



Information content in time series of litter decomposition studies and the transit time of litter in arid lands

Agustín Sarquis¹ and Carlos A. Sierra²

¹Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura, Facultad de Agronomía de la Universidad de Buenos Aires, CONICET, 1417 Buenos Aires, Argentina

²Department of Biogeochemical Processes, Max-Planck-Institut für Biogeochemie, 07745 Jena, Germany

Correspondence: Carlos A. Sierra (csierra@bgc-jena.mpg.de)

Received: 23 January 2023 – Discussion started: 30 January 2023

Revised: 19 April 2023 – Accepted: 20 April 2023 – Published: 15 May 2023

Abstract. Plant litter decomposition stands at the intersection between carbon (C) loss and sequestration in terrestrial ecosystems. During this process organic matter experiences chemical and physical transformations that affect decomposition rates of distinct components with different transformation fates. However, most decomposition studies only fit one-pool models that consider organic matter in litter as a single homogenous pool and do not incorporate the dynamics of litter transformations and transfers into their framework. As an alternative, compartmental dynamical systems are sets of differential equations that serve to represent both the heterogeneity in decomposition rates of organic matter and the transformations it can undergo. This is achieved by including parameters for the initial proportion of mass in each compartment, their respective decomposition rates, and mass transfer coefficients between compartments. The number of compartments as well as their interactions, in turn, determine the model structure. For instance, a one-pool model can be considered a compartmental model with only one compartment. Models with two or more parameters, in turn, can have different structures, such as a parallel one if each compartment decomposes independently or in a series if there is mass transfer from one compartment to another. However because of these differences in model parameters, comparisons in model performance can be complicated. In this context we introduce the concept of transit time, a random variable defined as the age distribution of particles when they are released from a system, which can be used to compare models with different structures. In this study, we first asked what model structures are more appropriate to represent decomposition from a publicly available database of decomposition studies in arid

lands: *aridec*. For this purpose, we fit one- and two-pool decomposition models with parallel and series structures, compared their performance using the bias-corrected Akaike information criterion (AICc) and used model averaging as a multi-model inference approach. We then asked what the potential ranges of the median transit times of litter mass in arid lands are and what their relationships with environmental variables are. Hence, we calculated a median transit time for those models and explored patterns in the data with respect to mean annual temperature and precipitation, solar radiation, and the global aridity index. The median transit time was 1.9 years for the one- and two-pool models with a parallel structure and 5 years for the two-pool series model. The information in our datasets supported all three models in a relatively similar way and thus our decision to use a multi-model inference approach. After model averaging, the median transit time had values of around 3 years for all datasets. Exploring patterns of transit time in relation to environmental variables yielded weak correlation coefficients, except for mean annual temperature, which was moderate and negative. Overall, our analysis suggests that current and historical litter decomposition studies often do not contain information on how litter quality changes over time or do not last long enough for litter to entirely decompose. This makes fitting accurate mechanistic models very difficult. Nevertheless, the multi-model inference framework proposed here can help to reconcile theoretical expectations with the information content from field studies and can further help to design field experiments that better represent the complexity of the litter decomposition process.

1 Introduction

Plant litter decomposition is the process through which plant-derived organic matter is broken down into smaller components. The main biotic driver of decomposition is the metabolic activity of fungi and bacteria (Bradford et al., 2017), but soil fauna can be important too (García-Palacios et al., 2013; Zanne et al., 2022). The magnitude of biotic decomposition is further determined by climate (Gholz et al., 2000) and litter quality (Cornwell et al., 2008). Additionally, abiotic drivers of decomposition like solar radiation can have a large contribution to this process (Méndez et al., 2022). Altogether, plant litter decomposition releases carbon that was fixed by plants back to the atmosphere and mediates soil organic-matter formation (Cotrufo et al., 2015). This puts decomposition at a crucial intersection between C loss and sequestration in terrestrial ecosystems. It is thus of great interest to gain a better understanding on how decomposition influences the terrestrial C balance and how this process would be affected by global change.

Plant litter is composed of material of different physical and chemical properties that decays at different rates (Adair et al., 2008; Tuomi et al., 2009). However, litter decomposition models commonly assume a single pool that considers the decomposition of organic matter as if it was a homogenous mass pool with a single decomposition constant (Adair et al., 2010). Alternatively, organic-matter dynamics can be modeled using compartmental dynamical systems, which are sets of differential equations that serve to represent both the heterogeneity of organic-matter chemical quality and the transformations plant residues can undergo (Sierra and Müller, 2015). This is achieved with the inclusion of different pools that decompose at different rates. This allows us to model the dynamics of labile C compounds that are more readily available for microbial consumption like sugars and other compounds that have a longer persistence in the litter pool like tannins or lignin. Additionally, it is possible to include interactions between these pools, like C transfers from one pool to another. This mass transfer between pools represents the transformation of molecules in litter without actual mass loss from the litter system (Prescott and Vesterdal, 2021). The number of compartments as well as their interactions finally determine model structure. Compartmental models of decomposition have been successfully applied for decades (Chappelle et al., 2023; Parton et al., 1987; Tuomi et al., 2009), and it has been proven many times that they can be an improvement on the traditional one-pool model (Adair et al., 2008; Cornwell and Weedon, 2014; Derrien and Amelung, 2011; Manzoni et al., 2012).

Despite the richness of information that can be learned from compartmental models, there are still limitations for their widespread application. One main limitation is parameter identifiability. This happens because more complex models usually have more parameters, and, in some cases, the information contained in time series of litter mass loss may

not be enough to estimate those parameters unambiguously (Brun et al., 2001). Depending on the resolution and extension of the time series, it might be possible to obtain different number of parameters from the available data (Sarquis et al., 2022a; Sierra et al., 2015). Consequently, different studies developed under different methodologies and sampling schemes may provide information on different model structures. Further, this limits the application of compartmental models to data from extensive heterogeneous databases, since not all parameters might be identifiable for all datasets (Sarquis et al., 2022a).

It is common to compare model parameters like the decomposition constant when the same model has been applied to many datasets. But comparing the behavior of models with different structures in the same way is not possible because decomposition constants of single homogenous pools are not comparable to decomposition constants of specific pools, such as those in compartmental models. Thus, a metric that can be used to compare models with different structures is the transit time of mass in a complex heterogeneous system. Transit time represents the mean age of particles when they are released from a system (Sierra et al., 2017). In the context of litter decomposition studies, transit time can tell us about how long it has taken for mass to exit litter since the start of an experiment. Transit time is a random variable with its own probability distribution, and thus mean and median transit times can be calculated (Sierra et al., 2018). Unlike a single decomposition rate, transit time can be calculated for the bulk of litter when using compartmental models. Transit time contains information from all different mass compartments (Lu et al., 2018), and so it becomes a more useful parameter when making comparisons from models that have different structures.

In this study we used the *aridec* database, which is an open-access database of published decomposition studies in arid lands from around the world (Sarquis et al., 2022a). The focus of this database on arid lands stems from how widespread arid lands are, since around 41 % of the land surface is classified as arid to some extent (Safriel and Adeel, 2005). This large area represents a wide range of diverse ecosystems, with many shared functional characteristics. For instance, arid lands are usually more sparsely vegetated (Guttal and Jayaprakash, 2007), and this produces a shift in the importance of decomposition drivers in comparison to humid ecosystems. Plant litter under these conditions is more susceptible to solar radiation (Austin and Vivanco, 2006) and desiccation by wind (D'Odorico et al., 2019). Further, water sources other than rain can become more relevant when mean annual precipitation is low (Evans et al., 2020). These unique traits of arid ecosystems probably explain why decomposition rates are not correlated to mean annual precipitation in these systems (Austin, 2011), contrary to what was proposed in the traditional literature (e.g., Meentemeyer, 1978). Furthermore, arid-land processes are thought to become more widespread in the future because of arid-land ex-

pansion (Feng and Fu, 2013) and drought intensification of humid ecosystems (Grünzweig et al., 2022).

Hence, we used the *aridec* database to address the following questions: given the information content in time series of litter decomposition studies, what model structures are more appropriate to represent decomposition from arid ecosystems? From the set of models obtained, what are the potential ranges of the median transit times of litter mass? Moreover, what are the potential relationships between the median transit time and environmental variables? We fit one- and two-pool decomposition models with parallel and series structures, compared their performance using AICc, and used model averaging as a multi-model inference approach. We further calculated transit times for those models and explored patterns in the data in relation to environmental variables.

2 Methods

2.1 Model fitting

First, we used the *aridec* database to fit a group of candidate decomposition models. The *aridec* database is a publicly available database of decomposition studies from arid lands across the world (Sarquis et al., 2022a). This database contains bulk litter mass loss data, but it lacks mass loss dynamics of different litter organic-matter pools that decompose at different rates (e.g., soluble carbohydrates, cellulose, lignin). Because of this, we took an inverse-modeling approach that allowed us to estimate the parameters of these unknown pools by fitting the models to mass loss data. This model calibration procedure constitutes a non-linear optimization problem, where the objective is to find parameter values that minimize a measure of badness of fit, like a weighted sum of squared residuals (Soetaert and Petzoldt, 2010). Following this procedure, we obtained a group of parameters for each dataset and fit the dynamics of mass loss for different pools. We did this with the SoilR (Sierra et al., 2012) and the FME (Soetaert and Petzoldt, 2010) packages in R (R Core Team, 2020).

SoilR is a modeling framework that contains a wide set of functions and tools to model soil organic-matter decomposition within the R computing platform. Organic-matter decomposition in SoilR is represented by systems of linear differential equations that generalize most compartment-based models. A simple general structure to represent litter decay with no inputs follows Eq. (1):

$$\begin{aligned} \frac{d\mathbf{C}(t)}{dt} &= \mathbf{A}\mathbf{C}(t), \\ \mathbf{C}(t) &= [C_{\text{pool } 1}, \dots, C_{\text{pool } m}]^T, \\ \mathbf{A} &= \begin{bmatrix} -k_1 & \cdots & a_{1i} \\ \vdots & \ddots & \vdots \\ a_{j1} & \cdots & -k_m \end{bmatrix}, \end{aligned} \quad (1)$$

where $\mathbf{C}(t)$ is a $m \times 1$ vector with m pools of litter mass observed at time t and \mathbf{A} is a square $m \times m$ matrix that contains decomposition rates (k_m) for each pool and transfer rates (a_{ij}) between them. These different pools may correspond to different ways in which the quality of the litter is expressed in different studies. For example, they may correspond to different compounds obtained from a specific extraction method (e.g., water-soluble sugars or acid detergent lignin), or they can be defined by general decay classes such as fast- and slow-decay compounds. The linear dynamical system represented by Eq. (1) has many different solutions, but we are only interested in the solution that satisfies

$$\mathbf{C}(t=0) = \mathbf{C}_0 = [\text{total } C_0 \cdot p_1, \dots, \text{total } C_0 \cdot p_m]^T, \quad (2)$$

where C_0 is a $m \times 1$ vector with the value of initial litter mass content in the different compartments m . We set total initial C_0 to be 100 % for this analysis, and the resulting p_m parameters are the initial proportions of litter in m pools.

Before fitting the models, we run a collinearity test following the procedure by Soetaert and Petzoldt (2010), and the results are presented in Sarquis et al. (2022a). Briefly, when parameters are functionally related, changes in one of them can be compensated for by changes in others. This produces different parameter sets that have similar probability distributions; thus it is impossible to determine a single parameter set for a model (Brun et al., 2001; Sierra et al., 2015). From this analysis, we were able to choose three models: a one-pool model, a two-pool parallel model, and a two-pool series model (Fig. 1). The one-pool model represents mass loss data as a single homogenous mass compartment and has a single parameter, the decomposition rate k . The two-pool model with parallel structure considers litter mass as two distinct compartments that decompose at different rates. Hence, its parameters are the two decompositions rates (k_1 and k_2) and the initial proportion of litter mass in pool 1 (p_1 , from which the proportion of mass in pool 2 can be calculated as $p_2 = 1 - p_1$). Finally, the two-pool series model is similar to the parallel model, but it incorporates the transfer of matter from pool 1 to pool 2 after its transformation. This is indicated in the model by the parameter a_{12} (i.e., the transfer rate from pool 1 to pool 2).

Specifically for the two-pool series model our collinearity analysis showed that only 20.1 % of the datasets produced identifiable results for this model and only did so when we restricted parameter p_1 . Restricting or fixing parameters to known values is a way of avoiding collinearity issues. For this purpose, we decided to use initial litter lignin content as a proxy for the p_2 parameter (the initial proportion of mass in pool 2), which is complementary to p_1 ($p_1 + p_2 = 1$). We were limited by the number of datasets that provided initial lignin values in *aridec*. We searched for this missing information in the TRY database, which contains plant trait data for ecology and earth system sciences (Kattge et al., 2020). We could only find information for three of these datasets in

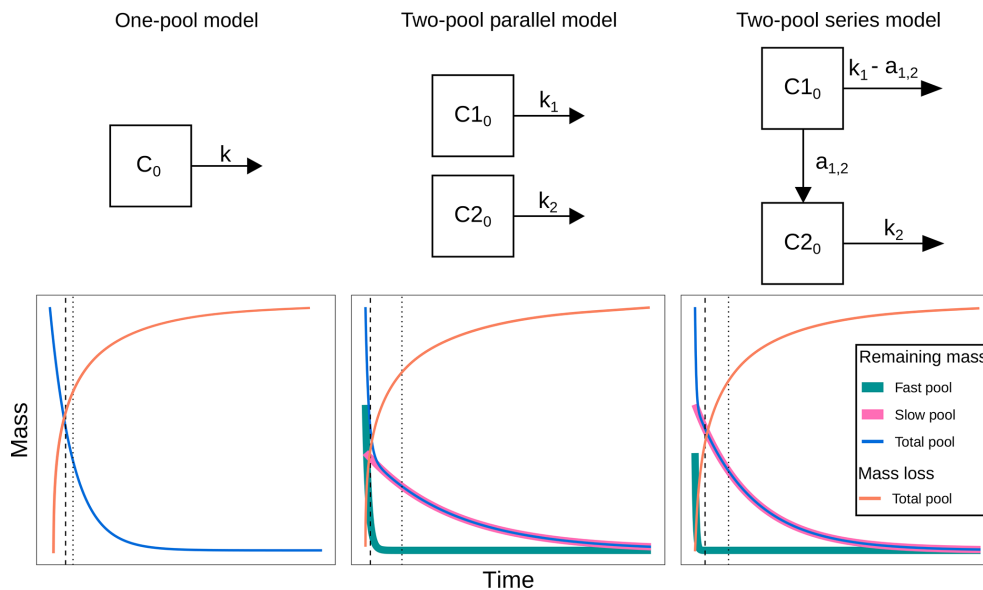


Figure 1. Decomposition models fitted in this study. C_0 : total initial litter mass; C_{10} : initial litter mass in the fast-decomposing pool; C_{20} : initial litter mass in the slow-decomposing pool; k , k_1 , k_2 : decomposition rates of the total, fast-, and slow-decomposing litter pools, respectively; $a_{1,2}$: mass transfer coefficient from the fast-decomposing pool to the slow-decomposing pool; dashed lines denote median transit time; dotted lines denote mean transit time.

the TRY database. We then completed some of the missing values by averaging lignin data of the same litter types that were already present in *aridec*. Having all the data ready, we proceeded to fit the models mentioned above. All time variables were transformed to monthly timescales to achieve more consistent comparisons.

2.2 Transit time

For each model, we calculated litter mass transit time (Sierra et al., 2017). This concept represents the mean age of the particles when they are released from the bulk litter. Another way to interpret this is the time it has taken particles to transit the litter system since the beginning of the experiment. We used a modified version of the mean transit time (MTT) from Sierra et al. (2017) without new litter inputs:

$$\text{MTT} = - (1, \dots, 1) A^{-1}. \quad (3)$$

For both two-pool models, we used the function `transitTime` in the `SoilR` package. This function calculates the mean and median of the distribution of the transit time as well as other quantiles of the distribution. The transit time median is interpreted as the time it takes half the litter mass in a sample to decompose. As a special case, for the one-pool model the MTT can be simply calculated as

$$\text{MTT} = \frac{1}{k}, \quad (4)$$

while the median transit time (mTT) can be calculated as

$$\text{mTT} = \frac{\ln 2}{k}. \quad (5)$$

We found that MTT was usually overestimated in our models (Supplement S4 in Sarquis and Sierra, 2023, pre-averaging results table), possibly due to the already slow decomposition rates of arid lands and the inclusion of the a_{12} parameter that prolonged the time that molecules remained in the litter system in the two-pool series models. Instead, values of mTT were usually lower, so we decided to only work with mTT hereafter. However, some of the mTT values obtained were also overestimated and so we decided to make a cut-off at an mTT of 14.5 years. This value came from fitting the two-pool series model to the longest dataset in *aridec*, which is 10 years long and corresponds to average data of different species at the Central Plains Experimental Range in Adair et al. (2017) (Supplement S1 in Sarquis and Sierra, 2023). We excluded from this study the datasets that exceeded this median transit time cutoff. Finally, after accounting for collinearity, the availability of initial litter lignin data, and the mTT cutoff, we were left with 128 datasets from 12 *aridec* entries (Table A1).

2.3 Model selection and multi-model inference

As a first attempt at model selection, we calculated the bias-corrected Akaike information criterion, which is used for small sample sizes (AICc; Burnham and Anderson, 2002). We used the formula from Shumway and Stoffer (2017):

$$\text{AICc} = \log \sigma^2 k + \frac{n+k}{n-k-2}, \quad (6)$$

where $\sigma^2 k$ is the variance of the model (in this case the mean squared residuals, i.e., sum of squared residuals divided by

sample size), k is the number of parameters in the model, and n is the sample size or the number of points in each time series. We accounted for the variance as one of the parameters in the formula as Burnham and Anderson (2002) recommend.

A common way of choosing the model with the best fit is by looking at the model with the lowest Akaike information criterion (AIC) value. We did this by using the `akaike.weights` function from the `qpcR` package. Additionally, we calculated the difference in AICc between the model with the lowest AICc and the other two candidate models (ΔAICc). Since we did not have enough information to choose a single model structure based on AICc (see the Results section), we decided to follow a multi-model inference approach (Burnham and Anderson, 2002). We first calculated Akaike weights using the function `weights` from the `MuMinR` package for each model. Akaike weights can be interpreted as the probability that a model j is the best of all i candidate models given the data (Lukacs et al., 2010), and they are calculated as

$$w_j = \frac{\exp\left(-\frac{1}{2}\Delta\text{AICc}_j\right)}{\sum_{i=1} \exp\left(-\frac{1}{2}\Delta\text{AICc}_i\right)}. \quad (7)$$

We then calculated new average estimators for the mean and the median transit times as

$$\hat{\beta}_i = \sum_{j=1} w_j \hat{\beta}_{ij}, \quad (8)$$

where $\hat{\beta}_{ij}$ is the i parameter estimator $\hat{\beta}$ for each j model. This results in estimators of mean (avgMTT) and median (avgmTT) transit times averaged across models for each database entry.

We also calculated the unconditional variance for each averaged estimator (Burnham and Anderson, 2002; Lukacs et al., 2010) as

$$v\hat{a}r\left[\hat{\beta}_i\right] = \sum_{j=1} w_j \left[\text{MSR}_j + \left(\hat{\beta}_{ij} - \hat{\beta}_i\right)^2 \right]. \quad (9)$$

Finally, we estimated 95 % confidence intervals as

$$\hat{\beta}_i \pm cv \sqrt{v\hat{a}r\left[\hat{\beta}_i\right]}, \quad (10)$$

where cv stands for the critical value of a t distribution for a particular number of degrees of freedom.

We made non-parametric Kendall's rank correlation tests between study duration in days and avgMTT and avgmTT, respectively. We also plotted data against environmental variables to explore potential relationships between avgMTT and calculated Pearson r correlation coefficients. We used data already available in *aridec* like mean annual temperature and mean annual precipitation. We additionally used the global aridity index as calculated in Sarquis et al. (2022a)

for *aridec* entries and annual downward shortwave radiation (hereafter annual solar radiation) from the TerraClimate database (Abatzoglou et al., 2018). We only used data from litter decomposed in ambient conditions (without manipulative treatments) for data exploration.

Further, to test whether the data fit an exponential distribution, we calculated the ratio between avgmTT and $\ln 2 \times \text{avgMTT}$. In an exponential distribution, the median equals $\ln 2$ times the mean. So, if the ratio between the median from our models (avgmTT) and the median calculated as $\ln 2 \times \text{avgMTT}$ equals 1, that would imply that both medians are equal, and the model follows an exponential distribution. All calculations, modeling, and figures were made using R (R Core Team, 2020).

3 Results

We fit three different candidate models for 128 time series of decomposition, which totaled 384 models. The information in our datasets supported all three models in a similar way. Most times the one-pool model had the lowest AICc values, but close to one-third of the times the two-pool series model had the best fit according to AICc (Fig. 2a and Supplement Table S2 in Sarquis and Sierra, 2023). Our ΔAICc values were very low (ΔAICc of the third quartile: 1.515), so we would have not been able to apply a $\Delta\text{AICc} = 2$ cutoff criterion if we wanted to, even when this practice is not recommended (Anderson, 2008; Burnham and Anderson, 2002). All of this showed that the information available was not enough to choose a single model with the best fit. Additionally, we obtained root mean squared residuals for all 128 datasets. For the one-pool model this indicator ranged from 1.1 to 12.9, for the two-pool parallel model it ranged from 1.1 to 12.3, and for the two-pool series model it ranged from 0.3 to 6.6 (Fig. 2b). The first two models performed similarly according to this parameter, but the series model had considerably lower residuals. Following this, we decided to implement a multi-model inference approach using model averaging, which left us with 128 individual models (see Supplement Table S3 in Sarquis and Sierra, 2023 for model variance and confidence intervals).

The median transit time of plant litter in arid lands after model averaging was within the range of the original models (Fig. 3). In this analysis, we only used data from litter decomposed in ambient conditions (without manipulative treatments). One and two-pool parallel models had similar mTT (23.27 ± 9.28 and 23.04 ± 9.65 months, mean \pm standard deviation, respectively). The two-pool series model had near 3-fold mTT values of 60.21 ± 45.80 months. After model averaging, mTT (i.e., avgmTT) dropped to 36.15 ± 22.20 months.

Looking at the avgmTT alone showed the wide range of time that litter takes to decompose in arid ecosystems (Fig. 4). Correlation between the duration in days and the

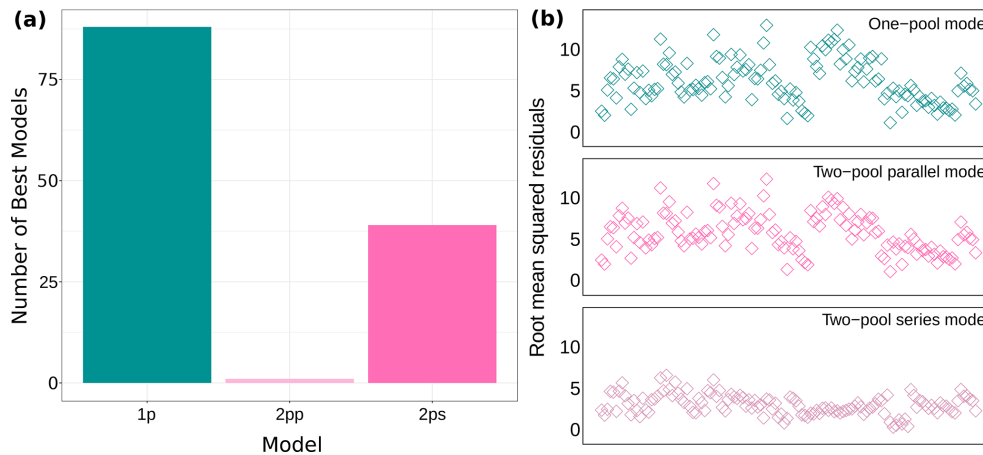


Figure 2. Model fit for all 128 datasets. (a) Number of models with the lowest AICc values and (b) root mean squared residuals for each model structure. 1p: one-pool model; 2pp: two-pool parallel model; 2ps: two-pool series model.

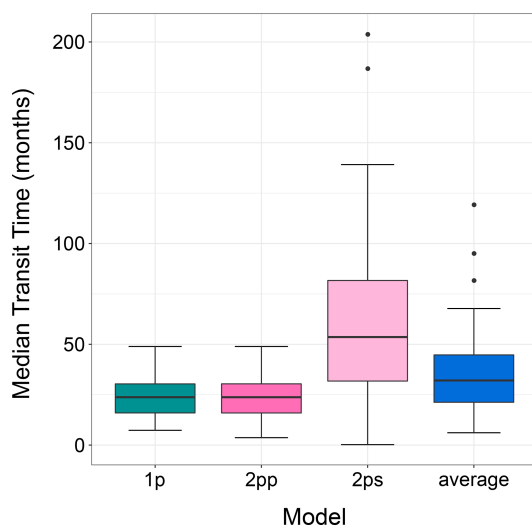


Figure 3. The median transit time (months) for three different models and for the averaged model. Only data for control or ambient treatments were used for this figure. 1p: one-pool model; 2pp: two-pool parallel model; 2ps: two-pool series model.

avgMTT was positive ($\tau = 0.2$, $p = 0.002$) but it was not significantly different from zero for avgMTT ($p = 0.3$; Fig. B1). An exploration of patterns of transit time in relation to environmental variables yielded weak correlation coefficients, except for mean annual temperature, which was moderate but significant ($r = -0.56$, $p = 0.047$). Values of avgMTT at the coldest end ranged between 37 and 65 months, while the warmest site showed values of 8 months (Fig. 4a). This shows that plant litter in warmer arid lands decomposes faster than at colder sites.

Calculating the quotient between the avgMTT and avgMTT times, the natural logarithm of 2 showed contrasting results (Fig. 5). Forty-two percent of the models in this

analysis had values near 0, which suggests that those models did not follow an exponential distribution. This is because in an exponential distribution the median equals $\ln 2$ times the mean, and the ratio of the median and $\ln 2$ times the mean, if equal, should result in 1. On the other hand, only 15 % of the models had values between 0.9 and 1.0. Complementarily, this suggests that those models did indeed have a near-exponential distribution.

4 Discussion

We asked as our first question of what model structures are more appropriate to represent decomposition in arid lands. After fitting three different models to the data in *aridec* we found that there was not enough information to choose a unique model judging by their AICc values (Fig. 2a). This limitation comes from the information contained in the original datasets, which constrains our capacity to distinguish between models. Simply put, we cannot force a model to reveal information that is not contained in the input data (Brun et al., 2001). As a workaround, we took a multi-model inference approach (Burnham and Anderson, 2002) that allowed us to incorporate the dynamics of all three models in our results by using AICc weights (Lukacs et al., 2010). In this way, our predictions of transit time in arid lands include the differences in litter chemistry and their effects on decomposition instead of just considering the bulk of litter as a homogeneous pool. This type of information theoretical approach, like model averaging, is not novel but is still underused in ecological studies (Grueber et al., 2011).

However, before fitting complex compartmental models, researchers should take into consideration the issue of collinearity. In a previous study, we found that most of the time series in the *aridec* database could only be fitted to simpler models with less than three parameters (Sarquis et al., 2022a). This was because the information contained in those

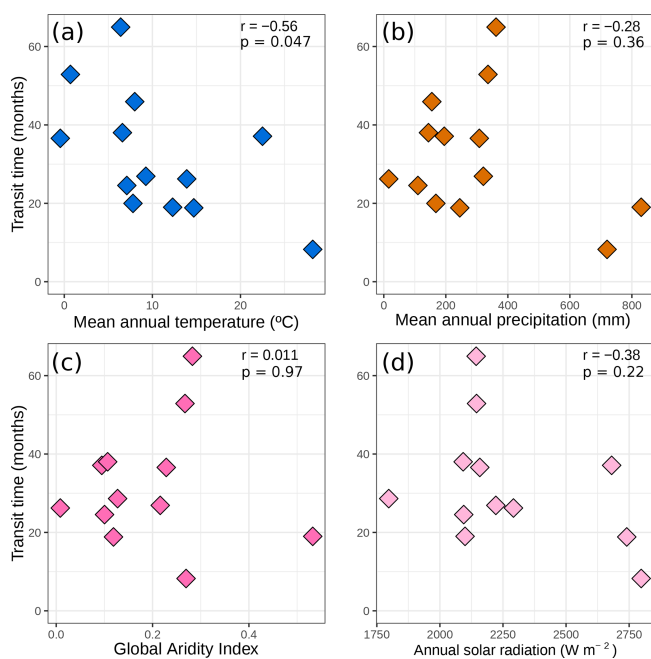


Figure 4. Transit time (months) Pearson correlations with (a) mean annual temperatures ($^{\circ}\text{C}$), (b) mean annual precipitation (mm), (c) global aridity index, and (d) annual solar radiation (W m^{-2}). Only data for control or ambient treatments were used for this figure. Each diamond represents the mean avgmTT for each site. Pearson correlation coefficients (r) and p values are displayed.

time series of litter decomposition was not sufficient to inform more complex models, for example, models with three distinct litter mass pools with transfer coefficients between them. This lack of information in the data caused collinearity between parameters, which in turn made it impossible to identify a single set of parameters for each model (Brun et al., 2001; Sierra et al., 2015). Some of these limitations probably come from the small number of sampling points in most decomposition studies (Sarquis et al., 2022a), which lowers the degrees of freedom available and limits our capacity to model complex organic-matter dynamics. The fact that complex models cannot be obtained from the data suggests that we should focus more attention on designing field experiments that can provide better information about model structures that are more consistent with our current understanding of litter heterogeneity and transformations (Prescott and Vesterdal, 2021).

Our second question was the following: what are the potential ranges of the median transit times of C in litter for arid lands? This part of our study yielded some new insights into the biogeochemistry of arid environments. The median transit time from one- and two-pool decomposition models without interactions were similar and showed that half of the litter mass is lost after almost 2 years in the field (Fig. 3). However, results from the two-pool model with a series structure were almost 3 times higher. This is explained by the mass trans-

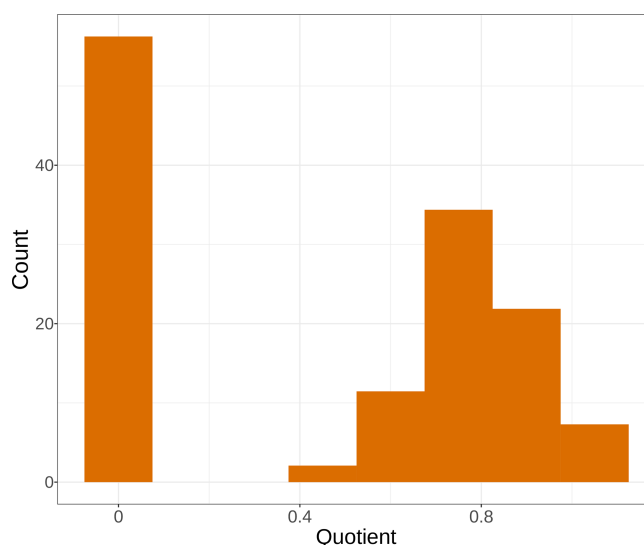


Figure 5. Histogram of frequency for the quotient of the median transit time and the natural logarithm of 2 times the mean transit time from average models. Bars represent the number of models for a range of values of the quotient.

fer from the fast-decomposing pool to the slow-decomposing pool, which slows down mass loss from litter. After model averaging, we obtained intermediate values of the median transit times of around 3 years (Fig. 3). Previously, estimations were made of the mean transit time for litter of between 3.4 and 3.8 years for the same models as in this study (Manzoni et al., 2012). However, their data did not come from an arid land. To our knowledge, our study is the first attempt to estimate litter transit time in arid environments.

The discrepancy between estimations from the two-pool series model and the other two models connects back to the issue of model parameter identifiability. Most decomposition studies carried out in arid lands last for only 1 year (Sarquis et al., 2022a). But our results show that decomposition of litter in arid environments can take on average 6 times longer until all litter mass exits the system. This means that most field decomposition studies are not capturing the entire dynamics of mass release through time. Most decomposition studies must usually compromise between measurement resolution and study length. Usually, studies that describe fine-scale dynamics of chemical compounds in leaf litter do not last for the entire decomposition process. By contrast, longer studies usually focus on broad-scale processes and represent litter as a homogenous pool. In turn, this has consequences for potential future research because the information that is not contained in data cannot be retrieved by modeling techniques (Brun et al., 2001). Similar to this study, Derrien and Amelung (2011) concluded that future continuous isotope labeling studies should make more measurements in time and with a finer time resolution in order to make more reliable estimations of soil C fluxes and reservoirs from models. If we

aim to incorporate field data into complex Earth system models, we need to take into consideration the study time length and resolution to capture both broad- and fine-scale mechanisms of decomposition. We acknowledge this might seem excessive given academic timescales are usually shorter than litter decomposition in arid lands. However, successful long-term litter decomposition projects exist and can be a potential solution to this issue (e.g., LIDET; Gholz et al., 2000).

We asked as our third question what the relationships between the median transit time and environmental variables are. From the set of four variables that we used to explore these relationships, only mean annual temperature showed a moderate correlation with the median transit time from average models (Fig. 4a). The importance of temperature as a climatic driver of decomposition is well documented (Zhang and Wang, 2015), both through its positive effects on microbial activity (Sinsabaugh et al., 1991) and its increase in photochemical emissions (Day and Bliss, 2020). Moreover, the correlation with mean annual precipitation was weak (Fig. 4b). This was more or less expected since it has been long known that precipitation fails to explain patterns of decomposition rates in arid lands (Austin, 2011).

As a final remark, we explored what transit time can teach us about the distribution of decomposition models. We calculated the quotient of the median transit time and the natural logarithm of 2 times the mean transit time from average models. Since the median of an exponential distribution equals $\ln 2$ times the mean, this ratio should equal 1 for models that are close to a single exponential distribution. But only 15 % of the models had values close to 1 (Fig. 5), which indicates that for most cases models did not follow an exponential distribution. The negative exponential model of decomposition has been the standard for litter and soil organic-matter decomposition studies for at least the last 5 decades (Olson, 1963). This connects back to our first results where the one-pool exponential model was not chosen by our information theoretical approach (Fig. 2). Previous studies found similar results where the negative exponential one-pool model did not rank first for the entirety of the datasets considered (Adair et al., 2008; Cornwell and Weedon, 2014; Manzoni et al., 2012). One alternative to exponential models has been a linear function relating mass loss and time, as it has performed statistically well in the past, especially in photodegradation experiments carried out in arid lands (Brandt et al., 2010). However, such linear functions lack any theoretical support as they imply that litter keeps losing mass even after all mass has decayed away in the long term. In contrast, the compartmental approach used here can account for chemical and physical transformations of litter as it decays and has strong theoretical support. Future studies could take advantage of the compartmental modeling framework to test multiple model structures that would represent a different mechanism of litter transformation and decay, having the one-pool model structure as a null model that can be contrasted against

more complex structures suggested by the information content in the data.

5 Conclusions

Although our theoretical understanding of the litter decomposition process is based on the assumption that plant litter is chemically and physically heterogeneous and undergoes multiple transformations, time series of litter decomposition studies contain only relatively little information on litter heterogeneity and its transformation rates. However, we have shown that a multi-model inference approach helps to reconcile theoretical understanding with information content in observed datasets of litter decomposition. In particular, the combination of AIC model averaging applied to a metric that is independent of model structure, the transit time, provides an inference framework that is useful to understand decomposition dynamics. This framework could help us get a better insight into the chemical transformations of organic matter in litter and soil and into how soil organic matter responds to changes in the environment.

We recognize that some limitations for modeling these complex structures arise from field study designs that do not capture the entire decomposition process. This limits the quantity and the quality of the information that can be extracted from empirical data. We recommend that future field decomposition studies incorporate in their designs some strategy to better capture the dynamics of different organic-matter pools in litter. This could be done by either measuring the proportion of each compound through time or by increasing sampling times and study length. The latter two can help gain a better fit and avoid collinearity when using an inverse-modeling approach as in this study. We further encourage researchers to fit models other than the one-pool model, when possible.

Appendix A

Table A1. Entry name in the *aridec* database, study site, decimal coordinates, and citation of the datasets included in this study.

Entry Name	Study Site	Coordinates	Citation
Austin2006a	Chubut, Argentina	Latitude: -45.7 Longitude: -70.3	Austin et al. (2006)
Berenstecher2021	Chubut, Argentina	Latitude: -45.7 Longitude: -70.3	Berenstecher et al. (2021)
Brandt2007	Colorado, USA	Latitude: 40.8 Longitude: -104.8	Brandt et al. (2007)
Day2018	Arizona, USA	Latitude: 33.5 Longitude: -111.8	Day et al. (2018)
Giese2009	Inner Mongolia, China	Latitude: 43.6 Longitude: 116.7	Giese et al. (2009)
Huang2017	Xinjiang, China	Latitude: 44.4 Longitude: 87.9	Huang et al. (2017)
	Xinjiang, China	Latitude: 45.3 Longitude: 87.6	
	Xinjiang, China	Latitude: 42.9 Longitude: 89.2	
Li2016	Inner Mongolia, China	Latitude: 43.0 Longitude: 120.7	Li et al. (2016)
Manlay2004	Kaolack, Senegal	Latitude: 13.8 Longitude: -15.7	Manlay et al. (2004)
Qu2020a	Inner Mongolia, China	Latitude: 41.5 Longitude: 107.0	Qu et al. (2020)
Santonja2017	Provence-Alpes-Côte d'Azur, France	Latitude: 44.0 Longitude: 5.9	Santonja et al. (2017)
Smith2018	New Mexico, USA	Latitude: 32.5 Longitude: -106.8	Smith and Throop (2018)
WangY2020	Inner Mongolia, China	Latitude: 44.2 Longitude: 116.5	Wang et al. (2020)

Appendix B

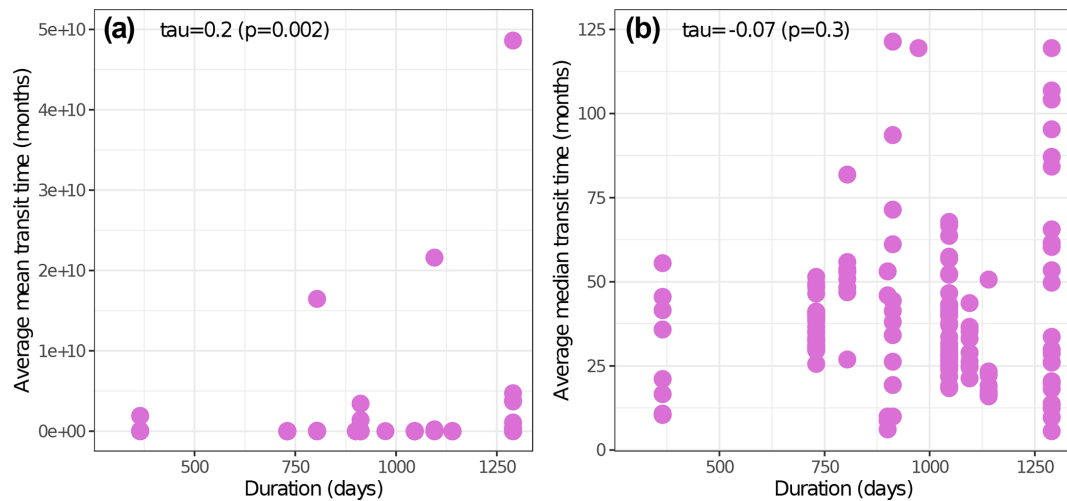


Figure B1. Non-parametric Kendall's rank correlation tests between study duration in days and avgMTT (a) and avgmTT (b), respectively.

Code and data availability. The *aridec* database version 1.0.2 is archived and publicly available at <https://doi.org/10.5281/zenodo.6600345> (Sarquis et al., 2022b). Result tables and code are stored at <https://doi.org/10.5281/zenodo.7799585> (Sarquis and Sierra, 2023).

Author contributions. CAS supervised the study. CAS and AS conceptualized the study. AS curated the data and carried out the analysis. AS wrote the original draft of the paper. CAS and AS revised and edited further versions of the paper.

Competing interests. The contact author has declared that neither of the authors has any competing interests.

Disclaimer. Publisher's note: Copernicus Publications remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Acknowledgements. We thank two anonymous referees, who made substantial contributions to the quality of this publication. We thank Mina Azizi-Rad for early discussions on model fitting and selection. We also thank Ignacio Siebenhart for providing annual solar radiation data. We thank Amy Austin, Soledad Méndez, and Ignacio Siebenhart for making revisions of early versions of this paper.

Financial support. Financial support for the project came from the University of Buenos Aires (grant no. UBACyT 2020) and the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT; projects PICT 2015-1231, PICT 2016-1780, and PICT 2019-02645). Agustín Sarquis was funded by the University of Buenos Aires (grant no. UBACyT 2018; res. no. 1245/18) and the German Academic Exchange Service (DAAD; Research Grants – Short-Term Grants program 2021, grant no. 57552337). Additional financial support was given by the Max Planck Society.

The article processing charges for this open-access publication were covered by the Max Planck Society.

Review statement. This paper was edited by Edzo Veldkamp and reviewed by two anonymous referees.

References

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., and Hegewisch, K. C.: TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015, *Sci. Data*, 5, 170191, <https://doi.org/10.1038/sdata.2017.191>, 2018.
- Adair, E. C., Parton, W. J., Del Grosso, S. J., Silver, W. L., Harmon, M. E., Hall, S. A., Burke, I. C., and Hart, S. C.: Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates, *Glob. Change Biol.*, 14, 2636–2660, <https://doi.org/10.1111/j.1365-2486.2008.01674.x>, 2008.
- Adair, E. C., Hobbie, S. E., and Hobbie, R. K.: Single-pool exponential decomposition models: potential pitfalls in their use in ecological studies, *Ecology*, 91, 1225–1236, <https://doi.org/10.1890/09-0430.1>, 2010.

- Adair, E. C., Parton, W. J., King, J. Y., Brandt, L. A., and Lin, Y.: Accounting for photodegradation dramatically improves prediction of carbon losses in dryland systems, *Ecosphere*, 8, e01892, <https://doi.org/10.1002/ecs2.1892>, 2017.
- Anderson, D. R.: *Model Based Inference in the Life Sciences: A Primer on Evidence*, Springer, New York, ISBN: 9780387740737, 2008.
- Austin, A. T.: Has water limited our imagination for arid-land biogeochemistry, *Trends Ecol. Evol.*, 26, 229–235, <https://doi.org/10.1016/j.tree.2011.02.003>, 2011.
- Austin, A. T. and Vivanco, L.: Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation, *Nature*, 442, 555–558, <https://doi.org/10.1038/nature05038>, 2006.
- Austin, A. T., Sala, O. E., and Jackson, R. B.: Inhibition of Nitrification Alters Carbon Turnover in the Patagonian Steppe, *Ecosystems*, 9, 1257–1265, <https://doi.org/10.1007/s10021-005-0039-0>, 2006.
- Berenstecher, P., Araujo, P. I., and Austin, A. T.: Worlds apart: Location above- or below-ground determines plant litter decomposition in a semi-arid Patagonian steppe, *J. Ecol.*, 109, 1365–2745, <https://doi.org/10.1111/1365-2745.13688>, 2021.
- Bradford, M. A., Veen, G. F. (Ciska), Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., Crowther, T. W., De Long, J. R., Freschet, G. T., Kardol, P., Manrubia-Freixa, M., Maynard, D. S., Newman, G. S., Logtestijn, R. S. P., Viketoft, M., Wardle, D. A., Wieder, W. R., Wood, S. A., and Van Der Putten, W. H.: A test of the hierarchical model of litter decomposition, *Nat. Ecol. Evol.*, 1, 1836–1845, <https://doi.org/10.1038/s41559-017-0367-4>, 2017.
- Brandt, L. A., King, J. Y., and Milchunas, D. G.: Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem, *Glob. Change Biol.*, 13, 2193–2205, <https://doi.org/10.1111/j.1365-2486.2007.01428.x>, 2007.
- Brandt, L. A., King, J. Y., Hobbie, S. E., Milchunas, D. G., and Sinsabaugh, R. L.: The Role of Photodegradation in Surface Litter Decomposition Across a Grassland Ecosystem Precipitation Gradient, *Ecosystems*, 13, 765–781, <https://doi.org/10.1007/s10021-010-9353-2>, 2010.
- Brun, R., Reichert, P., and Künsch, H. R.: Practical identifiability analysis of large environmental simulation models, *Water Resour. Res.*, 37, 1015–1030, <https://doi.org/10.1029/2000WR900350>, 2001.
- Burnham, K. P. and Anderson, D. R.: *Model Selection and Multi-model Inference*, edited by: Burnham, K. P. and Anderson, D. R., Springer New York, New York, NY, ISBN: 978-0-387-95364-9, 2002.
- Chappelle, G., Hastings, A., and Rasmussen, M.: Pool dynamics of time-dependent compartmental systems with application to the terrestrial carbon cycle, *J. R. Soc. Interface*, 20, 200, <https://doi.org/10.1098/rsif.2022.0843>, 2023.
- Cornwell, W. K. and Weedon, J. T.: Decomposition trajectories of diverse litter types: a model selection analysis, edited by: Oksanen, J., *Method. Ecol. Evol.*, 5, 173–182, <https://doi.org/10.1111/2041-210X.12138>, 2014.
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, *Ecol. Lett.*, 11, 1065–1071, <https://doi.org/10.1111/j.1461-0248.2008.01219.x>, 2008.
- Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., and Parton, W. J.: Formation of soil organic matter via biochemical and physical pathways of litter mass loss, *Nat. Geosci.*, 8, 776–779, <https://doi.org/10.1038/ngeo2520>, 2015.
- D’Odorico, P., Porporato, A., and Runyan, C. W.: *Dryland Ecohydrology*, edited by: D’Odorico, P., Porporato, A., and Wilkinson Runyan, C., Springer International Publishing, Cham, ISBN: 978-3-030-23268-9, 2019.
- Day, T. A. and Bliss, M. S.: Solar Photochemical Emission of CO₂ From Leaf Litter: Sources and Significance to C Loss, *Ecosystems*, 23, 1344–1361, <https://doi.org/10.1007/s10021-019-00473-8>, 2020.
- Day, T. A., Bliss, M. S., Tomes, A. R., Ruhland, C. T., and Guénon, R.: Desert leaf litter decay: Coupling of microbial respiration, water-soluble fractions and photodegradation, *Glob. Change Biol.*, 24, 5454–5470, <https://doi.org/10.1111/gcb.14438>, 2018.
- Derrien, D. and Amelung, W.: Computing the mean residence time of soil carbon fractions using stable isotopes: impacts of the model framework, *Eur. J. Soil Sci.*, 62, 237–252, <https://doi.org/10.1111/j.1365-2389.2010.01333.x>, 2011.
- Evans, S., Todd-Brown, K. E. O., Jacobson, K., and Jacobson, P.: Non-rainfall Moisture: A Key Driver of Microbial Respiration from Standing Litter in Arid, Semiarid, and Mesic Grasslands, *Ecosystems*, 23, 1154–1169, <https://doi.org/10.1007/s10021-019-00461-y>, 2020.
- Feng, S. and Fu, Q.: Expansion of global drylands under a warming climate, *Atmos. Chem. Phys.*, 13, 10081–10094, <https://doi.org/10.5194/acp-13-10081-2013>, 2013.
- García-Palacios, P., Maestre, F. T., Kattge, J., and Wall, D. H.: Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes, edited by: Klironomos, J., *Ecol. Lett.*, 16, 1045–1053, <https://doi.org/10.1111/ele.12137>, 2013.
- Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., and Parton, W. J.: Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition, *Glob. Change Biol.*, 6, 751–765, <https://doi.org/10.1046/j.1365-2486.2000.00349.x>, 2000.
- Giese, M., Gao, Y. Z., Zhao, Y., Pan, Q., Lin, S., Peth, S., and Brueck, H.: Effects of grazing and rainfall variability on root and shoot decomposition in a semi-arid grassland, *Appl. Soil Ecol.*, 41, 8–18, <https://doi.org/10.1016/j.apsoil.2008.08.002>, 2009.
- Grueber, C. E., Nakagawa, S., Laws, R. J., and Jamieson, I. G.: Multimodel inference in ecology and evolution: challenges and solutions, *J. Evol. Biol.*, 24, 699–711, <https://doi.org/10.1111/j.1420-9101.2010.02210.x>, 2011.
- Grünzweig, J. M., De Boeck, H. J., Rey, A., Santos, M. J., Adam, O., Bahn, M., Belnap, J., Deckmyn, G., Dekker, S. C., Flores, O., Gliksmann, D., Helman, D., Hultine, K. R., Liu, L., Meron, E., Michael, Y., Sheffer, E., Throop, H. L., Tzuk, O., and Yakir, D.: Dryland mechanisms could widely control ecosystem function-

- ing in a drier and warmer world, *Nat. Ecol. Evol.*, 6, 1064–1076, <https://doi.org/10.1038/s41559-022-01779-y>, 2022.
- Guttal, V. and Jayaprakash, C.: Self-organization and productivity in semi-arid ecosystems: Implications of seasonality in rainfall, *J. Theor. Biol.*, 248, 490–500, <https://doi.org/10.1016/j.jtbi.2007.05.020>, 2007.
- Huang, G., Zhao, H., and Li, Y.: Litter decomposition in hyper-arid deserts: Photodegradation is still important, *Sci. Total Environ.*, 601–602, 784–792, <https://doi.org/10.1016/j.scitotenv.2017.05.213>, 2017.
- Kattge, J., Bönisch, G., Díaz, S., et al.: TRY plant trait database – enhanced coverage and open access, *Glob. Change Biol.*, 26, 119–188, <https://doi.org/10.1111/gcb.14904>, 2020.
- Li, Y., Ning, Z., Cui, D., Mao, W., Bi, J., and Zhao, X.: Litter Decomposition in a Semiarid Dune Grassland: Neutral Effect of Water Supply and Inhibitory Effect of Nitrogen Addition, edited by: Hui, D., *PLoS One*, 11, e0162663, <https://doi.org/10.1371/journal.pone.0162663>, 2016.
- Lu, X., Wang, Y.-P., Luo, Y., and Jiang, L.: Ecosystem carbon transit versus turnover times in response to climate warming and rising atmospheric CO₂ concentration, *Biogeosciences*, 15, 6559–6572, <https://doi.org/10.5194/bg-15-6559-2018>, 2018.
- Lukacs, P. M., Burnham, K. P., and Anderson, D. R.: Model selection bias and Freedman’s paradox, *Ann. Inst. Stat. Math.*, 62, 117–125, <https://doi.org/10.1007/s10463-009-0234-4>, 2010.
- Manlay, R. J., Masse, D., Chevallier, T., Russell-Smith, A., Friot, D., and Feller, C.: Post-fallow decomposition of woody roots in the West African savanna, *Plant Soil*, 260, 123–136, <https://doi.org/10.1023/B:PLSO.0000030176.41624.d7>, 2004.
- Manzoni, S., Piñeiro, G., Jackson, R. B., Jobbágy, E. G., Kim, J. H., and Porporato, A.: Analytical models of soil and litter decomposition: Solutions for mass loss and time-dependent decay rates, *Soil Biol. Biochem.*, 50, 66–76, <https://doi.org/10.1016/j.soilbio.2012.02.029>, 2012.
- Meentemeyer, V.: Macroclimate and Lignin Control of Litter Decomposition Rates, *Ecology*, 59, 465–472, <https://doi.org/10.2307/1936576>, 1978.
- Méndez, M. S., Ballaré, C. L., and Austin, A. T.: Dose–responses for solar radiation exposure reveal high sensitivity of microbial decomposition to changes in plant litter quality that occur during photodegradation, *New Phytol.*, 235, 2022–2033, <https://doi.org/10.1111/nph.18253>, 2022.
- Olson, J. S.: Energy Storage and the Balance of Producers and Decomposers in Ecological Systems, *Ecology*, 44, 322–331, <https://doi.org/10.2307/1932179>, 1963.
- Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands, *Soil Sci. Soc. Am. J.*, 51, 1173–1179, <https://doi.org/10.2136/sssaj1987.03615995005100050015x>, 1987.
- Prescott, C. E. and Vesterdal, L.: Decomposition and transformations along the continuum from litter to soil organic matter in forest soils, *Forest Ecol. Manag.*, 498, 119522, <https://doi.org/10.1016/j.foreco.2021.119522>, 2021.
- Qu, H., Zhao, X., Lian, J., Tang, X., Wang, X., and Medina-Roldán, E.: Increasing Precipitation Interval Has More Impacts on Litter Mass Loss Than Decreasing Precipitation Amount in Desert Steppe, *Front. Environ. Sci.*, 8, 1–11, <https://doi.org/10.3389/fenvs.2020.00088>, 2020.
- R Core Team: R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/> (last access: 9 May 2023), 2020.
- Safriel, U. and Adeel, Z.: Dryland Systems, in: *Ecosystems and Human Well-being: Current State and Trends, Volume 1*, edited by: Hassan, R., Scholes, R., and Ash, N., 623–662, Island Press, Washington, ISBN: 1559632283, 2005.
- Santonja, M., Fernandez, C., Proffitt, M., Gers, C., Gauquelin, T., Reiter, I. M., Cramer, W., and Baldy, V.: Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest, edited by: McCulley, R., *J. Ecol.*, 105, 801–815, <https://doi.org/10.1111/1365-2745.12711>, 2017.
- Sarquis, A. and Sierra, C. A.: Supplementary Material for Sarquis & Sierra 2023 (v1.0.1), Zenodo [data set and code], <https://doi.org/10.5281/zenodo.7799585>, 2023.
- Sarquis, A., Siebenhart, I. A., Austin, A. T., and Sierra, C. A.: Aridec: an open database of litter mass loss from aridlands worldwide with recommendations on suitable model applications, *Earth Syst. Sci. Data*, 14, 3471–3488, <https://doi.org/10.5194/essd-14-3471-2022>, 2022a.
- Sarquis, A., Siebenhart, I. A., Austin, A. T., and Sierra, C. A.: AgustinSarquis/aridec: aridec (v1.0.2), Zenodo [data set and code], <https://doi.org/10.5281/zenodo.6600345>, 2022b.
- Shumway, R. H. and Stoffer, D. S.: *Time Series Analysis and Its Applications*, 4th Edn., edited by: DeVeaux, R., Fienberg, S. E., and Olkin, I., Springer International Publishing, Cham, ISBN: 978-3-319-52451-1, 2017.
- Sierra, C. A. and Müller, M.: A general mathematical framework for representing soil organic matter dynamics, *Ecol. Monogr.*, 85, 505–524, <https://doi.org/10.1890/15-0361.1>, 2015.
- Sierra, C. A., Müller, M., and Trumbore, S. E.: Models of soil organic matter decomposition: the SoilR package, version 1.0, *Geosci. Model Dev.*, 5, 1045–1060, <https://doi.org/10.5194/gmd-5-1045-2012>, 2012.
- Sierra, C. A., Malghani, S., and Müller, M.: Model structure and parameter identification of soil organic matter models, *Soil Biol. Biochem.*, 90, 197–203, <https://doi.org/10.1016/j.soilbio.2015.08.012>, 2015.
- Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., and Trumbore, S. E.: The muddle of ages, turnover, transit, and residence times in the carbon cycle, *Glob. Change Biol.*, 23, 1763–1773, <https://doi.org/10.1111/gcb.13556>, 2017.
- Sierra, C. A., Hoyt, A. M., He, Y., and Trumbore, S. E.: Soil Organic Matter Persistence as a Stochastic Process: Age and Transit Time Distributions of Carbon in Soils, *Global Biogeochem. Cy.*, 32, 1574–1588, <https://doi.org/10.1029/2018GB005950>, 2018.
- Sinsabaugh, R. L., Antibus, R. K., and Linkins, A. E.: An enzymic approach to the analysis of microbial activity during plant litter decomposition, *Agr. Ecosyst. Environ.*, 34, 43–54, [https://doi.org/10.1016/0167-8809\(91\)90092-C](https://doi.org/10.1016/0167-8809(91)90092-C), 1991.
- Smith, J. G. and Throop, H. L.: Animal generation of green leaf litter in an arid shrubland enhances decomposition by altering litter quality and location, *J. Arid Environ.*, 151, 15–22, <https://doi.org/10.1016/j.jaridenv.2017.11.003>, 2018.
- Soetaert, K. and Petzoldt, T.: Inverse Modelling, Sensitivity and Monte Carlo Analysis in R Using Package FME, *J. Stat. Softw.*, 33, 1–28, <https://doi.org/10.18637/jss.v033.i03>, 2010.

- Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J. A., Sevanto, S., and Liski, J.: Leaf litter decomposition—Estimates of global variability based on Yasso07 model, *Ecol. Modell.*, 220, 3362–3371, <https://doi.org/10.1016/j.ecolmodel.2009.05.016>, 2009.
- Wang, Y., Li, F. Y., Song, X., Wang, X., Suri, G., and Baoyin, T.: Changes in litter decomposition rate of dominant plants in a semi-arid steppe across different land-use types: Soil moisture, not home-field advantage, plays a dominant role, *Agr. Ecosyst. Environ.*, 303, 107119, <https://doi.org/10.1016/j.agee.2020.107119>, 2020.
- Zanne, A. E., Flores-Moreno, H., Powell, J. R., et al.: Termite sensitivity to temperature affects global wood decay rates, *Science*, 377, 1440–1444, <https://doi.org/10.1126/science.abo3856>, 2022.
- Zhang, X. and Wang, W.: Control of climate and litter quality on leaf litter decomposition in different climatic zones, *J. Plant Res.*, 128, 791–802, <https://doi.org/10.1007/s10265-015-0743-6>, 2015.