https://doi.org/10.5194/egusphere-2026-5013
Preprint. Discussion started: 4 September 2026

A Framework for Representing Biodegradation in Atmospheric Multiphase Models

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Abstract. Biodegradation is a key process in natural ecosystems through which microorganisms recycle organic matter. Cloud water can host metabolically active microorganisms, opening the possibility that biodegradation contributes to atmospheric processing of organics. However, the extent to which microbial activity occurs in the atmosphere and modifies carbon budgets, and the parameters that control the rates, remain poorly constrained. We present a framework to quantify the key parameters of biodegradation of six major cloud-water organics (methanol, ethanol, formaldehyde, acetaldehyde, formic and acetic acids) and for unspecified organics. Using a multiphase box model, we perform sensitivity analyses to evaluate the dependence of biodegradation rates on bacterial abundance (N_{bact}), Henry's law constants ($K_{H(eff)}$) and biodegradation rate constants (k_{bact}). Biodegradation scales proportionally with N_{bact}, while fits indicate weaker sensitivities to $K_{H,\text{eff}}$ and k_{bact} with slopes of 0.89 and 0.39 in log–log space, respectively. Biodegradation of compounds with $K_H > 10^5$ M atm^{-1} and/or $k_{\text{bact}} > 2 \times 10^{-13}$ L cell^{-1} s^{-1} is limited by insufficient substrate replenishment in bacteria-containing droplets. Biodegradation rates normalized by cell concentration are consistent in magnitude with values reported for other aqueous environments, resulting in an effective rate constant of $k_{\text{bact,DOM}} \sim 10^{-13}$ L cell^{-1} s^{-1} for dissolved organic matter (DOM). Comparison of predicted biodegradation rates with atmospheric chemical loss processes and biodegradation in other aquatic environments indicates that atmospheric biodegradation may be a significant sink for some individual compounds (C_2H_5OH, HCOOH, CH_3COOH) but generally represents a minor sink (< 1%) under the conditions explored. Overall, the empirical relationships and sensitivities derived here provide a framework for implementing biodegradation in atmospheric multiphase models of different complexity, enabling assessment not only of its contribution to atmospheric carbon cycling but also of how environmental conditions may affect microbial functioning of the airborne portion of Earth' microbiome.

1 Introduction

Microbial biodegradation is a well-established process that strongly influences the budgets of monofunctional C_1 and C_2 compounds in aquatic environments. In freshwater and marine systems, bacteria metabolize these compounds through enzymatic pathways, converting them into intermediate metabolites and ultimately mineralizing them to CO_2 (de Bruyn et al., 2020; Cory and Kling, 2018). The efficiency of these processes is supported by high microbial abundances in aquatic systems, where

https://doi.org/10.5194/egusphere-2026-5013
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bacterial concentrations exceed those typically found in the atmosphere by several orders of magnitude (Whitman et al., 1998; Burrows et al., 2009; Ervens et al., 2025).

In the atmosphere, by contrast, photochemical oxidation is generally considered the dominant degradation pathway for volatile organic compounds (VOCs) and other trace gases (Seinfeld and Pandis, 1998). Oxidation processes initiated by radicals, such as OH and NO_3 are major atmospheric pathways in both the gas and aqueous phases and are included in atmospheric chemistry models at different levels of detail (Ervens et al., 2003; Herrmann et al., 2005; Barth et al., 2021). The atmosphere hosts metabolically active microorganisms which implies the possibility that biological transformations may also contribute to the cycling of atmospheric trace compounds (Amato et al., 2005; Sattler et al., 2001). This idea has stimulated increasing interest in the concept of an active atmospheric microbiome and the potential role of biodegradation as an additional sink for selected organic compounds (Vaïtilingom et al., 2010, 2013; Jaber et al., 2021; Khaled et al., 2021).

Over the past two decades, laboratory, field and model studies have provided evidence that microbial activity in clouds and fogs may influence the budgets of organic compounds under specific environmental conditions (Ariya et al., 2002; Fankhauser et al., 2019; Khaled et al., 2021; Ervens and Amato, 2020; Nuñez López, 2025; Nuñez López et al., 2024; Cao et al., 2025, 2026). Clouds have been of particular interest as potential air masses for biodegradation processes in the atmosphere. Despite highly oligotrophic and stressful conditions, cloud droplets are more likely to contain sufficient liquid water and dissolved substrates to sustain metabolic activity as compared to aerosol particles at humidity below saturation (Amato, 2017). Such studies suggest that atmospheric microorganisms can metabolize a range of chemical compounds that are present in the atmosphere, including organics (Amato et al., 2007), nitrogen-containing species (Mathonat et al., 2026a), and oxidants such as H_2O_2 (Wirgot et al., 2019). Cloud water analyses indicate that at least a subset of airborne microorganisms is viable and metabolically active outside clouds as well (Péguilhan et al., 2025). The importance of assessing biodegradation and microbial activity in the atmospheric environment extends beyond its potential influence on atmospheric chemical budgets. It also helps address broader questions regarding microbial survival, maintenance and ecological functioning in the atmosphere.

Monofunctional C_1 and C_2 compounds are ubiquitous atmospheric constituents and often represent a substantial fraction of dissolved organic matter in cloud and fog water (Herckes et al., 2013). They have been shown to be essential nutrients for microorganisms in other environments such as the surface of plants which act as strong sources of airborne microorganisms (Vorholt, 2012). These compounds originate from both primary emissions (vegetation, biomass burning, anthropogenic sources) and secondary photochemical production through oxidation of volatile organic compounds. Their high solubility enables efficient partitioning into atmospheric aqueous phases such as cloud droplets where they are efficiently oxidized. Recent model studies have come to different conclusions regarding the overall importance of microbial biodegradation on the atmospheric budgets of these compounds: Sensitivity studies using simple box models, such as Khaled et al. (2021); Nuñez López et al. (2024); Cao et al. (2025), suggest limited importance of biodegradation in fog and clouds on organic concentrations in the atmospheric multiphase system, whereas other studies that focused primarily on comparing biodegradation and chemical loss rates in the aqueous phase concluded that the two processes can be of comparable magnitude (Pailler et al., 2023; Vaïtilingom et al., 2010, 2013; Jaber et al., 2020, 2021) . All these studies relied on simplified representations of cloud microphysics,

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microbial abundance and environmental conditions, and they were constrained by the limited biodegradation data available for atmospheric microorganisms.

The rate constants on which these estimates are often based are usually obtained from laboratory incubations of microorganisms isolated from cloud water or aerosol samples that were subsequently cultured in the lab (Vaïtilingom et al., 2010, 2011). Such experiments are usually conducted under conditions that are more favorable than those encountered in natural clouds, particularly with respect to nutrient and water availability, temperature and exposure to environmental stressors. Consequently, laboratory-derived biodegradation rates likely represent upper-limit estimates of microbial activity in the atmospheric aqueous phases. Nonetheless, such data are valuable because they provide a means to assess the maximum potential influence of biodegradation processes on atmospheric chemical budgets on relevant temporal and spatial scales. Biodegradation is currently not represented in atmospheric chemistry models, and thus its potential relevance across a range of atmospheric conditions remains largely unexplored. To identify sensitivities and parameter ranges, biodegradation needs to be represented by simplified descriptions and parameterizations that can be included in atmospheric chemistry models of different complexity. Such approaches will enable the systematic assessment of environmental conditions and regions where biodegradation may be relevant.

Based on this motivation, the present study builds on our previous work , in which we investigated the impact of bacterial biodegradation on the atmospheric budgets of formic and acetic acids (Nuñez López et al., 2024). Here, we describe biodegradation of additional compounds (C_1 and C_2 aldehydes and alcohols) and further explore the extent to which biodegradation and substrate characteristics need to be known for meaningful prediction in atmospheric models. Overall, our proposed framework provides guidance for model implementation and to motivate future experimental and modeling efforts to better constrain biodegradation as a potential sink of small organic compounds, alongside chemical and physical loss processes.

2 Methodology

2.1 Box model description and set-up

We use the same multiphase chemistry box model with detailed gas- and aqueous-phase chemistry as in our previous studies (Khaled et al., 2021; Nuñez López et al., 2024; Nuñez López, 2025). The chemical module includes 58 reactions in the gas phase and 34 in the aqueous phase. Fifteen of the 31 chemical species are transferred between the gas and aqueous phases using a mass transfer coefficient k_{mt} that is defined as

$$k_{mt} = \left(\frac{r_d^2}{3\,D_g} + \frac{r_d}{3\,\alpha} \sqrt{\frac{2\pi\,M_g}{R\,T}} \right)^{-1} \tag{1}$$

whereas r_d is the drop radius [cm], D_g the gas phase diffusion coefficient [$\mathrm{cm^2\,s^{-1}}$], α the dimensionless mass accommodation coefficient, and M_g the molecular weight [$\mathrm{g\,mol^{-1}}$].

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We use the standard equations to describe the change in chemical concentrations during each 1-second model time step in the multiphase chemistry system:

$$\frac{dC_{aq,g}}{dt} = \underbrace{k_{mt}\ LWC\left(C_g - \frac{C_{aq,g}}{LWC\ K_{H(eff)}\ R\,T}\right)}_{phase\ transfer} + \underbrace{S_{aq,chem} - L_{aq,chem}}_{chemical\,processes} - L_{bact} \tag{2}$$

$$\frac{dC_g}{dt} = -\underbrace{k_{mt}\ LWC\left(C_g - \frac{C_{aq,g}}{LWC\ K_{H(eff)}\ R\,T}\right)}_{phase\ transfer} + \underbrace{S_{g,chem} - L_{g,chem}}_{chemical\,processes} \tag{3}$$

whereas LWC is the liquid water content (vol vol^{-1}), $K_{H(eff)}$ is the (effective) Henry's law constant [M atm^{-1}], and R the constant for ideal gases (0.082 L atm (mol K)$^{-1}$). All concentrations are expressed in units related to the gas phase volume, mol g$_{\text{air}}^{-1}$. The terms S_{aq}, L_{aq}, S_g, L_g denote the chemical sources and losses in the aqueous (aq) and gas (g) phases. L_{bact} denotes the loss by biodegradation occurring in a subset of droplets. The box model includes a monodisperse drop population with a constant liquid water content of 0.42 g m^{-3}. Simulations are performed at constant temperature (286 K) and air density (1.032·10^{-3} g cm^{-3}). Drop diameter D_d, drop number concentration N_d and pH value are kept constant throughout each simulation. Model simulations are performed for one hour comparing results from simulations with and without bacteria cells (i.e. L_{bact} > 0 and L_{bact} = 0, respectively). The predicted difference in total mixing ratios (gas + aqueous) predicted in the two simulation sets ($C_{t,nocell}$, $C_{t,cell}$) yields the loss rate due to biodegradation in ppt h^{-1}

$$R_{bio}\,[ppt\,h^{-1}] = \frac{C_{t,nocell} - C_{t,cell}}{1h} \tag{4}$$

The relative contribution of biodegradation as compared to chemical losses is accordingly defined as $X_{aq,bio}$:

$$X_{aq,bio} = \frac{L_{bact}}{L_{bact} + L_{aq,chem} + L_{gas,chem}} \tag{5}$$

where L_{bact} denotes microbial loss in cloud water, and $L_{aq,chem}$ and $L_{gas,chem}$ denote chemical loss in the aqueous and gas phases, respectively, with all rates expressed in identical units.

2.2 Biodegradation kinetics

Following our previous model approach, biodegradation is represented as a second-order loss process (Khaled et al., 2021; Nuñez López et al., 2024):

$$L_{bact} = -\frac{d[Org]}{dt} = k_{bact}[Org][Cell] \tag{6}$$

where $[Org]$ is the concentration of the organic compound [mol L^{-1}], $[Cell]$ is the bacterial cell concentration [cell L^{-1}] and k_{bact} is the biodegradation rate constant [L^{-1} cell^{-1} s^{-1}]. Even if available for some of the data, the temperature dependence of biodegradation rates was not taken into account as this effect is likely small over the range of experimental and cloud

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temperatures (Nuñez López et al., 2024). Rate constants were derived from lab-based biodegradation measurements for formic acid, acetic acid, methanol and formaldehyde in cloud water (Vaïtilingom et al., 2011, 2013; Husárová et al., 2011). Reported biodegradation rates in these studies [mol cell^{-1} s^{-1}] were converted into second-order rate constants k_{bact} (Khaled et al., 2021).

For ethanol and acetaldehyde, no measurements in cloud water (or its proxies) were available. To obtain data for these compounds, a literature compilation of biodegradation rates in other aquatic environments was performed for all six compounds (Table S1, Figure S1). This compilation was used to evaluate whether kinetic data derived from other aquatic environments, such as lakes, rivers, estuaries, and seawater, are generally comparable to those performed in cloud water.

In many studies on surface aquatic environments, biodegradation is reported as a first-order loss rate R_{bio}^{1st} [h^{-1}], together with corresponding substrate and bacterial concentrations. Substrate-to-cell ratios in the various aquatic environments span several orders of magnitude (10^{-16}–10^{-10}, Fig. S1b), with values for cloud water in the mid-range ($\sim 10^{-10}$). The measurements of these ratios are based on bulk aqueous samples, in which substrate and microbial abundances are homogeneously mixed across the full aqueous volume, unlike dispersed droplets in natural clouds. Surface waters inherently represent bulk aqueous systems, and for practical reasons also cloud water is sampled in bulk since the in-situ investigation of individual cloud droplets is not yet feasible. In the atmospheric aqueous phase of clouds, however, bacteria are not uniformly distributed among cloud droplets. Only a small fraction of droplets contains a bacterial cell, in which case the substrate-to-cell ratio differs from bulk conditions (Ervens et al., 2025). This difference can be quantified according to

$$\left(\frac{Org}{Cell}\right)_{bulk} = \frac{1}{f}\left(\frac{Org}{Cell}\right)_{droplet}. \tag{7}$$

where f is the fraction of bacteria-containing droplets in the total droplet population. Thus, under conditions where one out of 1000 cloud droplets contains an active bacterial cell ($N_{dr} = 100\,\mathrm{cm}^{-3}$; $N_{bact} = 0.1\,\mathrm{cm}^{-3}$), the bulk substrate-to-cell ratio is a factor of 1000 higher than in individual bacteria-containing droplets (Ervens et al., 2025). The extent to which such differences in substrate-to-cell ratio affect microbial activity cannot be assessed directly for the concentration ranges and gradients in cloud droplets. It should be noted that, generally, at low substrate concentration, the rates of enzymatic processes linearly scale with the substrate concentration, whereas at higher concentrations the rate becomes less sensitive (Michaelis-Menten kinetics). However, in the current analysis, these dependencies are not taken into account due to the lack of detailed data. Instead, since lab experiments under 'cloud water' conditions are typically conducted as bulk aqueous phase systems, we use the kinetic data derived from such measurements as the best available representation for biodegradation kinetics in clouds.

Under this assumption, biodegradation rates reported for other aquatic environments are compared to cloud-water measurements to evaluate whether they yield similar biodegradation kinetics when normalized by bacterial abundance. To ensure consistency across datasets, reported rates were converted to second-order rate constants using:

$$k_{bact} = R_{bio}^{1st}[Cell]^{-1} \tag{8}$$

The concentration of cells is defined differently across studies. They are commonly reported as total cell counts (including non-viable cells) or colony-forming units (CFU), which is the fraction of cells that are capable of developing under the specific incubation conditions. The resulting biodegradation rate constants for the six compounds are listed in Table 1.

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Table 1. Biodegradation rate constants used in this study. Data for CH_3OH, HCHO, HCOOH and CH_3COOH were taken form measurements in cloud water proxies, the values for CH_3CHO and C_2H_5OH were taken from other auqatic environments (Table S1, converted using Eq.-8).

Organic compound	k_{bact} [$\mathrm{L\,cell^{-1}\,s^{-1}}$]
CH_3OH	1.5×10^{-18}
C_2H_5OH	7.2×10^{-12}
HCHO	3.7×10^{-17}
CH_3CHO	2.5×10^{-12}
HCOOH	1.5×10^{-13}
CH_3COOH	8.7×10^{-14}

3 Results and discussion

3.1 Relationship of R_{bio} with N_{bact}

Atmospheric bacterial concentrations are highly variable, ranging from ~0.001 to 1 $\mathrm{cm^{-3}}$. Reported values of N_{bact} do not only depend on the environment but also on the measurement technique, including differences in sampling efficiency, detection limits, and whether total cell counts or other proxies of microbial abundance are reported. Consequently, reported values of N_{bact} represent different operational definitions of bacterial abundance and may actually present different quantities. Only a small fraction of atmospheric particles contains a bacterial cell. These particles are assumed to act as cloud condensation nuclei (CCN), thereby providing the aqueous volume in which microbial processes occur (Amato, 2017). Each bacteria-containing droplet is assumed to host a single cell, consistent with the comparable size range of bacterial cells and typical cloud condensation nuclei.

In previous model studies, a value of $N_{bact} = 0.1\,\mathrm{cm^{-3}}$ was assumed, corresponding to the upper end of reported measurements (Khaled et al., 2021; Nuñez López et al., 2024). In the present study, N_{bact} was varied from 0.005 to 0.5 $\mathrm{cm^{-3}}$, while keeping the total number of droplets constant ($N_{dr} = 100\,\mathrm{cm^{-3}}$).

As shown in Figure 1, the biodegradation loss rate increases linearly with N_{bact} across the full range. This linearity suggests that only a small fraction of the available organic material is consumed over the simulation time, such that substrate depletion remains negligible relative to the total substrate budget. Non-linear behavior would only be expected at substantially higher bacterial concentrations, where biodegradation would deplete a significant fraction of the available organic material. Under such conditions, substrate limitation would reduce the amount of organic matter degraded per cell. However, such cell concentrations are unlikely in the atmosphere. The results further show that the biodegradation rate scales proportionally with N_{bact} (slope of unity in log-log space), and can therefore be described by

$$R_{bio} = 10^{a} N_{bact} \tag{9}$$

where a is a compound-specific empirical coefficient which are listed in Table 2.

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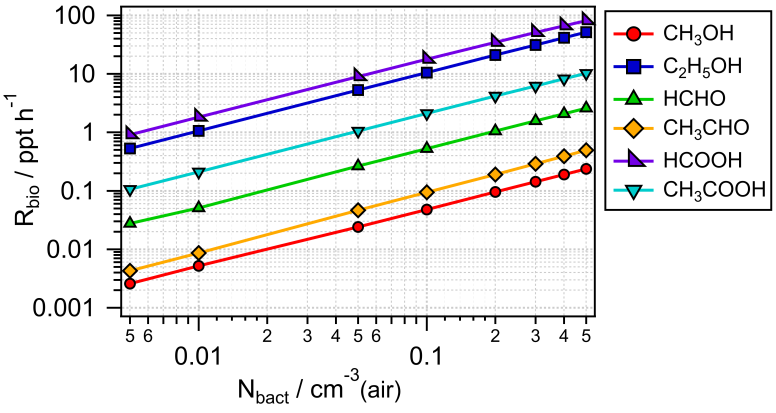

Figure 1. Predicted biodegradation rates R_{bio} for six C_1 and C_2 organic compounds as a function of bacteria concentration N_{bact}

Overall, despite the uncertainties in N_{bact} due to the different measurement techniques and quantities, Eq. 9 provides a practical means to estimate an upper bound of R_{bio} for the six individual compounds across the full range of N_{bact}.

Table 2. Compound-specific coefficients describing the dependence of the biodegradation rate R_{bio} on N_{bact} (Eq. 9) for the model conditions as used in the present study.

Compound	a
CH_3OH	-0.3126
C_2H_5OH	2.0207
HCHO	0.7209
CH_3CHO	0.003027
HCOOH (pH = 4.5)	2.2404
CH_3COOH (pH = 4.5)	1.3199

3.2 Relationship of ΔC with $K_{H(eff)}$

The Henry's law constants of the organic substrates control the amount of dissolved material available for biodegradation (Khaled et al., 2021; Nuñez López et al., 2024). Figure 2 shows ΔC as a function of the Henry's law constants of the six substrates. For formic and acetic acids, effective Henry's law constants at pH = 4.5 and pH = 5.5 are considered, respectively, to represent a typical cloud water pH range. ΔC generally increases with increasing Henry's law constant up to approximately $K_{H(eff)} = 10^5\ \mathrm{M\,atm^{-1}}$. Although ethanol and acetaldehyde appear to follow a similar trend, their ΔC values are higher than expected from the correlation defined by methanol, formaldehyde, formic acid (pH = 4.5) and acetic acid. Notably these are the compounds, for which k_{bact} was derived from other aquatic environments from data sets in different aquatic environments (Figure S1). Thus, this deviation from the linear trend may be related to different biodegradation kinetics. Specific reasons for

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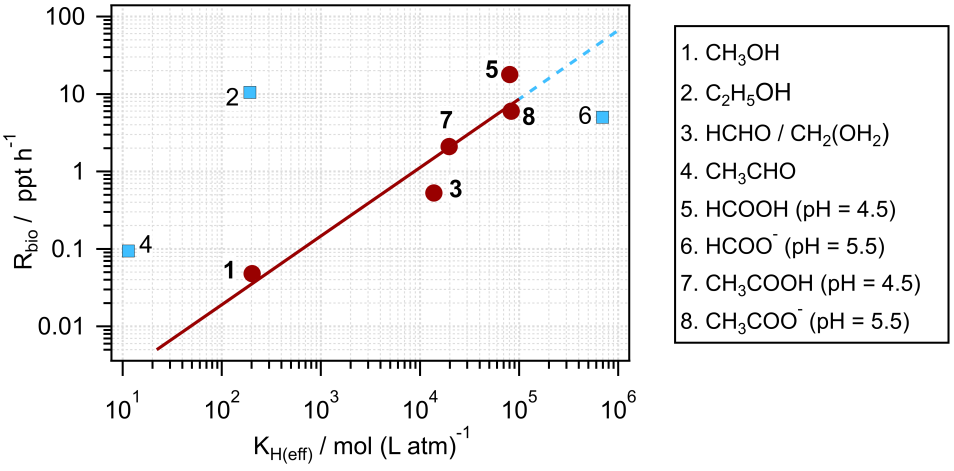

Figure 2. Predicted biodegradation rates R_{bio} as a function of the (effective) Henry's law constant $K_{H(eff)}$). The red points are included in the linear regression in log–log space (Eq. 12), whereas the blue points are shown for completeness only. The red line represents the fitted relationship up to a threshold value of $K_H = 10^5 M\,atm^{-1}$, above which R_{bio} decreases due to limited replenishment of the organic substrate in the bacteria-containing droplets.

this discrepancy cannot be clearly determined; they may include different bacteria populations and/or environmental conditions. The Henry's law constants of these compounds are comparably well constrained values as given in large literature data bases (Sander, 2023). The remaining five compounds exhibit a linear trend within the log-log space, which can be described by

$$\log R_{bio} = -3.49\,(\pm 0.71) + (0.89(\pm 0.17)\,\log K_{H(eff)}) \tag{10}$$

where the uncertainty represents one standard deviation.

The fitted slope of 0.89 is slightly lower than the unity slope expected from simple equilibrium partitioning: Under gas–aqueous equilibrium, the dissolved concentration is proportional to the gas-phase partial pressure via Henry's law:

$$C_{aq} = K_{H(eff)}\,p_g \tag{11}$$

Because the gas-phase partial pressure p_g is small and approximately constant, variations in C_{aq} scale directly with $K_{H(eff)}$, implying a theoretical slope of unity in log–log space under equilibrium conditions:

$$\log C_{aq} = \log K_{H(eff)} + \log p_g \tag{12}$$

The deviation from unity slope therefore indicates that the aqueous-phase concentration alone does not fully control the biodegradation rate. It suggests an influence of additional processes such as limited gas–liquid mass transfer or aqueous-phase loss pathways that reduce R_{bio}.

Equation 12 is applicable up to $K_{H(eff)} \sim 10^5$ M atm^{-1}. The predicted rate for the single point above this range (HCOOH at pH = 5.5, $\Delta C \sim 5$ ppt h^{-1}) lies approximately one order of magnitude below the predicted value based on Eq. 10. As

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discussed by Nuñez López et al. (2024), biodegradation of highly soluble compounds may become transport-limited when the supply of material from the gas phase and/or the chemical production inside the droplet is not sufficiently fast to maintain equilibrium between the gas and aqueous phases. Under these conditions, the aqueous-phase concentration is no longer controlled solely by Henry's law partitioning, but also by the rate at which gas-phase species are replenished, which can reduce the effective availability of substrate and, thus, the biodegradation rate.

The comparison with the ΔC–N_{bact} relationship shows that ΔC is less sensitive to $K_{H(eff)}$ than to N_{bact}. Given that $K_{H(eff)}$ is comparatively well constrained for 1000s of atmospherically relevant compounds, Eq. 10 provides a useful predictive relationship to identify compounds for which biodegradation is expected to be most relevant. In particular, it allows an initial screening of compounds. for which further investigation of biodegradation processes may be warranted. However, a full assessment of biodegradation also requires consideration of the biodegradation kinetics, as the rate is not solely determined by the physicochemical properties of the substrate.

3.3 Relationship of R_{bio} with k_{bact}

3.3.1 k_{bact} for individual compounds

The substrate available for biodegradation is controlled not only by source processes (e.g., uptake from the gas phase and in-droplet chemical production), but also by the rate at which microorganisms consume the substrate. Figure 3 shows R_{bio} as a function of the biodegradation rate coefficient k_{bact}. An empirical fit yields

$$\log R_{bio} = 5.85\,(\pm 1.03) + 0.39\,(\pm 0.07)\,\log k_{bact} \tag{13}$$

where uncertainties denote one standard deviation. Relative to the ΔC–$K_{H(eff)}$ relationship, the larger uncertainties reflect the narrow range of k_{bact} values available for most compounds ($\sim 10^{-14}$–10^{-13} L cell^{-1} s^{-1}). Despite substantial scatter, the positive slope indicates that higher k_{bact} values are generally associated with larger biodegradation rates. However, the slope of 0.39 implies that changes in k_{bact} translate into comparatively smaller changes in R_{bio} as compared to those caused by variations in N_{bact} or $K_{H(eff)}$.

This behavior indicates that the overall biodegradation rate is not controlled by k_{bact} alone. In the loss term L_{bact} (Eq. 6), cell concentration and k_{bact} are constant for a given simulation, implying that deviations from proportionality must arise from variations in the organic substrate concentration. The response of R_{bio} to k_{bact} indicates that $[Org]$ decreases as k_{bact} increases. This trend suggests that the organic substrate cannot be replenished sufficiently fast through gas-phase uptake or chemical production inside the droplet. Above a threshold of $k_{bact} \sim 10^{-13}$ L cell^{-1} s^{-1}, this limitation becomes increasingly pronounced, leading to decreasing R_{bio} with increasing k_{bact}. This behavior is consistent with the trend observed at high $K_{H(eff)}$, where limited replenishment of the substrate inside a droplet restricts substrate availability and thereby results in reduced biodegradation rates.

Overall, R_{bio} shows the weakest sensitivity to k_{bact} among the parameters tested ($K_{H(eff)}$ and N_{bact}). Given that the available k_{bact} values are relatively sparse compared to the other parameters, this identified trend seems relatively robust despite large uncertainties which translate into relatively small differences in predicted R_{bio}.

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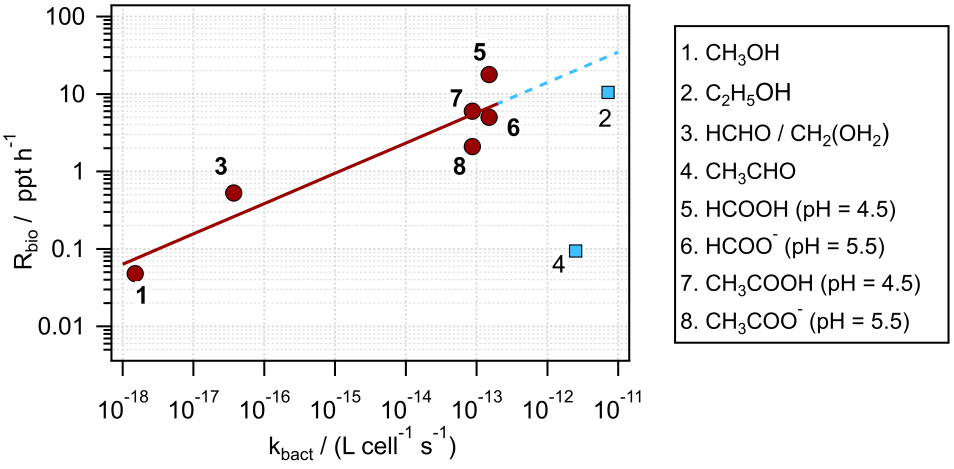

Figure 3. Predicted biodegradation rates R_{bio} as a function of the biodegradation rate constant k_{bact}. The red points are included in the linear regression in log–log space (Eq. 13), whereas the blue points are shown for completeness only. The red line represents the fitted relationship up to a threshold value of k_{bact} = 10^{-13} $\mathrm{Lcell^{-1}s^{-1}}$, above which R_{bio} decreases due to limited replenishment of the organic substrate in the bacteria-containing droplets.

This weak sensitivity can be quantified by comparing the scaling exponents of the different parameters. For example, an uncertainty of two orders of magnitude in k_{bact} results in a change in R_{bio} by only a factor of ~ 6 (= $100^{0.39}$), i.e., sufficient for an order-of-magnitude estimate, whereas the same uncertainty translates into a factor of ~ 60 (= $100^{0.89}$) for $K_{H(eff)}$ and 100 for N_{bact}. In light of this weak dependency, biodegradation rates derived from experiments in various bulk aquatic environments, including cloud water, may result in similar predicted R_{bio} even if the experimental values differ due to differences in bacteria community composition and activity. However, whether biodegradation rate constants representative in dispersed cloud droplets also fall within this range remains to be established.

3.3.2 Biodegradation of dissolved organic matter (DOM)

The compound-specific biodegradation rates discussed in the previous section provide mechanistic insight into microbial substrate utilization in atmospheric aqueous systems. Such compound-specific rates may be used to predict the microbial removal and lifetime of individual organic pollutants. However, atmospheric and environmental microbial communities are typically exposed to complex mixtures of organic compounds. Thus, compound-resolved rates alone do not capture the overall magnitude of microbial carbon processing. In addition, comprehensive compound-specific biodegradation datasets are not available for all relevant species, analogous to the incomplete representation of chemical pathways in atmospheric chemical mechanisms.

To overcome this limitation, the turnover of dissolved organic matter (DOM) is commonly used as a bulk metric of organic carbon processing in aquatic systems. In this context, DOM turnover is often interpreted as a proxy for net microbial carbon processing, although it may also include abiotic transformation pathways. DOM represents the total reservoir of dis-

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solved organic carbon available to microbial communities, and its turnover reflects the combined effect of substrate uptake, transformation including integration into biomass, and respiration to CO_2. This bulk representation is useful because it links microbial activity to total carbon processing without requiring complete knowledge of the underlying molecular composition. This is particularly relevant in atmospheric aqueous systems, where only a subset of organic compounds can explicitly be represented, yet microbial activity acts on the entire dissolved organic carbon pool. DOM-based metrics therefore provide a way to bridge compound-specific processes and bulk carbon budgets across environments with potentially very different organic matter composition.

Biodegradation studies in surface waters often do not resolve individual compounds or microbial taxa, as they are not intended to constrain compound-specific loss rates. Nevertheless, many bacterial taxa occur across aquatic and atmospheric environments (e.g., *Pseudomonas*), suggesting that microbial carbon utilization may be comparable across systems. Therefore, DOM-based biodegradation rates from aquatic environments may be used as constraints on microbial DOM processing in the atmospheric aqueous phase. This approach is supported by the relatively low sensitivity of R_{bio} to k_{bact} (Section 3.3.1), which reduces the impact of uncertainties related to differences in microbial communities and substrate composition.

Catalán et al. (2017) derived biodegradation rate constants for dissolved organic matter in river water and showed that biodegradation rates increase with the fraction of low-molecular-weight substances (LMWS) in total DOM, indicating that substrate composition influences bulk microbial carbon processing. They expressed this relationship as

$$\ln k\,[h^{-1}] = 0.06\,LMWS - 10.36 \tag{14}$$

where LMWS denotes the fraction of low molecular weight species. Assuming LMWS = 1, .e. assuming a large fraction of C_1 and C_2 compounds, yields a rate constant of $3.4 \cdot 10^{-5}$ h^{-1}. Using the reported bacterial concentrations in their study ($\sim 5.9{-}8.6 \cdot 10^6$ cells mL^{-1}), this corresponds to a second-order rate constant of $5 \cdot 10^{-16}$ L $cell^{-1}$ s^{-1}.

Similarly, DOM biodegradation rates reported by Chupakov et al. (2024) can be converted into the same units, yielding values of $6.3 \cdot 10^{-16}$ L $cell^{-1}$ s^{-1} for humic waters and substantially higher values in lake waters of $1.7 \cdot 10^{-13}$ L $cell^{-1}$ s^{-1} (Table S1). This trend is consistent with stronger biodegradation in lake waters, which typically contain a higher fraction of readily metabolized organic matter compared to humic waters, where DOM is more terrestrially derived and less bioavailable.

Most available biodegradation data measured in cloud water are obtained from experiments involving specific bacterial strains and/or individual organic compounds. To the best of our knowledge, the only exception is the study by Vaïtilingom et al. (2013) which was conducted using the natural, unspecified bacterial community present in cloud water samples.

To represent such an overall biodegradation rate in cloud water, we therefore consider representative mixtures of microorganisms and organic substrates as they occur in cloud water. Cloud water composition is often dominated by organic acids, with smaller contributions from aldehydes and alcohols (Herckes et al., 2013). These low-molecular-weight compounds are generally readily metabolized and therefore constitute preferred substrates for microbial activity. Figure 4 shows cloud water composition at three different locations. Based on these compositions, the overall biodegradation rate can be expressed as

$$k_{bact,DOM} = \sum_i x_{org,i}\, k_{bact,i} \tag{15}$$

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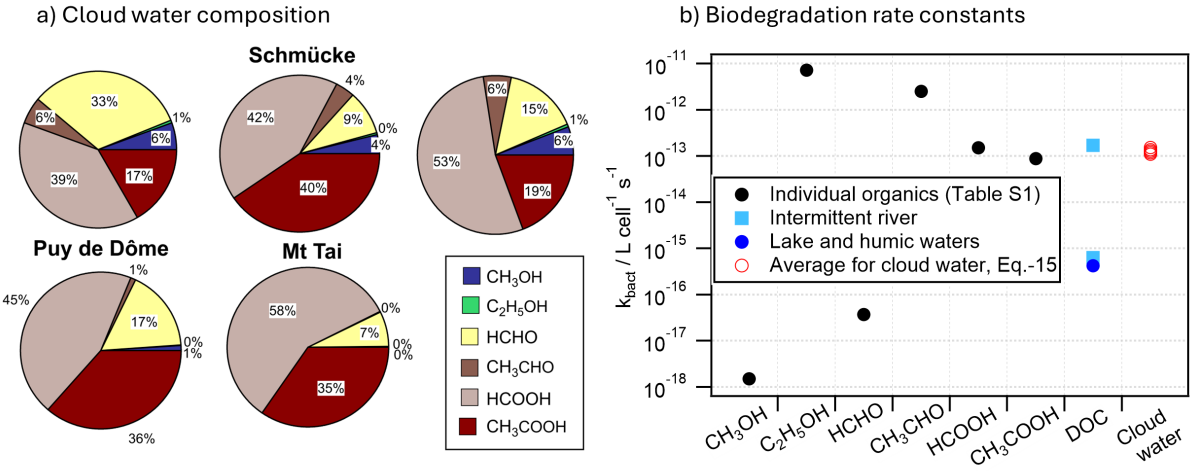

Figure 4. a) Relative proportions of C_1 and C_2 organics in cloud water at three locations: three samples at Schmücke (van Pinxteren et al., 2005), Puy de Dôme (Deguillaume, 2014) and Mt. Tai (Li et al., 2020); b) biodegradation rate constants for the six C_1 and C_2 monofunctional organic compounds (Table 1). Data for intermittent river water (dark blue) were derived based on Catalán et al. (2017), and lake and humic waters (light blue) based on Chupakov et al. (2024); respectively. The averaged k_{bact} values calculated using Eq. 15 for cloud water composition at the three locations in panel a, using Equation 15.

where $x_{org,i}$ denotes the fraction of organic compound i in total dissolved organic matter, and $k_{bact,i}$ is the corresponding compound-specific biodegradation rate constant. For the selected cloud water compositions, $k_{bact,DOM}$ yields values in the range shown by the red circles in Figure 4 (the circles are overlapping). This corresponds to a value of $k_{bact,DOM} \sim 2 \cdot 10^{-13}$ L cell^{-1} s^{-1} which may be considered being representative for cloud water across wide conditions. This estimate is consistent with previous order-of-magnitude estimates by Ervens and Amato (2020).

The derived atmospheric value is also in general agreement with the values derived for river and humic waters, supporting the assumption that bulk microbial carbon processing may occur at a comparable rate (normalized by cell concentration) across aquatic environments, despite differences in substrate composition. At the same time, this value lies near the lower end of the range derived from biologically active lake waters, suggesting that cloud water may represent a relatively substrate-limited environment. Given that $k_{bact,DOM}$ is close to the threshold above which biodegradation becomes transport-limited, this may provide a tentative explanation for observations that microorganisms experience starvation conditions in clouds (Péguilhan et al., 2025). Overall, these considerations indicate that microbial carbon processing in cloud water occurs under conditions close to a limiting regime in which substrate availability and transport constraints control the overall rate reflecting the combined influence of substrate availability, transport limitations and microbial kinetics.

https://doi.org/10.5194/egusphere-2026-5013
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4 Recommendations for implementation of biodegradation in atmospheric multiphase models

Biodegradation is not commonly included in atmospheric multiphase models despite its potential relevance for organic carbon processing for selected compounds and conditions. The analysis in Section 3 shows that biodegradation can be represented at different levels of complexity, ranging from compound-specific rate constants over fits to substrate or bacteria-relevant parameters to bulk DOM-based expressions, each constrained by different types of observational data and intended for different modeling purposes.

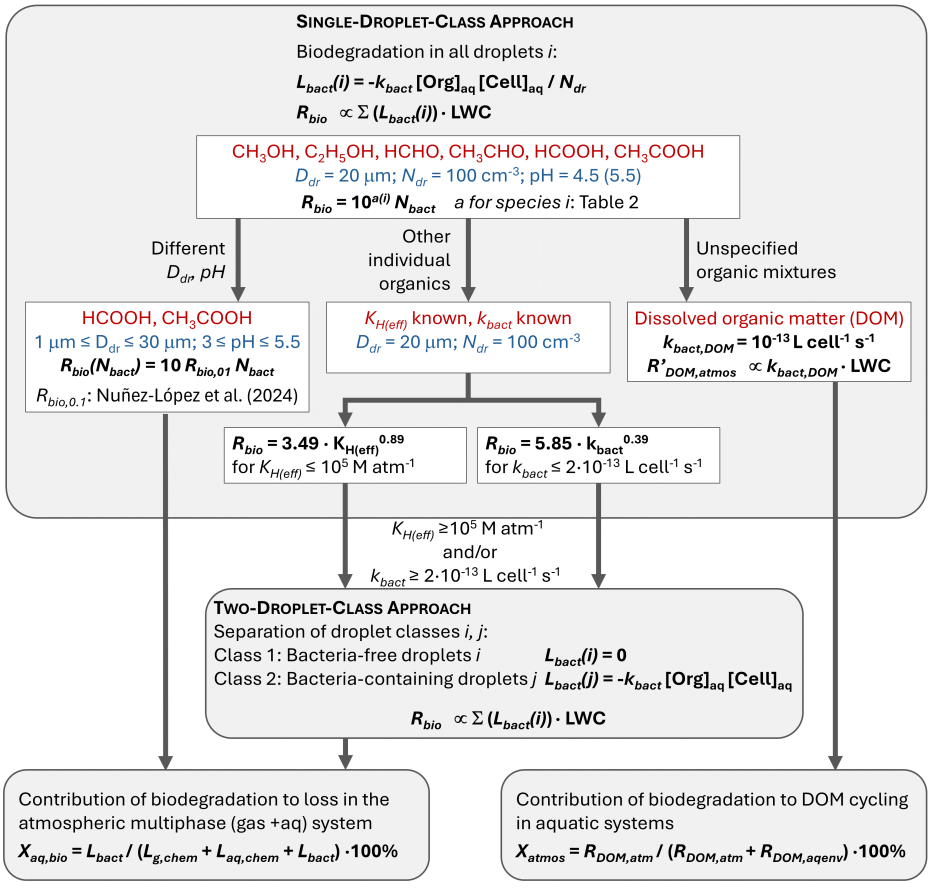

Figure 5. Schematic of the full framework of modeling options with increasing complexity for calculating biodegradation rates in the atmosphere based on the sensitivity studies in the previous sections. The upper part includes empirical parameterizations to predict R_bio as a function of N_{bact}, $K_{H\,(\mathrm{eff})}$, and k_{bact}, which can be applied under the indicated conditions. All parameterizations can be used in bulk approaches, i.e. when all droplets are assumed to have identical properties (size, composition, microbial activity). The two-droplet approach corresponds to the box model used in the present study and previously applied in (Khaled et al., 2021; Nuñez López et al., 2024; Nuñez López, 2025). The lower section illustrates how the relative importance of biodegradation can be assessed in comparison to other atmospheric loss processes.

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To present these approaches into a consistent framework, we synthesize the different representations of biodegradation into a single scheme summarizing the results of the model sensitivity studies. Figure 5 provides an overview and guidance for selecting and implementing appropriate biodegradation parameterizations in atmospheric models.

4.1 Estimating biodegradation rates from empirical relationships of R_{bio} as a function of N_{bact}, $K_{H(eff)}$ and k_{bact}

The relationships derived in the previous sections provide different but complementary ways to estimate biodegradation rates under atmospheric conditions, depending on the available input data. Figure 1 illustrates the dependence of R_{bio} on microbial abundance for a reference set of conditions. Such scaling seems reasonable and valid also for other conditions as they had been applied by (Nuñez López et al., 2024) who performed model sensitivity studies over wide ranges of cloud water pH values (3 - 6) and droplet sizes (1–30 μm) for a constant N_{bact} of 0.1 cm^{-3}. Thus, any of these previous results can be directly scaled for different N_{bact} by

$$R_{bio}(N_{bact}) = R_{bio}(N_{0.1})\frac{N_{bact}}{0.1} \tag{16}$$

where $N_{0.1} = 0.1$ cm^{-3} is the reference concentration. This linear scaling provides a simple means to assess whether biodegradation may represent a relevant sink of individual organic compounds under ambient bacterial concentrations. If compound-specific parameters are available, biodegradation rates can alternatively be estimated from empirical relationships with physicochemical and kinetic properties. Equations 10 and 13 can be rewritten in non-logarithmic form as

$$R_{bio} = 10^{3.49\pm0.71}\, K_{H(eff)}^{0.89}, \quad K_{H(eff)} \leq 10^5 \text{ M atm}^{-1} \tag{17}$$

and

$$R_{bio} = 10^{5.85\pm1.03}\, k_{bact}^{0.39}, \quad k_{bact} \leq 2\times10^{-13} \text{ L cell}^{-1}\text{s}^{-1} \tag{18}$$

These expressions are convenient to estimate R_{bio} for compounds beyond those investigated in the present study, provided that their effective Henry's law constants and/or biodegradation rate constants are known. However, the validity of the Equations 17 and 18 is limited to the parameter ranges up to the thresholds identified above. Beyond these thresholds, the linear scaling relationships break down because microbial consumption can no longer be maintained due to limited substrate replenishment through gas-phase uptake and in-droplet production.

4.2 Explicit representation of bacteria-containing and bacteria-free droplets

For compounds with very large $K_{H(eff)}$ values or high k_{bact}, substrate replenishment within bacteria-containing droplets becomes limiting, and the linear scaling relationships break down. Such compounds include formic acid at pH > 5 due to its high effective Henry's law constant and ethanol and acetaldehyde if the biodegradation rate constants as derived here is applicable to clouds (cf blue points towards the right-hand side of Figure 2 and Figure 3 respectively). Capturing this behavior requires an explicit representation of the distribution of microorganisms across the cloud droplet population. The droplet

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population must be separated into bacteria-containing and bacteria-free droplets to account for the strong local depletion of substrates that occurs within a subset of droplets.

Such behavior cannot be reproduced in model approaches in which all cloud droplets are treated as identical, implying a uniform distribution of microbial activity across the droplet population, e.g., (Pailler et al., 2023). In such models, biodegradation is effectively averaged over all droplets, which corresponds to a 'fractional' microbial activity per droplet (i.e. such 'cell concentration' would correspond to 0.001 cells in each droplet for the base case conditions in our simulations). While this has no direct physical meaning at the level of individual droplets, this simplification may be justified if the chemical concentrations remain homogeneous across the droplet population. However, it becomes invalid once strong differences in aqueous phase concentrations exist between bacteria-containing and bacteria-free droplets.

This limitation also applies to the simplistic estimates of the importance of biodegradation that are based on direct comparisons between $L_{aq,chem}$ and L_{bact}, e.g., (Vaïtilingom et al., 2010; Jaber et al., 2021; Liu et al., 2023). Such comparisons implicitly assume that the substrate concentration available for biodegradation is identical to the bulk cloud-water concentration. As a consequence, they inherently overestimate biodegradation rates whenever substrate depletion occurs within bacteria-containing droplets. As a result, single-class or bulk approaches are unable to reproduce the onset of substrate limitation that emerges at high $K_{H(eff)}$ and k_{bact} values. The empirical relationships derived above therefore not only provide estimates of R_{bio}, but also allow quantifying the magnitude of this bias. For example, single-droplet-class model may overestimate biodegradation rates of acetaldehyde and ethanol by factors of up to $\sim$100 and $\sim$5, respectively, while deviations for formic acid at pH 5.5 can reach approximately one order of magnitude (blue dashed lines in Figures 2 and 3).

The explicit separation of bacteria-containing and bacteria-free droplets is therefore recommended whenever highly soluble compounds or rapidly biodegraded substrates are considered, as these conditions are most likely to lead to substrate limitation within individual droplets. However, its implementation may be challenging in models that represent cloud water as a single bulk phase and do not explicitly resolve cloud droplet classes.

These recommendations are based solely on model simulations that employ biodegradation rates derived from bulk experiments. Whether substrate limitation actually occurs across natural cloud droplet populations remains to be demonstrated. Although *in situ* measurements in ambient clouds remain extremely challenging, controlled cloud chamber experiments may provide a feasible alternative, allowing the chemical composition and microbial activity of individual droplets to be monitored and the model predictions to be tested.

4.3 Importance of atmospheric biodegradation relative to other processes

4.3.1 Comparison of biodegradation to chemical losses in the atmosphere

The absolute biodegradation rates discussed so far do not provide direct information on how important atmospheric biodegradation is relative to other loss processes. To address this, in the following we compare biodegradation rates to (i) chemical rates in the atmosphere, using Equation 5 and (ii) to biodegradation rates in other aquatic environments. The resulting values from our model studies are summarized in Table 3. The results show that biodegradation contributes only marginally to the

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loss of methanol, formaldehyde and acetaldehyde, whereas it may account for several percent of the total loss of ethanol and carboxylic acids, in particular formic and acetic acid. However, it should be cautioned that the rate constant for ethanol has been derived under conditions very different from cloud water (Table S1). Thus, the kinetics may not be comparable. Obviously, $X_{aq,bio}$ is sensitive to the assumed oxidant levels and may increase under conditions of reduced chemical reactivity, such as nighttime or periods of low OH radical concentrations.

Table 3. Importance of biodegradation relative to chemical losses in the atmosphere ($N_{bact} = 0.1$ cm^{-3}).

Compound		X_{bio} **(%)**
CH_3OH		< 0.1
C_2H_5OH		16
HCHO		< 0.1
CH_3CHO		< 0.1
HCOOH	pH = 4.5	20
	pH = 5.5	5
CH_3COOH	pH = 4.5	1
	pH = 5.5	3

4.3.2 Comparison of DOM biodegradation in the atmosphere and other aquatic environments

To compare microbial DOM loss in cloud and surface waters, we calculaterates for selected parameter sets for different aqueous environments:

$$L_{\text{bact}} = k_{\text{bact}} \cdot N_{\text{aq,bact}} \cdot C_{\text{org}} \tag{19}$$

where L_{bact} is in mol L(aq)$^{-1}$ s^{-1}, k_{bact} in L cell^{-1} mol^{-1} s^{-1}, N_{cells} in cells L(aq)$^{-1}$, and C_{org} in mol L(aq)$^{-1}$. The input parameters and resulting rates are summarized in Table 4. The cell concentration of 0.01 cm$^{-3}_{air}$ represents a global mean estimate for the atmosphere (Burrows et al., 2009). Combined with a global mean liquid water content of 0.3 g m^{-3}, this corresponds to a cloud water cell concentration of 3.3×10^7 cells L(aq)$^{-1}$. The resulting L_{bact} values are of comparable magnitude across the three aquatic environments, with the lowest rates in lakes. However, this comparison can be misleading because cloud liquid water represents only a small fraction of the atmospheric volume (< 10^{-4}%). When scaling to bulk environmental volumes, the atmospheric rate per air volume is correspondingly smaller by six orders of magnitude.

To obtain an approximate, order-of-magnitude estimate of the global absolute DOM loss, the per-volume loss rates L_{bact} and L_{air} are multiplied by the total volumes of the respective environments. The total atmospheric volume is approximately 5×10^9 km^3, while global surface freshwater (lakes and rivers) is approximately 1×10^5 km^3 (Shiklomanov and Rodda, 2003). The resulting values R [mol s^{-1}] are listed in the last column of Table 4. This back-of-the-envelope estimate suggests that global atmospheric DOM biodegradation in clouds is on the order of $\sim 1\%$ of that in surface freshwater systems.

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Table 4. Microbial DOM loss rates in different environments expressed on volumetric and absolute bases.

System	N_{cells}	C_{org}	k_{bact}	L_{bact}	L_{air}	R
	L(aq)$^{-1}$	mol L(aq)$^{-1}$	L cell^{-1} mol^{-1} s^{-1}	mol L(aq)$^{-1}$ s^{-1}	mol L(air)$^{-1}$ s^{-1}	(mol s^{-1})
Lake	1.5×10^{5}	2.0×10^{-5}	1.7×10^{-13}	5.1×10^{-13}		
River	7.4×10^{9}	2.40×10^{-5}	4.4×10^{-16}	7.81×10^{-11}		7.8×10^{6}
Cloud	3.3×10^{7}	2.0×10^{-5}	1.0×10^{-13}	6.6×10^{-11}	2.0×10^{-17}	1.5×10^{4}

This estimate is highly uncertain, as it extrapolates sparse data points in all aquatic environments to global scales. While there are considerable uncertainties about biodegradation in cloud water as outlined in the previous sections, also the microbial activity in surface waters is possibly similarly uncertain and heterogeneous due to gradients in nutrient availability and biophysicochemical parameters. Overall, all parameters have substantial spatial and temporal variability, including microbial abundance and activity, organic substrate concentrations and atmospheric (cloud) properties. In addition, it remains uncertain to what extent microbial activity is strictly confined to cloud water, or may also occur in deliquesced aerosol particles that are present at relative humidity < 100%.

5 Atmospheric and ecological implications

Overall, the direct role of biodegradation in the atmosphere may be arguably small for carbon budgets (Table 3). However, its importance may extend beyond a direct contribution to atmospheric carbon budgets, as clouds and fog may represent ecological environments that favor microorganisms capable of exploiting the limited pool of dissolved organic compounds available in atmospheric waters, in particular highly soluble compounds that partition efficiently into the aqueous phase. Since dispersed droplets in the atmosphere likely only host one cell (or at least a very small number), biological competition for substrates between individual cells in atmospheric waters may be absent, and therefore selection processes based on substrate availability can be expected. Dominant atmospheric taxa such as *Pseudomonas* and *Sphingomonas* are such metabolically versatile generalists, and are consistently often reported viable and active metabolically in the atmosphere (Amato, 2017). Atmospheric droplets may also represent ecological niches for more resource-specialized organisms, notably methylotrophs, i.e., microorganisms utilizing in particular C_1 compounds such as methanol and formaldehyde. Among these, *Methylobacterium* spp. usually thrive on plant leaves, e.g., (Vorholt, 2012), and are also often reported among viable members of atmospheric microbial communities. To support metabolic activity, certain photoheterotrophic *Methylobacterium* are capable of using light in addition to dissolved organic compounds, and this has been linked with increased survival in oligotrophic environments and in the atmosphere (Soora and Cypionka, 2013; Mathonat et al., 2026b). Thus, the feasibility of biodegradation and the atmospheric conditions that support it are important not only for atmospheric composition but also because they ultimately shape microbial activity, persistence, and community structure in the atmosphere.

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6 Conclusions

This study provides a quantitative framework for representing microbial biodegradation of small C_1 and C_2 organic compounds in atmospheric multiphase models. Motivated by the growing evidence that cloud water can host metabolically active microorganisms, we explored how biodegradation responds to variations in bacterial abundance, substrate solubility, and intrinsic microbial kinetics. By extending previous studies to a broader set of compounds and wider parameter ranges, the results show under which conditions microbial activity may influence the budgets of highly soluble organic species in clouds.

The biodegradation rate R_{bio} [ppth^{-1}] scales that denotes the total loss of a compound in the atmosphere, linearly with the concentration of active bacteria. This proportionality reflects that, under typical atmospheric conditions, only a small fraction of the available organic substrate is biodegraded. As a result, substrate depletion does not limit atmospheric microbial activity under typical conditions, and uncertainties in N_{bact} directly translate into uncertainties in R_{bio}. Given the large variability and methodological differences in reported atmospheric bacterial abundances, this dependence highlights the need for improved constraints on the microbially active portion of bacteria in cloud water. A key finding is that the sensitivity of R_{bio} to physicochemical properties is weaker with sensitivities of 0.89 and 0.39 for the Henry's law constants $K_{H(eff)}$ and biodegradation rate constant k_{bact}, respectively. R_{bio} increases with the $K_{H(eff)}$ of the dissolved substrate up to an approximate threshold of $K_{H(eff)} \sim 10^5$ M atm^{-1}. Above this value, however, biodegradation becomes limited by the rate at which dissolved material can be replenished from the gas phase or produced chemically within droplets. A similar limitation is predicted for k_{bact}: although higher values increase microbial consumption, the overall sensitivity is modest, and biodegradation decreases once k_{bact} exceeds $\sim 10^{-13}$ L cell^{-1} s^{-1} due to insufficient substrate supply. These results emphasize that biodegradation in clouds is not solely determined by microbial kinetics but also depends on the physicochemical properties of the substrate. Such findings in terms of potential substrate limitation may also help explain recent observations that atmospheric transport may selectively affect microbial biodiversity, favoring specific trophic modes, such as methylotrophy, either in generalized or specialized microorganisms.

Overall, our findings help reconcile previous estimates that reached different conclusions regarding the relative importance of biodegradation in the atmosphere. Much of the apparent discrepancy arose from differences in the approaches and assumptions considered in these earlier studies. For example, comparisons of biodegradation and chemical rates in the aqueous phase revealed that both processes can be of similar magnitude under certain conditionsJaber et al. (2021); Vaïtilingom et al. (2010); Liu et al. (2023), which is consistent with our results. Within the full atmospheric multiphase system, Cao et al. (2025) predicted only a minor contribution of biodegradation to formaldehyde loss despite the comparatively high bacterial concentrations reported in fog water. This finding is fully consistent with our results since the relative contribution of biodegradation (X_{bio}) to total compound removal does not increase proportionally with N_{bact}.

Using a multiphase box model, Pailler et al. (2023) proposed that biodegradation of formaldehyde and formic acid may significantly contribute to their loss in clouds. However, given that their analysis relied on the single-droplet-class approach their estimates for formic acid at pH > 5 were likely overestimated by approximately one order of magnitude because the bulk approach cannot account for the transport limitations. While Nuñez López et al. (2024) showed already that biodegradation

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may contribute up to 20% and 3% of the total loss of formic and acetic acids, respectively, the extension to a wider range of compounds demonstrates that biodegradation is indeed most relevant for these organic acids, and probably negligible for less oxygenated alcohols and aldehydes.

The biodegradation rate constants used here are derived largely from laboratory incubations conducted under conditions more favorable than those in real clouds, including higher nutrient availability and reduced environmental stress. As such, the modeled rates may represent upper-limit estimates of microbial activity. In addition, cloud water is sampled as a bulk aqueous phase, whereas in reality only a small fraction of droplets contain bacterial cells. The resulting differences in substrate-to-cell ratios cannot be directly assessed experimentally and introduce uncertainty by translating data based on bulk measurements to individual droplets. Despite these limitations, the comparison with biodegradation rates from other aquatic environments shows broad consistency, supporting the use of an effective rate constant of $k_{bact,DOM} \sim 10^{-13}$ L cell^{-1} s^{-1} for dissolved organic matter in the atmosphere.

Overall, the relationships derived in this work provide a practical and physically grounded framework for implementing biodegradation in atmospheric multiphase models. They enable the identification of environmental conditions under which microbial activity may influence the cycling of small organic compounds in clouds and help clarify when biodegradation can be neglected in affecting the atmospheric chemical composition. More broadly, the results contribute to ongoing efforts to understand the ecological functioning of airborne microorganisms and their potential role in atmospheric carbon processing. Future work combining targeted laboratory studies, field observations and model development will be essential to further constrain microbial activity in clouds and to assess its implications for atmospheric chemistry across spatial and temporal scales. Such efforts will also help reveal how atmospheric conditions influence generalist and specialized microbial strategies, and thereby shaping the composition, selection and functioning of airborne microbial communities.

Data availability. The data can be found in (Ervens, 2026)

Author contributions. LNL conducted the investigation, performed the analyses and wrote the thesis chapter on which this manuscript is based. BE conceived and developed the research idea together with LNL. BE supervised the work and contributed to the conceptualization, interpretation of results and manuscript development. PA contributed to the interpretation of the findings and provided critical comments and revisions throughout the preparation of the manuscript. All authors reviewed, edited and approved the final version of the manuscript.

Competing interests. One of the authors is a member of the editorial board of *Biogeosciences*.

https://doi.org/10.5194/egusphere-2026-5013
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