others 2013), and highlights different soil carbon sequestration potentials according to soil horizon. It also suggests that the positive effect of temperature on tea bag mass loss is directly dependent on moisture, with potential negative feedback loops if the soil becomes too dry to support microbial activity. Therefore, although our data do not challenge the validity of other studies following the tea bag protocol, our results emphasize that care must be taken when interpreting stabilization versus decomposition rate in a TBI approach because they strongly depend on local conditions at the microsite level.

CONCLUSIONS

The results of our large-scale decomposition experiment provide new insights into the relative effects of climate, soil and plant functional traits on the decomposition process. First, we highlight that litter quality is the predominant factor controlling decomposition rates at large spatial scales. This clearly demonstrates that shifts in plant species due to changes in climate, land use or environmental conditions will have a drastic impact on carbon and nutrient cycling because the resulting modifications in litter quality will change decomposition rates. Second, we found that decomposition of high-quality litter was strongly related to climatic factors, whereas decomposition of low-quality litter was more strongly related to edaphic factors and plant traits. This indicates that nutrient-rich and labile litter is mainly limited by temperature and moisture, whereas nutrient-poor and recalcitrant litter is primarily limited by nutrient, and particularly nitrogen availability. Third, we found that soil depth increased decomposition rates, but that this effect was more important for high-quality litter. This is because water availability limits the decomposition of high-quality litter at the soil surface, especially during dry periods. This finding suggests that the negative relationship between carbon sequestration and temperature observed within and between ecosystems depends on conditions at the microsite level. Finally, our results across nearly one hundred forest sites throughout France emphasize that the position at which soil communities perform decomposition (that is, surface vs. buried) can be as important as macroclimate in predicting decomposition rates. It is therefore necessary to consider the variability in the environmental conditions at the plot level to assess accurately decomposition rates, especially because in almost all ecosystems, biotic and abiotic factors may strongly vary along the soil profile from the top to the bottom.

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DATA AVAILABILITY

The data used in this manuscript were submitted to the TBI database that will be published online on www.teatime4science.org after publication of the meta-analysis. It was given file number 136 in this database. Until publication on this platform, the data can be obtained by emailing the corresponding author or the TBI team.

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