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**Key Points:**

- The LIDET decomposition data are simulated using reactivity continuum modeling
- Apparent temperature sensitivity varied across litter categories and time
- Changes in plant community composition will strongly affect decomposition

**Supporting Information:**

- Supporting Information S1
- Table S3
- Table S4

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# Reactivity continuum modeling of leaf, root, and wood decomposition across biomes

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**Abstract** Large carbon dioxide amounts are released to the atmosphere during organic matter decomposition. Yet the large-scale and long-term regulation of this critical process in global carbon cycling by litter chemistry and climate remains poorly understood. We used reactivity continuum (RC) modeling to analyze the decadal data set of the "Long-term Intersite Decomposition Experiment," in which fine litter and wood decomposition was studied in eight biome types (224 time series). In 32 and 46% of all sites the litter content of the acid-unhydrolyzable residue (AUR, formerly referred to as lignin) and the AUR/nitrogen ratio, respectively, retarded initial decomposition rates. This initial rate-retarding effect generally disappeared within the first year of decomposition, and rate-stimulating effects of nutrients and a rate-retarding effect of the carbon/nitrogen ratio became more prevalent. For needles and leaves/grasses, the influence of climate on decomposition decreased over time. For fine roots, the climatic influence was initially smaller but increased toward later-stage decomposition. The climate decomposition index was the strongest climatic predictor of decomposition. The similar variability in initial decomposition rates across litter categories as across biome types suggested that future changes in decomposition may be dominated by warming-induced changes in plant community composition. In general, the RC model parameters successfully predicted independent decomposition data for the different litter-biome combinations (196 time series). We argue that parameterization of large-scale decomposition models with RC model parameters, as opposed to the currently common discrete multiexponential models, could significantly improve their mechanistic foundation and predictive accuracy across climate zones and litter categories.

## 1. Introduction

During litter decomposition, most of the carbon (C) that is fixed by photosynthesis is released back into the atmosphere as carbon dioxide. Decomposition produces humic substances that contribute to soil fertility as well as long-term C storage in soils and is tightly linked to nutrient cycling. Prominent factors regulating the "reactivity" of litter toward decomposition are climate, litter chemistry, and the microbial community [*Tenney and Waksman*, 1929; *Olson*, 1963; *Meentemeyer*, 1978, 1984; *Aber et al.*, 1990]. On a continental scale, leaf decomposition rates are primarily regulated by climate, with actual evapotranspiration as a powerful predictor. At smaller geographic scales, effects of litter chemical-physical parameters, such as lignin content, are more evident [*Meentemeyer*, 1978; *Aerts*, 1997]. However, these findings stem from rather short-term decomposition experiments of a few months up to 2 years, mainly capturing the initial rapid decomposition phase [*Harmon et al.*, 2009]. The regulation of decomposition across large spatial and temporal scales remains poorly understood [*Adair et al.*, 2008; *Berg and McClaugherty*, 2008]. Also, Earth system models that simulate carbon cycle-climate feedbacks are largely untested with respect to litter decomposition [*Bonan et al.*, 2012]. Hence, projecting how changing environmental conditions influence decadal decomposition across biome types remains a difficult task.

Earlier comparative studies were often based on data from different decomposition experiments, with differing approaches, research foci, or study species [e.g., *Olson*, 1963; *Meentemeyer* 1978, 1984; *Aerts*, 1997]. To study decomposition on large temporal and spatial scales with uniform methodology, the "Long-term Intersite Decomposition Experiment Team" (LIDET) set up the LIDET study in 1989 [*LIDET*, 1995]. Decomposition of aboveground and belowground fine litter and wood was studied in biomes across North and Central America for up to 10 years. The LIDET decomposition data set has so far mostly been analyzed using discrete (multi)exponential decay models, which fit the data well [e.g., *Gholz et al.*, 2000; *Adair et al.*, 2008; *Harmon et al.*, 2009; *Currie et al.*, 2010]. Discrete (multi)exponential models describe organic matter decomposition by one or a sum of several exponential decay functions which represent differing reactivity classes [*Jenny et al.*, 1949; *Olson*, 1963; *Lousier and Parkinson*, 1976; *Currie et al.*, 2010]. The reactivity in each class is assumed to remain stable over time, allowing exponential decay constants to be fitted. These model analyses of the LIDET data provided a wealth of process information and revealed decomposition patterns across biomes. For example, it was found that, when analyzing the first-year LIDET data, the exponential decay constant was strongly influenced by climate. However, when analyzing the complete long-term data set, climate was only a weak predictor of decomposition [*Currie et al.*, 2010].

Discrete (multi)exponential modeling of decomposition is currently the most commonly applied approach when modeling decomposition. For example, in 343 out of 498 litterbag decomposition studies in which a model was fit to the data, the single-pool exponential model was used in 93% [*Adair et al.*, 2010]. Or, in the decomposition module of the current Community Land Model (CLM4.0; http://www.cgd.ucar.edu/tss/clm/), the litter is assumed to consist of three classes, representing a labile pool, cellulose, and lignin [*Bonan et al.*, 2012]. However, there are concerns about the assumptions of discrete (multi)exponential models. Although individual components of a heterogeneous substrate might show exponential decay [*Minderman*, 1968], bulk decomposition rates generally exceed the single-pool exponential prediction during early decomposition and fall below the prediction during later stages of decomposition [*Hunt*, 1977; *Godshalk and Wetzel*, 1978; *Vähätalo et al.*, 2010; *Cornwell and Weedon*, 2014] (supporting information Figure S1). For discrete multiexponential modeling, the number of assumed reactivity classes needs to be predefined, and the number of fit parameters increases with each added class. While dividing organic matter into reactivity classes may be conceptually useful [*von Lützow and Kögel-Knabner*, 2010], it has been argued that the derived reactivity and size of classes in multiexponential models are just fit parameters rather than representing true or apparent decay constants and fractions [*Middelburg*, 1989], and their estimates were shown to be sensitive to the amount of time points and to the experimental duration [*Vähätalo et al.*, 2010]. Hence, an alternative model approach to analyze decomposition data could be valuable.

Such an alternative statistical approach to describe decomposition is the “reactivity continuum” (RC) model. This approach was developed several decades ago in the fields of chemistry, chemical engineering, theoretical biology, and sedimentology [*Aris*, 1968; *Hutchinson and Luss*, 1970; *Carpenter*, 1981; *Braun and Burnham*, 1987; *Boudreau and Ruddick*, 1991; *Bosatta and Ågren*, 1995] and has been recently applied to decomposition time series [e.g., *Bruun et al.*, 2010; *Vähätalo et al.*, 2010; *Sierra et al.*, 2011; *Forney and Rothman*, 2012; *Koehler et al.*, 2012; *Manzoni et al.*, 2012; *Cornwell and Weedon*, 2014]. The RC model is set up as an integral of exponential decay functions weighted by an initial probability distribution of reactivity [*Boudreau and Ruddick*, 1991]. Since reactivity is treated as a continuous variable there is no need to predefine the number of assumed reactivity classes as in discrete multiexponential models, and the RC model is parameter-parsimonious with two fit parameters. Different probability distribution functions, e.g., gamma, beta, or lognormal, have been used when applying the RC model, and this choice has been investigated and discussed earlier [e.g., *Boudreau and Ruddick*, 1991; *Vähätalo et al.*, 2010; *Forney and Rothman*, 2012; *Manzoni et al.*, 2012]. The initial “apparent first-order decay coefficient” $k_0$ is calculated as the expected value of the initial probability distribution of reactivity, and the continuous decrease of $k$ over decomposition time is calculated based on the probability distribution [*Boudreau et al.*, 2008]. RC approaches introduce model properties and behaviors that cannot be obtained when using discrete (multi)exponential models with a small number of reactivity classes and are of fundamental importance to simulate long-term carbon dynamics [*Sierra et al.*, 2011]. Finally, robustness of parameter estimates and predictions and the extrapolation power beyond the experimental duration are better for RC models compared to discrete (multi)exponential models [*Vähätalo et al.*, 2010], which is highly relevant given that decomposition models are commonly used for extrapolation and projection of, for example, long-term steady state stocks [*Cornwell and Weedon*, 2014].

Recently, a lognormal RC model was for the first time applied to the LIDET decomposition data [*Forney and Rothman*, 2012]. The study investigated the initial regulation of the mean decomposition by (1) litter chemistry across study sites per litter species and (2) climate across litter species per study site. The initial litter chemistry set the time scale of the faster decomposition rates, while the slower decomposition rates were relatively independent of initial composition. Temperature and moisture sensitivity were similar across labile to refractory organic matter compounds [*Forney and Rothman*, 2012]. This is in conflict with the earlier finding, based on discrete (multi)exponential modeling of the LIDET data, that the influence of climate was higher initially—when the organic matter contains more labile compounds—than during later stages of decomposition [*Currie et al.*, 2010].

Here we applied a gamma RC model to the LIDET decomposition data. Differing from the previous, first RC model analysis of the LIDET decomposition data which focused on mean initial decomposition [*Forney and Rothman*, 2012], we conducted our analysis separately for each litter-biome combination. This allowed us to investigate litter-category and biome-type specific patterns and to assess how well the RC model parameters predict decomposition under similar conditions using an independent, literature-derived data set of 196 time series. Moreover, we analyzed the regulation of decomposition by climate and litter chemistry over time throughout the experimental duration, obtaining for the first time RC-based information about the regulation of large-scale long-term decomposition.

## 2. Materials and Methods

### 2.1. Data

Our analysis is based on data from the Long-term Intersite Decomposition Experiment [*LIDET*, 1995], obtained from the HJ Andrews Experimental Forest Database [*Harmon*, 2010]. The experiment was set up to investigate the influence of litter chemistry and climate on long-term decomposition of aboveground and belowground fine litter and wood in eight biome types across North and Central America. The biome types are boreal forest, grassland including woodland and shrubland, semidesert, temperate coniferous forest, temperate deciduous forest, tropical forest, tundra, and wetland/saltmarsh. A detailed description of the 27 study sites and a map showing their location can be found in *Harmon et al.* [2009]. Kellog Biological Station, which is classified as Agro Ecosystem in *Harmon et al.* [2009], was included in the grassland category in this study as in *Bontti et al.* [2009]. The experiment was a reciprocal litter transplant study determining mass loss in four-replicate fine root ($<2$ mm diameter) and leaf litterbags and wooden dowels per site, plant species (10), and sampling time. After placement in the field, litterbags and wooden dowels were collected in approximately yearly time intervals for generally 10 years except for in the tropical forest sites where they were retrieved at shorter time intervals until no mass was left after 2–5 years [*LIDET*, 1995; *Adair et al.*, 2008].

In 25 of the sites, two series of wood decomposition experiments were conducted. In the earlier one, the soil-exposed half of the wooden dowels was unwrapped. In the later one, the soil-exposed half of the wooden dowels was wrapped in mesh of 1 mm mesh size to facilitate complete recovery of the decomposing wood. In 78% of the sites the ash-free mass loss for soil-exposed wood did not differ between these experiments, and the data were pooled before model analysis of decomposition in this study. In four sites (Arctic Lakes, Alaska; Jornada Experimental Range, New Mexico; Sevilleta National Wildlife Refuge, New Mexico; and Santa Margarita Ecological Reserve, California), the mass loss for soil-exposed wood was larger in the unwrapped compared to the wrapped experiment (all $P < 0.006$; see section 2.3), and only the data from the wrapped experiment were included in this study. Further details concerning the experimental design have been previously reported [e.g., *LIDET*, 1995; *Harmon et al.*, 2009; *Smith et al.*, 2011].

From the LIDET decomposition data set, we used the fraction of ash-free remaining mass as response variable, similar as in earlier LIDET decomposition data model analyses [e.g., *Harmon et al.*, 2009; *Currie et al.*, 2010; *Forney and Rothman*, 2012]. We grouped the litter into five categories, i.e., leaf/grass, needle, fine root, air-exposed wood, and soil-exposed wood. Litter chemistry per sampling time as well as mean site-specific annual temperature (MAT), annual precipitation (MAP), actual evapotranspiration (AET), and potential evapotranspiration (PET) over the study period were obtained from *Harmon* [2010]. The mean site-specific climate decomposition index (CDI), a synthetic variable integrating moisture and temperature used in the ecosystem model CENTURY [*Parton et al.*, 1987], was obtained from *Bonan et al.* [2012] for the 20 sites included in that study and from *Currie et al.* [2010] for the remaining sites. Species-specific initial cellulose content of leaves and fine roots was obtained from *Adair et al.* [2008].

### 2.2. Modeling

For each study site and species, we averaged the fraction of ash-free remaining mass at each time point over the four replicate litterbags or wooden dowels. For the few time series in which the replicates were harvested on slightly differing days the average day was used. Only time series containing at least six time points, including the initial value of unity, were considered, similar as in the previous LIDET RC model analysis [*Forney and Rothman*, 2012] ($n = 260$ from 25 sites). This criterion excluded the "wildcard" species, a species from one site decomposing at random in usually one of the other sites, but included all nine "standard" species, those from which litter decomposed at each site (*Acer saccharum* (ACSA), *Andropogon gerardii* (ANGE), *Drypetes glauca* (DRGL), *Gonystylus bancanus* (GOBA), *Pinus elliottii* (PIEL), *Pinus resinosa* (PIRE), *Quercus prinus* (QUPR), *Thuja plicata* (THPL), and *Triticum aestivum* (TRAE)) [*Harmon et al.*, 2009].

An initial data screening suggested that the RC model assumption, i.e., that organic matter decomposition can be described by an integral of exponential decay functions, was not fulfilled in part of the LIDET data. Therefore, we conducted an initial model selection before proceeding with the final RC model analysis. For each time series we fitted three models, a linear regression model, a single-pool exponential model (equation (9) in *Olson* [1963]), and the RC model (equation (1) below) and calculated Akaike weights. The Akaike weight expresses the probability that a certain model is the best model in the sense of the Akaike information criterion, i.e., minimizing the Kullback-Leibler discrepancy, given the data and the set of candidate models [*Burnham and Anderson*, 2001; *Wagenmakers and Farrell*, 2004]. The RC model did not converge for 36 of the 260 time series; hence, the RC model parameters could not be estimated for these. Twelve of these 36 time series showed an unclear mass loss pattern/unclear data and were excluded. Sixteen and 8 of these 36 time series were better modeled using the single-pool exponential and linear model, respectively. Hence, we conducted our final RC model analysis with $n = 224$ time series from 25 sites, and 24 more time series are included in the alternative model groups, giving a total of 248 analyzed time series.

We used an RC model with a gamma probability distribution of reactivity, a two-parameter distribution that has wide application to problems where the variable has a physical lower bound of zero but no upper bound [*Thom*, 1958]. The gamma RC model is well documented and analyzed [e.g., *Boudreau and Ruddick*, 1991; *Boudreau et al.*, 2008] and has previously been used to describe decomposition of litter [*Manzoni et al.*, 2012; *Cornwell and Weedon*, 2014], sediment organic carbon [*Boudreau and Ruddick*, 1991; *Boudreau et al.*, 2008], soil organic carbon [*Bolker et al.*, 1998], and lake-dissolved organic carbon [*Vähätalo et al.*, 2010; *Koehler et al.*, 2012]. The relative mass ($Mass_t/Mass_0$; dimensionless) at time $t$ (day) is described as

$$\frac{Mass_t}{Mass_0} = \left(\frac{a}{a+t}\right)^v \tag{1}$$

where $a$ is the rate parameter, which is interpreted as the average lifetime of the more reactive compounds (days), and $v$ is the shape parameter, which describes the shape of the probability distribution of reactivity near a decay coefficient of zero (dimensionless). The model parameters were estimated for each time series using nonlinear least squares parameter estimation with R3.0.2 [*R Core Team*, 2013] and averaged for each litter-biome combination. The initial apparent first-order decay coefficient $k_0$ is the expected value, or first moment, of the gamma distribution calculated as $\upsilon/a$ ($d^{-1}$). The decrease of $k_0$ over time is calculated as $\upsilon/(a + t)$ [*Tarutis*, 1993; *Boudreau et al.*, 2008]. We refer to the decay coefficient as $k_t$ in the text, where $t$ indicates the years after the start of the experiment (i.e., $k_0$ to $k_{10}$). When using $k$ index-free we refer to the decay coefficient independent of the time during the experiment. To summarize information of the cumulative probability distribution of reactivity and for comparison purposes, we defined three reactivity classes characterized by $k > 0.005\ d^{-1}$, $0.001 < k < 0.005\ d^{-1}$, and $k < 0.001\ d^{-1}$. When interpreting RC model parameters one should be aware that different probability distributions can cause similar time dependencies of decomposition [*Hutchinson and Luss*, 1970; *Cornwell and Weedon*, 2014]. This statistical issue is not unique to the RC model but applies similarly when fitting other statistical models, e.g., discrete (multi)exponential models.

A previous RC model analysis of the LIDET data focused on initial mean decomposition, based on a lognormal probability distribution of reactivity. The authors numerically inverted the LIDET decomposition time series and, because the lognormal distribution function was marginally better suited than the gamma distribution function to model the inverted data (Kolmogorov-Smirnov $D$ test), used the lognormal RC model [*Forney and Rothman*, 2012]. However, the root-mean-square error between observed and predicted values when fitting the RC model to the original, noninverted time series was similar for both the lognormal and the gamma probability distribution (supporting information of *Forney and Rothman* [2012]). In general, it is difficult to reliably discriminate between similar candidate models with a small sample size [*Kappenman*, 1982; *Lawless*, 1982; *Fatima Vaz and Fortes*, 1988; *Marshall et al.*, 2001]. While for an exact lognormal distribution the log plot of the rate distribution should be symmetrical around the maximum [*Fatima Vaz and Fortes*, 1988], the gamma distribution allows for an asymmetrical rate distribution. Given that both distributions fitted the data well [*Forney and Rothman*, 2012], we preferred the gamma RC model considering that rates are typically skewed toward slow decomposition [*Boudreau and Ruddick*, 1991; *Koehler et al.*, 2012].

We compiled an independent data set to validate the performance of the RC model parameters to predict ash-free mass loss over time during decomposition for the different litter-biome combinations. We extracted 196 time series for leaves/grasses, needles, and fine roots (supporting information Table S1) from published tables and figures, digitized using the software Dagra (Blue Leaf Software, Hamilton, NZ). Since the wood decomposition experiment had a specific setup, i.e., wooden dowels of certain dimensions from a tropical hardwood species inserted vertically into the soil, it was not validated with independent data. We did not find independent ash-free mass loss data for boreal forest and tundra, for fine root decomposition in semidesert, and for needle decomposition in tropical forest and wetland/saltmarsh. Except for these cases, we found at least three independent time series of ash-free mass loss for each litter-biome combination (on average 13 ± 3 time series; Table S1). We stopped searching for further data of a litter-biome combination when reaching the study with which 10 time series were reached or exceeded.

### 2.3. Statistical Analyses

For statistical effect analysis we mostly used linear mixed-effect models (LMMs). Significance of the fixed effect(s) was evaluated using analysis of variance [*Crawley*, 2009]. For all multiple factor analyses, the explanatory variables $x$ were mean centered and normalized before analysis [$x^* = (x\text{-mean}(x))/\text{standard error}(x)$] and $P$ values were multiplicity adjusted using a single-step method [*Hothorn et al.*, 2008]. Specifically, LMMs were used to test for differences in (1) the RC model parameters and climate characteristics between the model groups, i.e., RC, linear regression and single-pool exponential model, or sites (random effect (RE): species nested in litter category); (2) initial litter chemistry between the model groups and $k_0$ between the ecosystem native and the other litter categories for each biome type (RE: site); (3) initial chemistry between litter categories and litter chemistry over time (RE: biome type); (4) $k_0$ between biomes for each litter category (RE: species nested in site or just site for wood); and (5) ash-free mass loss between the soil-exposed wood decomposition experiments, i.e., unwrapped versus mesh-wrapped wooden dowels, for each site in which the wrapped experiment lasted for more than 2 years [*Smith et al.*, 2011] ($n = 18$; RE: replication nested in time).

We also tested for relationships between $k_t$ and mean climate variables across sites for each litter category and in yearly sample time intervals (RE: species). Approximate confidence intervals were calculated using the *intervals* function of the R-package *nlme*, and marginal variance explained (i.e., the variance explained by the fixed factors; $R^2_{(m)}$) [*Nakagawa and Schielzeth*, 2013] was calculated using the r.squaredGLMM function of the R-package MuMIn. For analyzing climate regulation of wood decomposition we used linear models since the wood experiment was conducted with just one species. Finally, we tested for relationships between $k_t$ and chemistry across litter categories for each site and, depending on data availability, sampling time using linear regression. Regression analyses were only conducted for sites and sampling times with data from at least four species. In all analyses, right-skewed variables were logarithmically transformed before testing, and differences were considered significant if $P \leq 0.05$. During validation of the RC model parameters to predict independent decomposition data we used the linear regression model slope between observed versus predicted ash-free mass loss and the $R^2$ of the relationship as well as the normalized root-mean-square error as quality criteria. Mean values are given with ±1 standard error and with ±95% confidence intervals in regression equations. Analyses were conducted using R3.0.2 [*R Core Team*, 2013].

## 3. Results

### 3.1. Mass Loss Patterns and Decomposition Modeling

The RC model described the mass loss observed in the majority (72%) of the time series in the LIDET study well. When the RC model was fitted to the 23% and 5% of the time series which were better described by the single-pool exponential and linear model, respectively, the RC model parameter estimates were considerably larger than for the time series in which the RC pattern could be tracked, resulting in smaller estimates for $k_0$ ($P < 0.0001$; supporting information Table S2). Litter chemistry, expressed as fraction contained in the ash-free dry mass, differed between the groups of LIDET mass loss data that were better simulated using the RC model versus the linear or single-pool exponential model (supporting Results). Decomposing wood made up 35% and 34% of the time series in the linear and single-pool exponential model group, respectively, whereas wood was substantially weaker represented in the RC model group (9%). Hence, wood is poorly represented in the RC model data set with nine and six time series for soil- and air-exposed wood, respectively.

Besides the influence of litter chemistry (*supporting Results*), climate influenced the mass loss patterns observed in the LIDET study as well. Specifically, linear mass loss was observed in sites with smaller MAP ($P = 0.0083$) and AET ($P = 0.0015$) and was thus more strongly represented in biomes such as semidesert and arid grassland. In contrast, the climate variables did not differ between the litter that showed mass loss following the single-pool exponential versus RC model. However, single-pool exponential mass loss was frequent in tropical forests (30% of all time series in this model group) and grassland (27%). Unless stated differently all following results are based on the 161 LIDET time series in which the RC model assumption, i.e., that the mass loss can be described by an integral of exponential decay functions, was fulfilled.

In general, the RC model parameters described the respective mean decrease of ash-free mass over time accurately (Figure 1). Exceptions were fine root decomposition in semidesert and in wetland/saltmarsh, which was somewhat underestimated by the respective mean RC models (Figures 1c and 1h). We summarized information from the cumulative distribution functions of $k$ (Figure 2) by defining reactivity classes. The reactivity classes consistently reflected the information obtained from the decomposition time series. The litter-biome combinations with the highest and fastest mass loss over time had larger proportions in the reactivity classes 1 and 2 (defined as $k > 0.005\ \mathrm{d}^{-1}$ and $0.001 < k < 0.005\ \mathrm{d}^{-1}$, respectively), and the litter-biome combinations with the smallest mass loss over time had a larger proportion in reactivity class 3 (defined as $k < 0.001\ \mathrm{d}^{-1}$; Figure 1 and Table 1).

Compared to boreal forest, which was the biome type with the smallest $k_0$, $k_0$ for leaves/grasses was larger in tropical forest ($P < 0.001$; Figure 3). $k_0$ for fine root decomposition was larger in grassland, tropical forest, and wetland/saltmarsh than in boreal forest (all $P < 0.0050$; Figure 3). A general pattern was that the larger the $k_0$, the steeper the decline in $k$ over time and vice versa. $k_0$ for soil-exposed wood decomposition (only available for four biome types; Figure 1) was larger in temperate deciduous forest compared to grassland ($P = 0.0493$). $k_0$ was larger for (1) leaves/grasses than wood in grassland, semidesert, and tundra (all $P < 0.0289$; Figures 3b and 3c), (2) leaves/grasses than needles and air-exposed wood in temperate deciduous forest (both $P < 0.0060$; Figure 3e), (3) leaves/grasses than for all other litter categories in tropical forest (all $P < 0.0011$; Figure 3f), and (4) fine roots than for leaves/grasses in tundra ($P = 0.0303$; Figure 3g).

### 3.2. Litter Chemistry Regulation of Decomposition

Initial chemistry differed between the litter categories and changed over decomposition time (*supporting Results*; supporting information Table S3). Across litter categories, the coefficient of variation for $k_0$ ($\mathrm{CV}_{\mathrm{litter}}$) ranged from 0.4 for boreal forest to 1.5 for wetland/saltmarsh and averaged $0.9 \pm 0.2$ (Table 1). The initial acid-unhydrolyzable residue (AUR, formerly referred to as lignin) and AUR/N were the litter chemical variables that were most frequently related to $\log(k_0)$. A negative linear relationship with AUR and AUR/N, indicating a rate-retarding effect, was found in 32 and 46% of the 22 sites for which data availability allowed testing (supporting information Tables S3 and S4), respectively. The sites with initial rate-retarding effect of AUR were characterized by higher MAT ($P = 0.0001$) and PET ($P = 0.0061$) and a tendency for higher AET ($P = 0.0967$) compared to the remaining sites. The sites with initial rate-retarding effect of AUR/N had lower MAP ($P < 0.0001$), AET ($P = 0.0048$), and CDI ($P = 0.0113$) than the other sites. Moreover, a rate-retarding effect of the initial carbon (C) to nitrogen (N) ratio (C/N) was detected in 23% of the sites (supporting information Tables S3 and S4). After 1 year of decomposition, the initial decomposition rate-retarding effect of AUR was lost, and an effect of AUR/N persisted in just three sites. Most prevalent at later stages of decomposition were rate-stimulating effects of potassium (K), magnesium (Mg), and phosphorus (P) and a rate-retarding effect of C/N (Table S4).

### 3.3. Climate Regulation of Decomposition

Across biome types, along the gradient of 33°C in mean annual temperature between sites [*Harmon et al.*, 2009], the coefficient of variation for $k_0$ ($\mathrm{CV}_{\mathrm{biomes}}$) ranged from 0.4 for soil-exposed wood to 2.1 for fine roots and averaged $1.1 \pm 0.3$ (Table 1). For leaves/grasses and needles, $\log(k_0)$ was positively related to all

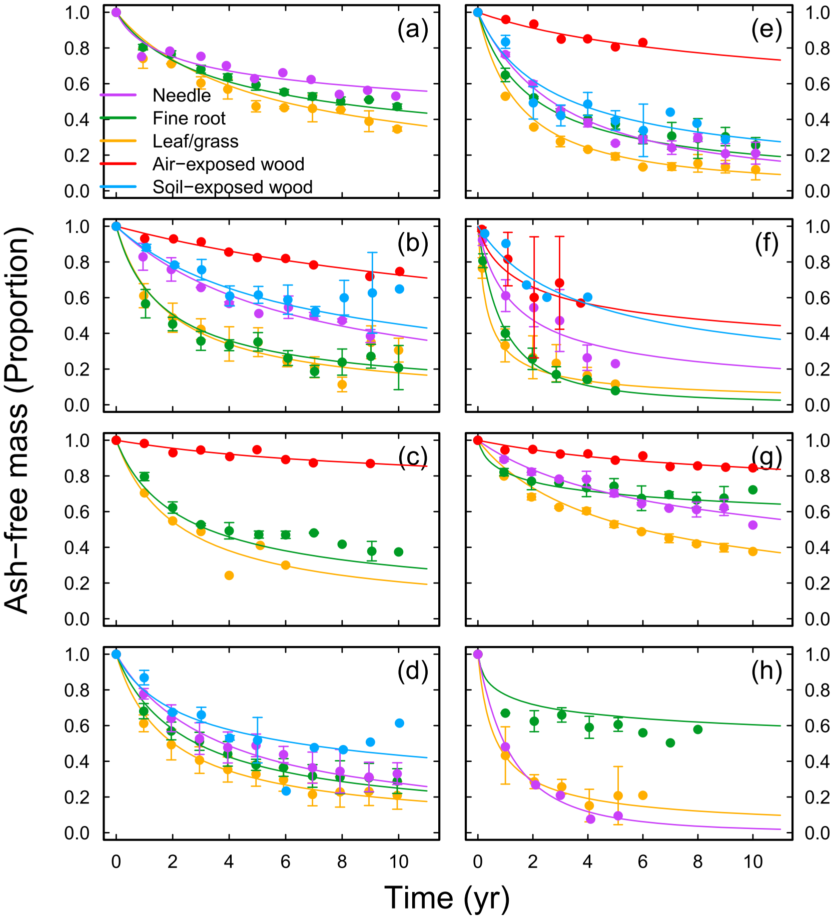

**Figure 1.** Mean (±SE) relative decrease in the ash-free mass over time of litter decomposing in (a) boreal forest, (b) grassland, (c) semidesert, (d) temperate coniferous forest, (e) temperate deciduous forest, (f) tropical forest, (g) tundra, and (h) wetland/saltmarsh. The lines show the ash-free mass simulated using reactivity continuum modeling. In tropical forest (Figure 1f), litterbags were collected more frequently than annually and with differing time intervals in the different sites. For clarity of the figure, we show the mean mass loss averaged per year.

tested climate variables (Figures 4a–4h). The climate regulation became continuously weaker over decomposition time, as indicated by a decrease in the slope of the regression line and an increase in the *P* value, and eventually became insignificant for most climate variables several years into the experiment (Table 2). For fine roots, the positive relationship was initially only significant with MAT (Figure 4h), AET (Figure 4i), and CDI (Figure 4l). In contrast to leaves/grasses and needles, log($k_t$) of fine root decomposition was better predicted by climate after an initial lag period. For air-exposed wood, log($k_0$) was positively related to MAP (Figure 4m), AET (Figure 4o), and CDI (Figure 4p). As for leaves/grasses and needles the climate influence became weaker over time (Table 2). MAT and PET did not influence the decomposition of air-exposed wood (Table 2). For soil-exposed wood, a climate influence was neither found initially (Figures 4m–4p) nor for later-stage decomposition (Table 2). Across litter categories, the climate decomposition index was the strongest predictor of both initial and later-stage log($k$) (based on the AIC; Table 2).

### 3.4. Reactivity Continuum Model Performance to Predict Decomposition

The accuracy of the LIDET-based RC model parameters to predict independent, literature-derived decomposition time series differed between litter-biome combinations (Figure 5). The mean fine root mass loss was smaller in the independent data set than predicted for temperate forests (Figures 5d and 5e), and mass loss was somewhat higher for leaves/grasses in the independent data set than predicted for wetland/saltmarsh (Figure 5h). Apart from these, the other 12 litter-biome combinations that we could

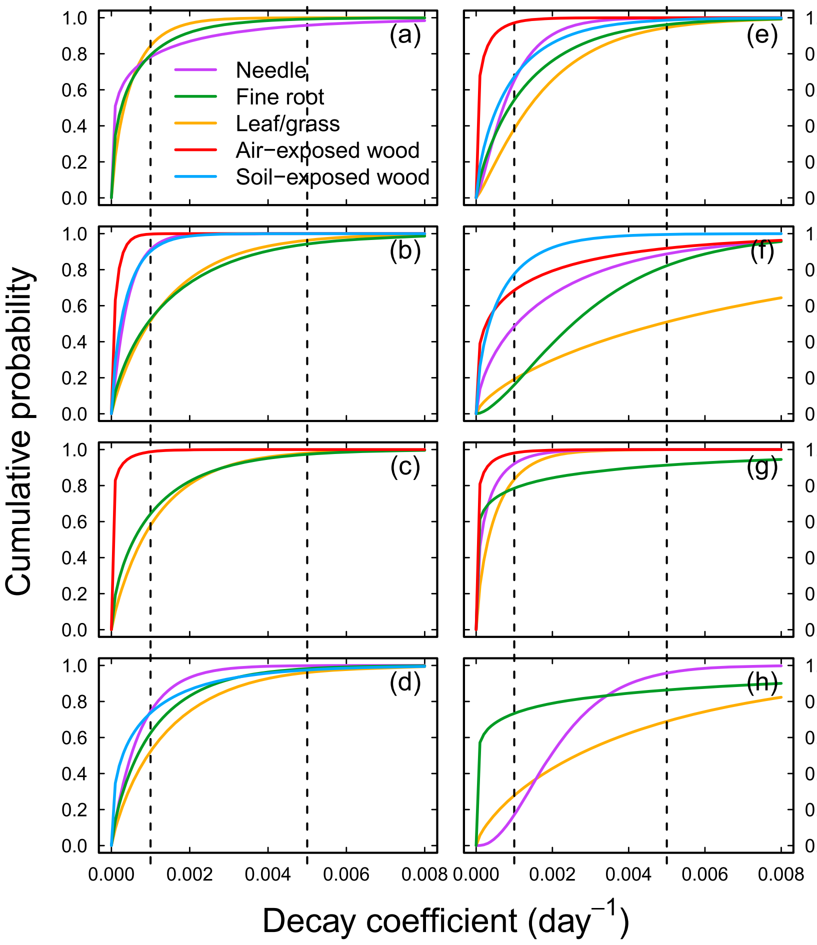

**Figure 2.** Cumulative distribution function of initial reactivity for ash-free mass from litter decomposing in (a) boreal forest, (b) grassland, (c) semidesert, (d) temperate coniferous forest, (e) temperate deciduous forest, (f) tropical forest, (g) tundra, and (h) wetland/saltmarsh. The dashed vertical lines mark $k = 0.001$ and $k = 0.005$ d$^{-1}$.

validate were satisfactorily predicted using RC model parameters derived from the LIDET decomposition data (Figure 5 and Table 3). Across biomes, the decomposition of leaves/grasses and needles was better predicted than that of fine roots (Table 3).

## 4. Discussion

### 4.1. Reactivity Continuum Modeling of Litter Decomposition

The RC model uses a probability distribution to describe the spectrum of reactivity in organic matter decomposition. A mass loss pattern well fitted by the RC model was found in 72% of the LIDET decomposition data (Table S2 and Figures 6a (green) and 6b). It is likely that a continuum of reactivity also existed for the remaining third of the decomposition experimental data. We suggest that there are two main reasons why these were not tracked in the respective time series, specifically (1) the RC pattern was not resolved by the data/experimental design or (2) the mass loss exhibited an apparent or real initial “lag phase” which the RC model is not able to simulate.

With respect to the first reason, our analysis suggests that it is more challenging to measure the RC pattern for bulk litter mass loss when the RC spectrum is narrow, i.e., when the organic matter behaves predominantly labile or predominantly recalcitrant under the given site conditions (Figure 6). Accordingly, the single-pool exponential model was often statistically preferred when litter mass loss was initially rapid, a clearly slower phase of decomposition was not reached or captured with the measurements, and the data exhibited high variability, e.g., often in tropical forests and grasslands. When litter-biome combinations create a

**Table 1.** Mean (±SE) (1) Proportion of Ash-Free Mass Loss Observed After 1 Year and at the End of the LIDET Study Period (See Also Figure 1), (2) Parameters of the Reactivity Continuum Model Used to Model Decomposition (Equations (1)), and (3) Proportion of Litter in Three Reactivity Classes[a,b]

| Litter Category ($CV_{biomes}$[c]) | Biome ($CV_{litter}$[d]) | Mass Loss Within the First Year (%) | Overall Mass Loss (%) | *a* (Days) | *v* (Dimensionless) | $k_0$ ($d^{-1}$) | Reactivity Class 1 (%) | Reactivity Class 2 (%) | Reactivity Class 3 (%) |
|---|---|---|---|---|---|---|---|---|---|
| Leaf/grass (1.0) | Boreal forest (0.4) | 25.9 ± 5.5 | 65.4 ± 1.2 | 1494.24 ± 972.06 | 0.78 ± 0.38 | 0.0014 ± 0.0008 | 0.8 ± 0.8 | 16.9 ± 5.8 | 82.4 ± 6.6 |
| | Grassland (1.1) | 38.9 ± 6.7 | 69.4 ± 6.7 | 616.41 ± 55.58 | 0.89 ± 0.16 | 0.0026 ± 0.0010 | 4.7 ± 1.9 | 43.2 ± 7.1 | 52.1 ± 8.9 |
| | Semidesert (0.8) | 29.5 ± not applicable (NA) | 69.9 ± NA | 734.29 ± NA | 0.88 ± NA | 0.0012 ± NA | 2.0 ± NA | 40.2 ± NA | 57.8 ± NA |
| | Temperate coniferous forest (0.5) | 38.7 ± 4.7 | 79.1 ± 7.8 | 578.35 ± 88.20 | 0.84 ± 0.12 | 0.0020 ± 0.0003 | 6.1 ± 2.6 | 42.7 ± 7.4 | 51.2 ± 9.4 |
| | Temperate deciduous forest (0.8) | 47.0 ± 0.4 | 88.1 ± 5.8 | 667.72 ± 201.94 | 1.23 ± 0.25 | 0.0033 ± 0.0007 | 7.3 ± 3.4 | 54.8 ± 3.5 | 37.9 ± 0.2 |
| | Tropical forest (1.1) | 66.8 ± 9.2 | 88.4 ± NA | 82.02 ± 15.48 | 0.69 ± 0.19 | 0.0118 ± 0.0033 | 48.3 ± 13.1 | 26.4 ± 3.8 | 25.4 ± 10.5 |
| | Tundra (1.4) | 20.0 ± 0.3 | 62.3 ± NA | 1347.94 ± 506.23 | 0.72 ± 0.20 | 0.0008 ± 0.0001 | 0.2 ± 0.2 | 16.8 ± 3.1 | 83.0 ± 3.2 |
| | Wetland/saltmarsh (1.5) | 56.7 ±16.0 | 79.0 ± NA | 159.94 ± 41.34 | 0.71 ± 0.12 | 0.0050 ± 0.0020 | 33.0 ± 13.7 | 38.4 ± 2.1 | 28.6 ± 11.6 |
| Needle (0.6) | Boreal forest | 24.8 ± NA | 46.9 ± NA | 229.71 ± NA | 0.20 ± NA | 0.0009 ± NA | 4.3 ± NA | 17.9 ± NA | 77.9 ± NA |
| | Grassland | 17.1 ± 7.5 | 61.5 ± 3.6 | 2602.40 ± 2383.53 | 1.09 ± 0.82 | 0.0008 ± 0.0004 | 3.2 ± 3.2 | 13.2 ± 9.6 | 83.7 ± 12.7 |
| | Temperate coniferous forest | 22.2 ± 3.0 | 66.9 ± 6.1 | 1323.47 ± 637.16 | 0.97 ± 0.32 | 0.0009 ± 0.0002 | 1.6 ± 1.1 | 26.9 ± 7.1 | 71.6 ± 8.0 |
| | Temperate deciduous forest | 23.7 ± 1.3 | 78.9 ± 6.1 | 1503.19 ± 690.41 | 1.38 ± 0.50 | 0.0010 ± 0.0001 | 0.7 ± 0.7 | 34.9 ± 2.7 | 64.4 ± 3.4 |
| | Tropical forest | 38.9 ± 8.9 | 76.9 ± NA | 287.77 ± 41.08 | 0.59 ± 0.19 | 0.0023 ± 0.0007 | 10.9 ± 3.1 | 37.6 ± 9.1 | 51.4 ± 12.0 |
| | Tundra | 10.7 ± 1.1 | 47.5 ± NA | 1380.80 ± 320.76 | 0.43 ± 0.10 | 0.0003 ± 0.000005 | 0.03 ± 0.03 | 7.9 ± 0.8 | 92.1 ± 0.8 |
| | Wetland/saltmarsh | 51.8 ± NA | 90.5 ±NA | 1217.27 ± NA | 2.71 ± NA | 0.0023 ± NA | 4.2 ± NA | 78.6 ± NA | 17.2 ± NA |
| Fine root (2.1) | Boreal forest | 19.5 ± 1.5 | 52.8 ± 1.4 | 676.95 ± 27.67 | 0.43 ± 0.02 | 0.0007 ± 0.0001 | 0.8 ± 0.2 | 20.2 ± 1.5 | 79.1 ± 1.7 |
| | Grassland | 43.4 ± 8.0 | 79.2 ± 12.4 | 452.02 ± 245.48 | 0.71 ± 0.23 | 0.0051 ± 0.0025 | 19.3 ± 9.4 | 34.3 ± 4.4 | 46.4 ± 6.0 |
| | Semidesert | 20.4 ± 2.3 | 62.5 ± NA | 546.26 ± 25.47 | 0.60 ± 0.01 | 0.0012 ± 0.00004 | 2.6 ± 0.3 | 33.0 ± 0.2 | 64.4 ± 0.4 |
| | Temperate coniferous forest | 31.9 ± 4.3 | 71.1 ± 6.9 | 697.75 ± 171.49 | 0.76 ± 0.23 | 0.0021 ± 0.0005 | 2.2 ± 0.8 | 33.7 ± 6.7 | 64.1 ± 6.7 |
| | Temperate deciduous forest | 35.1 ± 3.8 | 74.3 ± 4.2 | 566.21 ± 241.28 | 0.79 ± 0.23 | 0.0021 ± 0.0006 | 6.1 ± 2.8 | 40.1 ± 3.7 | 53.8 ± 2.5 |
| | Tropical forest | 60.0 ± 3.8 | 92.1 ± NA | 558.64 ± 264.27 | 1.74 ± 0.47 | 0.0045 ± 0.0010 | 28.9 ± 9.6 | 55.2 ± 9.2 | 16.0 ± 4.1 |
| | Tundra | 17.9 ± 2.1 | 27.7 ± NA | 72.89 ± 6.84 | 0.11 ± 0.03 | 0.0036 ± 0.0015 | 8.2 ± 1.6 | 12.2 ± 2.8 | 79.6 ± 4.4 |
| | Wetland/saltmarsh | 33.0 ± 0.2 | 42.1 ± NA | 38.17 ± 26.28 | 0.11 ± 0.01 | 0.0701 ± 0.0122 | 15.9 ± 5.3 | 12.7 ± 1.3 | 71.5 ± 4.1 |
| Air-exposed wood (1.4) | Grassland | 6.9 ± NA | 25.3 ± NA | 4808.62 ± NA | 0.56 ± NA | 0.0001 ± NA | $5.6 \times 10^{-10}$ ± NA | 0.2 ± NA | 99.8 ± NA |
| | Semidesert | 1.8 ± NA | 13.0 ± NA | 1631.01 ± NA | 0.13 ± NA | 0.0001 ± NA | $5.7 \times 10^{-4}$ ± NA | 1.2 ± NA | 98.8 ± NA |
| | Temperate deciduous forest | 4.0 ± NA | 16.9 ± NA | 1630.04 ± NA | 0.25 ± NA | 0.0002 ± NA | 0.0015 ± NA | 2.8 ± NA | 97.2 ± NA |
| | Tropical forest | 18.4 ± 15.0 | 43.0 ± NA | 182.32 ± 58.83 | 0.26 ± NA | 0.0011 ± 0.0009 | 6.5 ± 5.3 | 19.7 ± 16.6 | 73.4 ± 21.9 |
| | Tundra | 5.4 ± NA | 15.5 ± NA | 1338.09 ± NA | 0.13 ± 0.23 | 0.0001 ± NA | $2.9 \times 10^{-3}$ ± NA | 1.9 ± NA | 98.1 ± NA |
| Soil-exposed wood (0.4) | Grassland | 11.9 ± NA | 35.1 ± NA | 1815.60 ± 1041.14 | 0.72 ± 0.34 | 0.0005 ± 0.0001 | 1.2 ± 1.2 | 10.1 ± 3.1 | 88.7 ± 3.6 |
| | Temperate coniferous forest | 13.1 ± NA | 38.6 ± NA | 426.09 ± 20.83 | 0.37 ± 0.03 | 0.0009 ± 0.00002 | 2.5 ± 0.1 | 23.8 ± 1.0 | 73.7 ± 0.9 |
| | Temperate deciduous forest | 16.6 ± NA | 71.2 ± NA | 714.26 ± 300.37 | 0.68 ± 0.08 | 0.0012 ± 0.0003 | 4.3 ± 2.6 | 32.3 ± 6.6 | 63.4 ± 8.6 |
| | Tropical forest | 9.6 ± NA | 39.6 ± NA | 870.07 ± NA | 0.58 ± NA | 0.0007 ± NA | 0.4 ± NA | 22.0 ± NA | 77.6 ± NA |

[a] Obtained from the mean cumulative distribution functions of initial reactivity (Figure 2) with $k > 0.005$ $d^{-1}$ reactivity class 1, $0.001 < k < 0.005$ $d^{-1}$ reactivity class 2, and $k < 0.001$ $d^{-1}$ reactivity class 3.

[b] Please note that the fine roots stemmed from both coniferous and nonconiferous species and, when comparing the mass loss, that experimental duration differed between sites [*Harmon et al.*, 2009]. Litter-biome combinations for which the parameters could not be determined due to lack of suitable data are not included in the table. Please see *Harmon et al.* [2009] for species-specific remaining final masses.

[c] $CV_{biomes}$ is the coefficient of variation of $k_0$ for the different litter categories across biomes types.

[d] $CV_{litter}$ is the coefficient of variation of $k_0$ for the different biome types across litter categories (given at first occurrence of each biome type in the table).

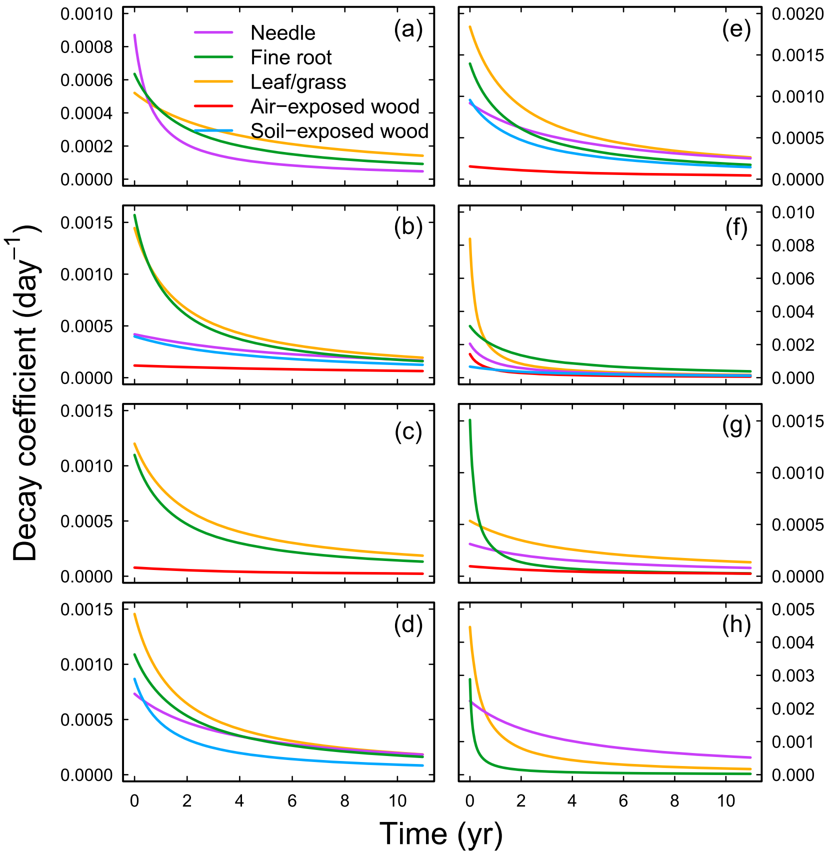

**Figure 3.** Time series of the apparent first-order decay coefficient *k* for ash-free mass loss during litter decomposition in (a) boreal forest, (b) grassland, (c) semidesert, (d) temperate coniferous forest, (e) temperate deciduous forest, (f) tropical forest, (g) tundra, and (h) wetland/saltmarsh.

narrow RC spectrum with a high $k_0$, a higher sampling frequency especially in the beginning of the experiment and higher measurement precision, e.g., a higher number of replicates per time point, might resolve the generally existent RC pattern of mass loss (Figures 6a (red) and 6b). The linear model was often statistically superior when litter mass loss was slow, such as for wood in biomes with adverse conditions for decomposition, e.g., dry sites. When litter-biome combinations create a narrow RC spectrum with a low $k_0$, a long experimental duration and high measurement precision might help to detect the expected RC pattern (Figures 6a (blue) and 6b). This has been achieved for example when applying the RC model to depth profiles of the C content in marine sediments, dating back hundreds to thousands of years [*Boudreau and Ruddick*, 1991]. In summary, successful application of the RC model to litter decomposition data requires that both the initial fast mass loss and the final slow mass loss are captured and well resolved with the data. While this is more challenging to achieve when the RC spectrum of reactivity is narrow it should in many cases be possible to optimize the experimental design for this purpose.

With respect to the second reason, i.e., an initially delayed mass loss, the subset of LIDET data not well described by the RC model was frequently wood and/or litter with small N content. For these litter types, an initial lag phase of mass loss may be rather typical [*Cornwell and Weedon*, 2014] and existed in part of these data (Figure 6a, magenta). While an initial lag phase cannot be simulated using the gamma RC model a recently advocated continuous quality model, which describes organic matter as a distribution of residence times assuming a Weibull distribution, can exhibit a sigmoidal curve shape of mass loss. However, the “Weibull residence time model” has, similarly to the single-pool exponential model, limitations in describing a slow late decomposition phase [*Cornwell and Weedon*, 2014] (Figure 6a and supporting information Figure S3). Also, there may be a risk of overemphasizing single data points which might result in an overpronounced or artificial sigmoidal shape of the fitted mass loss curve (Figure S3).

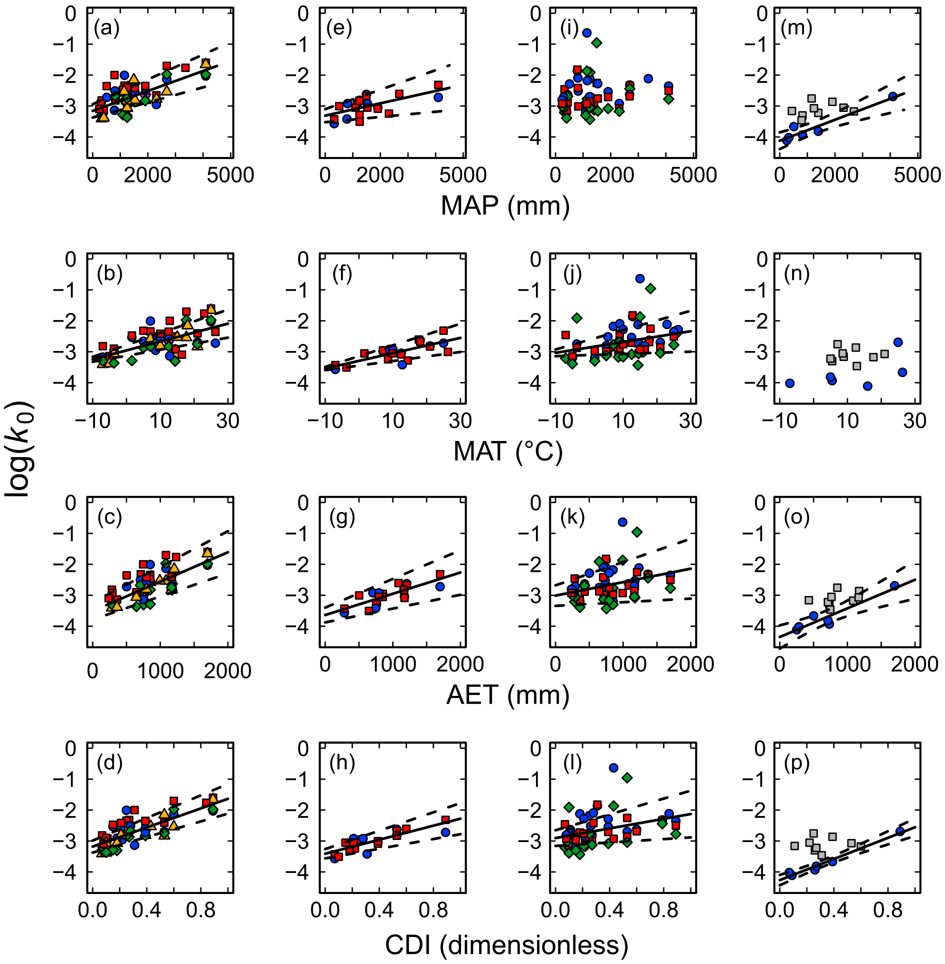

**Figure 4.** Scatterplots between the logarithmically transformed initial apparent first-order decay coefficient $k_0$ and the climate variables mean annual precipitation (MAP), mean annual temperature (MAT), actual evapotranspiration (AET), and climate decomposition index (CDI) for (a–d) leaves/grasses (species ACSA: blue circles, DRGL: red squares, TRAE: green diamonds, QUPR: orange triangles), (e–h) needles (species PIRE: blue circles, THPL: red squares), (i–l) fine roots (species ANGE: blue circles, DRGL: red squares, PIEL: green diamonds), and (m–p) soil-exposed wood (species GOBA). See section 2.2 for species acronyms. When significant, the regression line is plotted (solid, with ±95% CI as dashed lines) (Table 2). The two high $k_0$ for fine roots (Figures 4i–4l) are from wetland/saltmarsh, and model parameters were not sensitive to their exclusion. Air-exposed wood is not included because $k$ could only be estimated for three sites. The slope of the relationships between log ($k_0$) and MAT in Figures 4b, 4f, and 4j are referred to in the text as initial apparent temperature sensitivity (see Table 2).

Therefore, the Weibull model appears a flexible and promising model alternative to cover even initial lag phase cases of litter mass loss, which does however come about with a disadvantage regarding simulation of the late decomposition phase.

Since the RC model performed well in simulating multiyear decomposition for the majority of litter-biome combinations, when the RC spectrum was sufficiently broad and $k_0$ sufficiently high and mass loss proceeded without initial lag phase, we advocate its use for decomposition modeling. However, we recommend to first conduct a statistically founded model selection as exemplified in this study. If the RC model is applied to data which is statistically better modeled by a single-pool exponential or a linear model, the model parameter estimates become artificially inflated, causing the estimates of $k$ to be biased low. Artificial model parameter estimates or behavior for a small subset of time series has similarly been reported in other litter decomposition RC modeling studies [*Forney and Rothman*, 2012; *Cornwell and Weedon*, 2014]. We used model selection to identify the time series that do not fulfill the assumption of the RC model, i.e., that mass loss can be described by an integral of exponential decay functions. The purpose was not to compare curve fit with alternative decomposition models, such as discrete

**Table 2.** Model Parameter Estimates and Information About the Linear Mixed-Effect Models Used to Test the Influence of Climate on the Logarithmically Transformed Apparent First-Order Decay Coefficient $k_t$ in Annual Time Steps[a]

| Litter Category | Predictor Variable[b] | Intercept ± SE | Slope ± SE | $P_0$ | $AIC_0$ | $R^2_{(m)0}$ | $P_t$ | $AIC_t$ | $R^2_{(m)t}$ | Significance Over Time |
|---|---|---|---|---|---|---|---|---|---|---|
| Leaf/grass ($n = 60$) | AET | −3.51 ± 0.14 | 0.0010 ± 0.0001 | <0.0001 | 48.70 | 0.49 | $t_7$: 0.0466 | $t_7$: 8.79 | $t_7$: 0.06 | Insignificant after $t_7$ |
| | CDI | −3.18 ± 0.10 | 1.5444 ± 0.1420 | <0.0001 | 22.38 | 0.58 | $t_8$: 0.0474 | $t_8$: −4.49 | $t_8$: 0.06 | Insignificant after $t_8$ |
| | MAP | −3.16 ± 0.11 | 0.00032 ± 0.00004 | <0.0001 | 58.19 | 0.47 | $t_4$: 0.0311 | $t_4$: 5.30 | $t_4$: 0.07 | Insignificant after $t_4$ |
| | MAT | −2.96 ± 0.09 | 0.0289 ± 0.0047[c] | <0.0001 | 63.08 | 0.37 | $t_4$: 0.0235 | $t_4$: −4.44 | $t_4$: 0.08 | Insignificant after $t_6$ |
| | PET | −3.36 ± 0.17 | 0.0006 ± 0.0001 | <0.0001 | 81.91 | 0.25 | $t_4$: 0.0532 | $t_4$: 4.22 | $t_4$: 0.06 | Insignificant after $t_4$ |
| Needle ($n = 22$) | AET | −3.64 ± 0.11 | 0.0007 ± 0.0001 | <0.0001 | 17.34 | 0.63 | $t_{10}$: 0.0100 | $t_{10}$: 28.70 | $t_{10}$: 0.28 | Significant throughout experimental duration |
| | CDI | −3.41 ± 0.07 | 1.13 ± 0.17 | <0.0001 | −0.62 | 0.69 | $t_{10}$: 0.0457 | $t_{10}$: 16.70 | $t_{10}$: 0.18 | Significant throughout experimental duration |
| | MAP | −3.31 ± 0.101 | 0.0002 ± 0.0001 | 0.0018 | 29.73 | 0.39 | $t_6$: 0.0543 | $t_6$: 31.64 | $t_6$: 0.17 | Insignificant after $t_6$ |
| | MAT | −3.29 ± 0.07 | 0.0248 ± 0.0048[c] | 0.0001 | 13.77 | 0.56 | $t_5$: 0.0453 | $t_5$: 21.29 | $t_5$: 0.18 | Insignificant after $t_5$ |
| | PET | −3.79 ± 0.15 | 0.0007 ± 0.0001 | <0.0001 | 20.19 | 0.58 | $t_9$: 0.0488 | $t_9$: 31.12 | $t_9$: 0.17 | Insignificant after $t_9$ |
| Fine root ($n = 64$) | AET | −3.01 ± 0.17 | 0.0004 ± 0.0002 | 0.0081 | 115.13 | 0.10 | $t_{10}$: 0.0006 | $t_{10}$: 78.36 | $t_{10}$: 0.11 | Significant throughout experimental duration |
| | CDI | −2.91 ± 0.13 | 0.7772 ± 0.2519 | 0.0031 | 98.59 | 0.12 | $t_{10}$: <0.0001 | $t_{10}$: 57.46 | $t_{10}$: 0.17 | Significant throughout experimental duration |
| | MAP | - | - | 0.2233 | 122.59 | 0.02 | $t_{10}$: <0.0001 | $t_{10}$: 71.11 | $t_{10}$: 0.19 | Significant after $t_1$ and throughout experimental duration |
| | MAT | −2.86 ± 0.12 | 0.0175 ± 0.0069[c] | 0.0143 | 108.64 | 0.09 | $t_{10}$: 0.0002 | $t_{10}$: 68.27 | $t_{10}$: 0.14 | Significant throughout experimental duration |
| | PET | - | - | 0.2379 | 120.67 | 0.02 | $t_{10}$: 0.0033 | $t_{10}$: 81.40 | $t_{10}$: 0.09 | Significant after $t_1$ throughout experimental duration |
| Air-exposed wood ($n = 6$) | AET | −4.35 ± 0.14 | 0.0009 ± 0.0002 | 0.0044 | 0.64 | 0.89 | $t_5$: 0.0504 | $t_5$: 4.99 | $t_5$: 0.66 | Insignificant after $t_5$ |
| | CDI | −4.27 ± 0.06 | 1.71 ± 0.14 | 0.0003 | −7.73 | 0.97 | $t_1$: 0.0224 | $t_1$: 3.08 | $t_1$: 0.77 | Insignificant after $t_1$ |
| | MAP | −4.12 ± 0.10 | 0.0003 ± 0.0001 | 0.0032 | −0.25 | 0.91 | $t_5$: 0.0463 | $t_5$: 4.75 | $t_5$: 0.67 | Insignificant after $t_5$ |
| | MAT | - | - | 0.2061 | 11.40 | 0.36 | $t_{10}$: 0.8116 | $t_{10}$: 11.75 | $t_{10}$: 0.02 | Insignificant throughout experimental duration |
| | PET | - | - | 0.2451 | 11.82 | 0.32 | $t_{10}$: 0.8603 | $t_{10}$: 11.80 | $t_{10}$: 0.009 | Insignificant throughout experimental duration |

[a] Given are the $P$ values, Akaike information criterion (AIC), and marginal variance explained ($R^2_{(m)}$), as well as information about the temporal development of the relationships. The indices indicate the year after start of the experiment. Soil-exposed wood is not included because no significant relationships were found.

[b] AET: actual evapotranspiration (cm); CDI: climate decomposition index (unitless); MAP: mean annual precipitation (cm); MAT: mean annual temperature (°C); PET: potential evapotranspiration (cm).

[c] This slope is referred to in the text as "apparent temperature sensitivity."

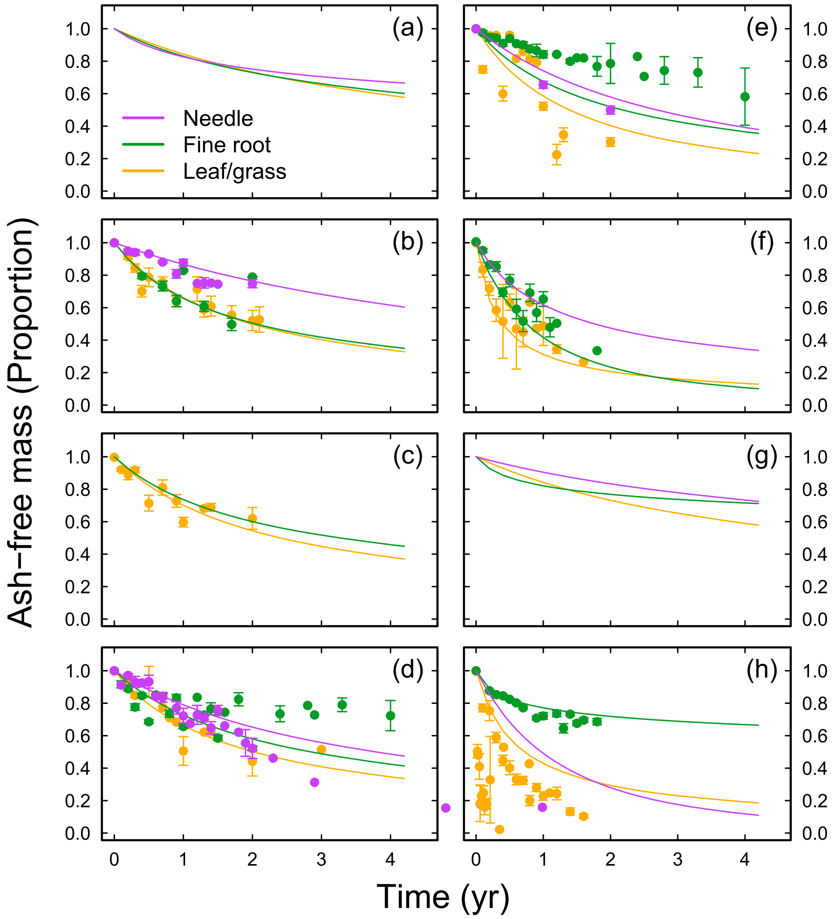

**Figure 5.** Mean (±SE) ash-free mass loss over time observed during litter decomposition from independent, literature-derived data (symbols; Table S1) and predicted (lines) using the reactivity continuum model parameters derived from the LIDET decomposition data analysis (Table 3) for leaves/grasses (orange), needles (violet) and fine roots (green) in (a) boreal forest, (b) grassland, (c) semidesert, (d) temperate coniferous forest, (e) temperate deciduous forest, (f) tropical forest, (g) tundra, and (h) wetland/saltmarsh.

multiexponential models. It was previously shown that discrete multiexponential models also fit the LIDET data well [e.g., *Gholz et al.*, 2000; *Adair et al.*, 2008; *Harmon et al.*, 2009; *Currie et al.*, 2010]. However, we chose the RC model a priori because it (1) does not require definition of the number of assumed reactivity classes but, more realistically, assumes a continuous reactivity distribution (Figure 2); (2) is more parameter-parsimonious than discrete multiexponential models allowing application even when the number of available decomposition time points is restricted; and (3) has model parameters which have an ecological interpretation (section 2.2) [*Boudreau and Ruddick*, 1991]. Also, directly estimating a long-term average decomposition rate from discrete multiexponential models is more difficult [*Harmon et al.*, 2009], and it was shown for dissolved organic carbon decomposition that the temporal change in the mean decay coefficient from discrete (multi)exponential models was not consistent with observations [*Vähätalo et al.*, 2010]. In contrast, the continuous change of $k$ over time is straightforward to calculate when using RC modeling (Figure 3) and was in agreement with observations [*Vähätalo et al.*, 2010]. These RC model characteristics were central for our analysis of the temporal development of climate and litter chemistry regulation of long-term decomposition.

### 4.2. Home Field Advantage

We found that $k_0$ was 3–5 times larger for leaves/grasses than needles in temperate deciduous and tropical forests, respectively (Figures 3e and 3f and Table 1). This suggests a home-field advantage [*Gholz et al.*, 2000] in these biomes, which are naturally void of coniferous plants. A home-field advantage was also found when

**Table 3.** Performance of the Mean Reactivity Continuum Model Parameters to Predict Ash-free Mass Loss During Decomposition for the Different Litter-Biome Combinations[a]

| Litter Category | Biome | $R^2$ | Slope | Intercept | Normalized RMSE % |
|---|---|---|---|---|---|
| Leaf/grass | Grassland | 0.91 | 0.87 ± 0.09 | n.s. | 10.26 |
| | Semidesert | 0.83 | 0.83 ± 0.13 | n.s. | 14.76 |
| | Temperate coniferous forest | 0.84 | 1.00 ± 0.13 | n.s. | 12.62 |
| | Temperate deciduous forest | 0.58 | 1.18 ± 0.29 | n.s. | 21.58 |
| | Tropical forest | 0.86 | 0.84 ± 0.10 | 0.17 ± 0.05 | 16.42 |
| | Wetland/saltmarsh[b] | 0.97 (0.20) | 1.33 ± 0.07 (0.48 ± 0.19) | −0.34 ± 0.04 (n.s.) | 19.65 (39.01) |
| | Mean ± SE | 0.83 ± 0.05 (0.70 ± 0.11) | 1.01 ± 0.08 (0.87 ± 0.10) | not applicable (NA) | 15.88 ± 1.74 (19.11 ± 4.28) |
| Needle | Grassland | 0.89 | 1.26 ± 0.14 | n.s. | 20.04 |
| | Temperate coniferous forest | 0.96 | 1.48 ± 0.06 | −0.43 | 14.17 |
| | Temperate deciduous forest | 0.99 | 1.20 ± 0.10 | n.s. | 13.56 |
| | Mean ± SE | 0.95 ± 0.03 | 1.32 ± 0.08 | NA | 15.92 ± 2.07 |
| Fine root | Grassland | 0.52 | 0.69 ± 0.27 | n.s. | 23.77 |
| | Temperate coniferous forest | 0.30 | 0.35 ± 0.12 | 0.53 ± 0.09 | 31.77 |
| | Temperate deciduous forest | 0.88 | 0.51 ± 0.04 | 0.50 ± 0.03 | 48.37 |
| | Tropical forest | 0.89 | 0.85 ± 0.09 | 0.18 ± 0.05 | 17.60 |
| | Wetland/Saltmarsh | 0.93 | 1.25 ± 0.10 | −0.23 ± 0.08 | 12.09 |
| | Mean ± SE | 0.70 ± 0.13 | 0.73 ± 0.15 | NA | 26.72 ± 6.33 |

[a] Given are the $R^2$, slope, and intercept (±SE, n.s. = not significant) of linear regressions between observed (independent, literature-derived data) versus predicted values and the normalized root-mean-square error (RMSE). Litter-biome combinations for which validation was not possible due to lack of independent data are not included in the table. No validation was conducted for the wooden dowels (see section 2.2).

[b] For leaves/grasses in wetland/saltmarsh the results are given both excluding and including (in brackets) one influential study in which most of the sites were flooded twice a day or the litterbags were incubated submerged [*Odum and Heywood*, 1978], conditions which are unrepresentative for those during the LIDET experiment.

analyzing the first 5 years of the LIDET data for one coniferous and one nonconiferous tree species [*Gholz et al.*, 2000]. Our study strengthens the evidence of home-field advantages for leaves/grasses, based on the multispecies 10 year LIDET data analysis. However, we could not trace a similar, general home-field advantage for needle decomposition in boreal or temperate coniferous forests; i.e., $k_0$ of needle decomposition did not differ significantly from $k_0$ of leaf/grass decomposition (Figures 3a and 3d). The presence of a home-field advantage is generally explained by specialization of litter and topsoil decomposer communities to break down litter encountered most often. Recently, it has been suggested that a home-field advantage is a special case of a more general theory termed “substrate quality-matrix quality interaction” (SMI). According to the SMI hypothesis, low-quality litter should show smaller intersite differences in decomposition rates than higher-quality litter [*Freschet et al.*, 2012]. Hence, the findings from our study are in accordance with the SMI hypothesis, given that differences in needle decomposition were not significant between biomes naturally supporting coniferous plants and those naturally void of coniferous plants, whereas differences in leave/grass decomposition were significant.

### 4.3. Regulation of Decomposition by Litter Chemistry and Climate

When interpreting the linear regression relationships between $k_t$ and litter chemistry or climate (Table 2, Table S4, and Figure 4), it needs to be considered that single factors can be useful indicators of decomposability but do not, on their own, determine decomposition rates. Thresholds exist at which one factor becomes rate-controlling, and inadequate conditions with respect to any of the regulating factors can slow down decomposition regardless of the adequacy of other factors [*Prescott*, 2010]. Nevertheless, our analysis confirms important rate-regulatory effects of (1) AUR and AUR/N and (2) the C/N ratio, as well as rate-stimulatory effects of macronutrient and micronutrient contents [*Melillo et al.*, 1982; *Weedon et al.*, 2009; *Zhang et al.*, 2008; *Prescott*, 2010]. The influence of AUR interacted with climate, with the decomposition rate-retarding effect appearing generally in the warmer and wetter sites, consistent with the literature [*Meentemeyer*, 1978; *Johansson et al.*, 1995]. Also, our study supports that actual evapotranspiration explains considerable variation in decomposition [*Meentemeyer*, 1984; *Aerts*, 1997]. In general, the climate decomposition index was the strongest climatic predictor of decomposition across litter categories and time (Table 2), supporting results from earlier LIDET data analyses [*Gholz et al.*, 2000; *Adair et al.*, 2008; *Cusack et al.*, 2008].

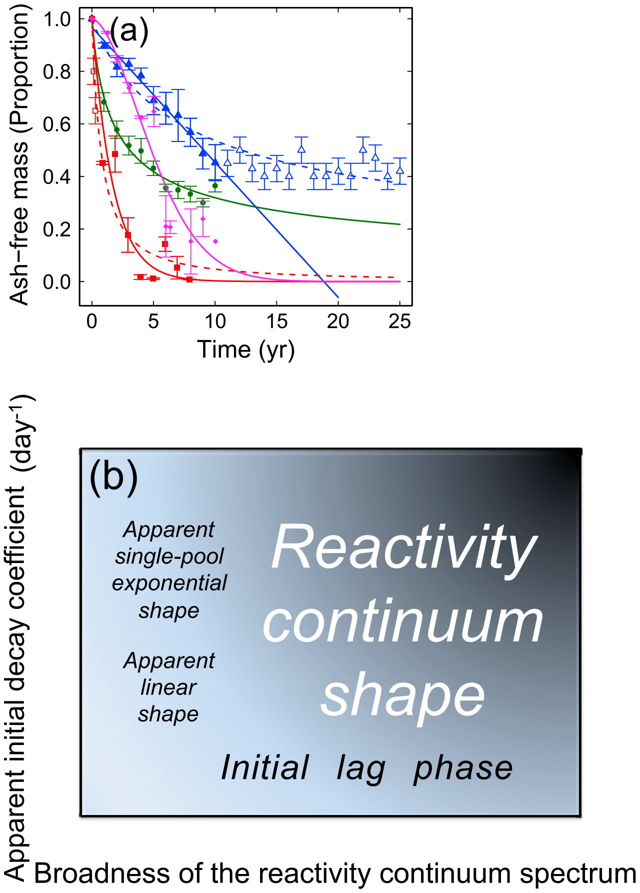

**Figure 6.** (a) Exemplary LIDET time series (solid symbols with model fits as solid lines) showing mass loss best modeled by the reactivity continuum model (RC; green circles), a linear model (blue triangles), and a single-pool exponential model (red squares). The open symbols are the hypothetical additional data points resulting in the RC model being superior (dashed lines). This exemplifies how, depending on site conditions and decomposing litter, the experimental design (e.g., sampling frequency and duration) may be optimized in order to trace the RC curve shape in litter mass loss data. Additionally, a time series showing an initial lag phase of decomposition as modeled by the Weibull residence time model is shown (magenta diamonds [*Cornwell and Weedon*, 2014]). (b) Conceptual relationship between RC properties of litter decomposing under given biome conditions, i.e., broadness of the RC spectrum and apparent initial decay coefficient, and the apparent shape of the mass loss time series/mathematically best model. It is more difficult to capture the RC dynamics of litter mass loss when the RC spectrum is narrow, and the RC model cannot simulate an initial lag phase of mass loss.

The decreasing influence of climate on aboveground litter mass loss as decomposition proceeds is consistent with the literature. Climate controls short-term leaf decomposition rates at the continental scale, whereas control by litter chemistry becomes evident at a smaller spatial scale [*Meentemeyer*, 1984]. It has been hypothesized that the same regulating principle should hold true on longer time scales [*Aerts*, 1997]. However, an earlier LIDET data analysis using discrete multiexponential modeling revealed that climate variables lose their predictive capacity for decomposition on a decadal time scale [*Currie et al.*, 2010]. We come to the same conclusion concerning leaf/grass and needle decomposition, which is also in line with observations that climate effects on late-stage decomposition are small [*Berg et al.*, 1993; *Berg and Meentemeyer*, 2002]. Hence, litter incubated in different climates reach similar late-stage decomposition rates [*Johansson et al.*, 1995]. Fine roots, however, exhibited a different pattern in our analysis; i.e., the relationship between *k* and climate variables seemed to strengthen after the initial decomposition phase and remained strong throughout the experiment. In support of this pattern, root chemistry was a more important regulator during the first year of decomposition, while climate played a secondary role [*Silver and Miya*, 2001]. It needs to be considered as well that root decomposition studies are typically performed using living roots harvested from soil, which may result in initially high-N and nonstructural carbohydrate concentrations which are rapidly exploited by microorganisms [*Anderson*, 1991]. This might have contributed to the high $k_0$ of fine roots in some biomes and the general strengthening of the regulating effect of climate over time.

### 4.4. Apparent Temperature Sensitivity of Decomposition

Regulation of mean initial decomposition was previously analyzed using the LIDET data and a lognormal RC model, which has different parameters and parameter interpretation than the gamma RC model used in this study [*Forney and Rothman*, 2012]. The correlation relationships between the mean of the initial reactivity distribution and climate as well as initial litter chemistry were generally in agreement with the literature and with our study. However, in the earlier lognormal RC model analysis the average standard deviation of the reactivity distribution was unrelated to MAT, which would justify the assumption of a common TS across labile and refractory components in decomposition models [*Forney and Rothman*, 2012]. In this gamma RC model analysis, in contrast, the apparent TS, defined as the slope of the increase of log($k$) with MAT, differed between litter categories and/or sites of decomposition (aboveground versus belowground). For example, while decomposition of soil- and air-exposed wood was temperature independent under the examined conditions, the initial apparent TS varied between 0.02 for fine roots and 0.03 for leaves/grasses (Figure 4 and Table 2). Also, the apparent TS changed over decomposition time (supporting information Figure S2). This finding is in agreement with earlier studies showing that the apparent TS depends on litter type and extent of litter decomposition [*Fierer et al.*, 2005] and that the influence of temperature on discrete multiexponential decay constants of decomposition decreases over time in the LIDET data [*Currie et al.*, 2010]. Therefore, we argue that it is not justified to use the same temperature-scaling factor across litter categories and time in decomposition models.

One should be aware of the difference between intrinsic and apparent TS and factors influencing the apparent TS such as environmental conditions, substrate availability, and enzyme affinities [*Davidson and Janssens*, 2006; *Kirschbaum*, 2006]. Extrapolation of decomposition rates into a future warmer world based on observations of current apparent TS is inadequate [*Davidson and Janssens*, 2006]. Finally, indirect effects via warming-induced shifts in plant growth-form composition also need to be considered [*Aerts*, 1997; *Vivanco and Austin*, 2006; *Cornelissen et al.*, 2007]. The LIDET study sites covered a range in mean annual temperature of 33°C, from −7°C in a tundra site in Alaska to 26°C in a tropical dry forest in Puerto Rico [*Harmon et al.*, 2009]. This range in mean annual temperature is great compared to the Intergovernmental Panel on Climate Change-predicted near-term increase in global mean surface air temperature of 0.3 to 0.7°C over 2016–2035 relative to the reference period 1986–2005 [*Kirtman et al.*, 2013]. Yet the variability in $k_0$ was similar within biome types across litter categories as within litter categories across biome types with their great gradient in mean annual temperature (Table 1), suggesting that future changes in litter decomposition may be dominated by warming-induced changes in plant community composition. In accordance with this conclusion, plant species traits dominated over climate effects in controlling litter decomposition rates within biomes worldwide [*Cornwell et al.*, 2008], and climate change effects on decomposition may be small unless they alter the present plant forms [*Prescott*, 2010].

### 4.5. Large-Scale Decomposition Modeling

Recently, the litter decomposition parameterization of the Community Land Model version 4 (CLM4.0) was validated against the LIDET data [*Bonan et al.*, 2012]. In CLM4.0, decomposition is parameterized based on data from laboratory microcosm studies using discrete multiexponential modeling. The litter is assumed to consist of three pools, i.e., labile, cellulose, and lignin, and their base decomposition rates are modified by environmental parameters such as moisture and temperature. Model validation revealed that the predicted exceeded the observed decomposition; i.e., lower decomposition rates are required to match the observations, as found in earlier multiexponential decomposition model validations with litterbag data as well [e.g., *Palosuo et al.*, 2005]. This may be a main reason why the CLM4 model underestimates soil carbon content [*Bonan et al.*, 2012]. An earlier discrete multiexponential LIDET data analysis concluded that the global litter store would be underestimated by at least one third if calculated using short-term decomposition rates [*Harmon et al.*, 2009]. RC models simulate the continuous decrease in decomposition rate over time more realistically than discrete multiexponential models [*Vähätalo et al.*, 2010]. We suggest that the RC model is superior in this sense compared to discrete multiexponential models and that this might explain part of the observed discrepancy between observed and simulated decomposition in, for example, CLM4.0.

A central aim of our LIDET data analysis is to provide RC model parameters suitable to predict decomposition for different litter-biomes combinations (Table 1). Validation using independent data supported that the reported RC model parameters are applicable (Figure 5 and Table 3). This is remarkable considering that the decomposing plant species were nonnative for most biomes. In support of this finding, decomposition rates did not differ between North and South American temperate grassland species [*Vivanco and Austin*, 2006]. An earlier LIDET data analysis also found that the exponential decay constants derived for nonnative litter decomposition in tropical forest were comparable to those from independent studies of native species decomposition [*Cusack et al.*, 2008]. Decomposition was more variable in temperate forest, especially for fine roots. Therefore, the LIDET-based RC model parameters indicate one plausible course of decomposition while mass loss may differ considerably in other temperate forest sites.

## 5. Conclusions

We conclude that the RC model (1) generally simulates decadal litter decomposition well, (2) is able to track mechanistic patterns of climate and litter chemistry regulation of large-scale decomposition over time, (3) can be valuable to predict decomposition for different litter-biome combinations, and (4) could improve the mechanistic foundation and predictive accuracy of large-scale and long-term decomposition models.

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