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LETTER **OPEN ACCESS**

Microbial Evolution Drives Adaptation of Substrate Degradation on Decadal to Centennial Time Scales Relevant to Global Change

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ABSTRACT

Understanding microbial adaptation is crucial for predicting how soil carbon dynamics and global biogeochemical cycles will respond to climate change. This study employs the DEMENT model of microbial decomposition, along with empirical mutation and dispersal rates, to explore the roles of mutation and dispersal in the adaptation of soil microbial populations to shifts in litter chemistry, changes that are anticipated with climate-driven vegetation dynamics. Following a change in litter chemistry, mutation generally allows for a higher rate of litter decomposition than dispersal, especially when dispersal predominantly introduces genotypes already present in the population. These findings challenge the common idea that mutation rates are too low to affect ecosystem processes on ecological timescales. These results demonstrate that evolutionary processes, such as mutation, can help maintain ecosystem functioning as the climate changes.

1 | Introduction

As primary drivers of Earth's biogeochemical cycles through organic matter decomposition and respiration, soil microbial communities determine how decomposition will affect future soil carbon stock changes, and carbon feedback on global warming through CO₂ released by soils (Falkowski, Fenchel, and Delong 2008). As the climate changes, evolution and dispersal are the only processes that can introduce new traits into microbiomes, and if these traits survive selection and stochasticity, they enable adaptation to new climatic conditions (Stegen et al. 2012). Mutations allow the appearance of new traits that enable a functional group for instance to decompose a given

substrate more efficiently. Dispersal can likewise spread functional traits that would change a community's ability to access and decompose carbon substrates at a given location. Whereas dispersal has already proven to be important for microbiome adaptation to global change (Barbour et al. 2023; Evans et al. 2020; Wang and Allison 2021), uncertainty surrounds the significance of mutations for biogeochemistry on 'global change' timescales of decades to centuries (Martiny et al. 2023). It remains unclear whether mutations can modify trait values at a pace that changes organic matter decomposition rates on these time scales. A key question is thus how does the rate of change of functional traits due to mutation compare to the spread of traits through dispersal?

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Theoretical studies suggest that mutations can dictate the response to environmental change if the mutation rate is high and/or if the environmental change leads to novel conditions (which can involve either new niche space or new ranges of environmental conditions). On the other hand, dispersal is the main driver of changes in community-level functioning if the dispersal rate is faster than mutation (Loeuille and Leibold 2008). Therefore, the question of whether mutations play a significant role in the microbial response to global change hinges largely on the difference between mutation and dispersal rates. Barbour et al. (2023) empirically measured dispersal in surface soil microbiomes to be 1000 dispersers per cm² per day. This rate means that dispersal could alter community composition and functioning at a typical ecosystem scale of 100 m within a few months. Considering that the mutation rate in bacteria is around 10⁻⁹ mutations per nucleotide site per generation and that there are about 10⁹ bacteria in a gram of soil (Yang et al. 2023), there are approximately twice as many mutations per cm² per day as dispersers. Thus, in microbiomes, mutations could impact composition and functional potential just as much as dispersal. However, given that mutation introduces new traits through evolutionary descent from a parent lineage whereas dispersal can potentially spread traits present in any extant microbe, it remains to be tested whether mutations and dispersal result in functional responses to environmental change of comparable magnitude or not.

Shifts in litter chemistry are expected to be a key component of climate change because litter composition integrates many factors, including climate- and CO₂-driven plant shifts of above and below-ground productivity affecting soil carbon inputs, as well as changes in nutrient availability at the ecosystem level. In particular, many ecosystems display shifts in vegetation composition driven by climate change, such as transitions from grassland to shrubland (Petrie et al. 2015) or from tundra to boreal forest (Elmhagen et al. 2015), resulting in altered litter chemistry. Moreover, litter chemistry is a very strong selection factor for microbiomes, often exerting more control over microbial decay than the direct effect of climate change (Malik et al. 2020). For example, higher net primary productivity leads to soil carbon loss through accelerated decomposition (priming) when litter quality is low, but to soil carbon gain when litter quality is high (Sulman et al. 2014).

We focused on a grassland-to-shrubland transition, modelled as a drop in cellulose content, and we hypothesized that mutation would facilitate greater adaptation to the new litter chemistry compared to dispersal. We used a continuum for dispersal, ranging from short to long range, wherein 100% short-range corresponded to reintroducing taxa previously present in the community. Short-range dispersal closely approximates a scenario of environmental filtering only, with the exception of the microbes' repositioning within the grid. As for mutation, we use the term as a shorthand for the evolutionary acquisition of new traits, which could result from either *de novo* mutation or horizontal gene transfer. In both the mutation and dispersal treatments, selection and stochasticity influenced changes in the community composition. Thus, we included the four processes most influential in community responses to environmental change (Stegen et al. 2012), and we compared the impact of the two processes that generate new trait diversity: mutation and dispersal.

To test our hypothesis, we used a numerical model of microbial decomposition of litter, known as DEMENT (Decomposition Model of Enzymatic Traits; Figure 1) (Allison 2012). This model represents trait diversity and substrate chemistry to simulate species sorting through selection and stochasticity. We incorporated dispersal and mutations, subjected populations to an idealised stepwise shift in litter chemistry, and examined whether populations responding with mutations caused greater litter mass loss compared to those experiencing dispersal (Figure 2).

Dispersal and mutation can increase trait diversity at both the community level (by introducing new species) and the population level (by introducing new alleles or populations). To our knowledge, the question of whether mutations can alter the response of any ecosystem process to changes in litter chemistry has not been addressed at any biological level. Therefore, we began with the simpler population level before expanding to the community level. To this end, we isolated the evolutionary question by modelling a single population containing multiple genotypes.

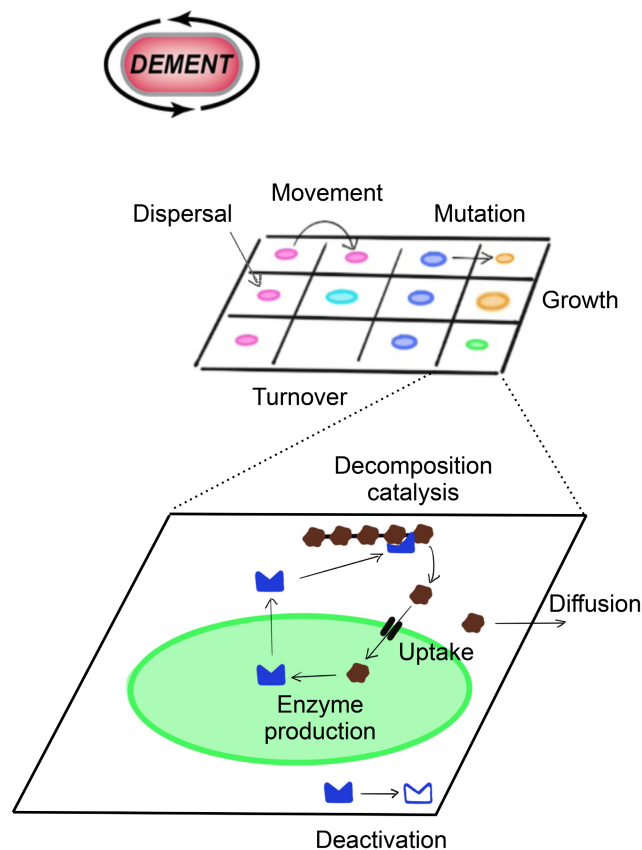


FIGURE 1 | Schematic overview of the DEMENTmut model. (Top) 2D grid domain on which individual microbes can grow, die, move from one grid point to another, disperse in and out of a grid, and mutate. (Bottom) Intra-cellular metabolism simulated for one type of microbe: Microbes take up nutrients and carbon that they use to produce enzymes (blue double-peak symbols) that are released out of the cell to decompose complex polymers (connected brown nuggets) into monomers (individual brown nuggets). The remaining monomers diffuse evenly across the grid.

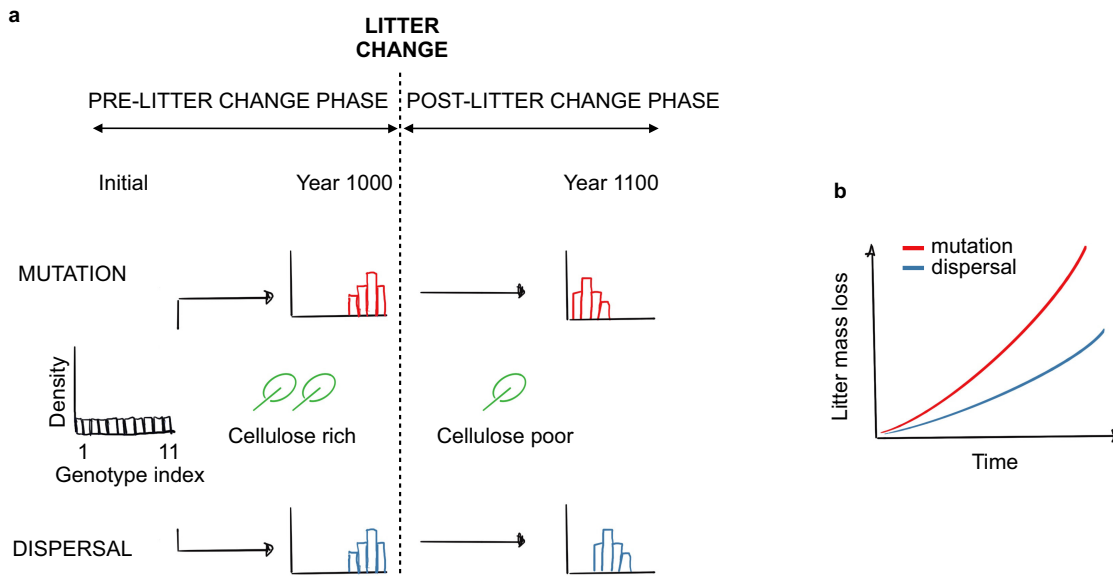


FIGURE 2 | Conceptual framework of the simulation experiment. (a) In the first 1000 years, the population is fed with cellulose-rich litter that should select for high cellulase producers and for the last 100 years with cellulose-poor litter that should select for low cellulase producers. Populations are initialized with 11 genotypes from index 1 to 11, in equal abundance. We let both litters select genotypes arising with either mutation or dispersal. (b) The experimental setup is used to test the hypothesis that mutation leads to greater adaptation than dispersal, as quantified by a faster litter mass rate loss during days 1 to 100 of year 1100.

2 | Material and Methods

2.1 | Model Description

DEMENT is a spatially explicit, individual- and trait-based microbial model that simulates leaf litter decomposition emerging from both microbial cell-level physiology and community-level interactions (Allison 2012; Figure 1). The model includes different genotypes and is typically run with 5–100 genotypes. We used a new version of the model in Python, called DEMENTmut, that allows for mutation processes (see Data Availability Statement).

Each day during the simulation, microbes produce new enzymes, substrate compounds are decomposed into monomers, and these monomers diffuse on the grid. Each genotype produces 12 different enzymes, one per substrate. Each substrate compound is decomposed into one type of monomer. The mass of monomers taken up by microbes drives microbial growth. Reproduction occurs when the biomass of a single genotype in a grid cell reaches a threshold. Initially, the biomass of a taxon is 1 mg cm^{-3} , and it grows solely through monomer uptake. Once the biomass reaches 2 mg cm^{-3} , it divides into two individuals. All the genotypes die at the same constant death rate. In this study, microbial movement between grid cells is decoupled from reproduction, as daughter microbes remain within the same location where division occurred. Microbes move across the grid at a rate averaged from Wang and Allison (2021) to one of the eight adjacent grid boxes, so that a microbe will take a minimum of 500 days to cross the grid. Mortality and movement of microbes are both partially stochastic processes in the model code.

We held temperature and water potential constant for this study at 15.7°C and -0.01 MPa respectively (Earth averages), to focus on the sole effect of litter chemistry change. Enzyme kinetics depended on temperature as per the Arrhenius equation. New litter is added on the first day of each year because we are interested in the decay of one leaf by one microbiome every year. DEMENT simulated 100 years of decomposition by a diverse population on a grid of 1 mm^2 in $\sim 4 \text{ h}$.

2.2 | Initialization

We initialized the simulation on a spatial grid domain of 96×96 boxes ($10 \mu\text{m}$ on a side) representing the surface of a litter substrate. The 12 compounds that comprise leaf litter, such as cellulose and lignin, were initially homogeneously distributed on the grid. To track the effects of mutation versus dispersal on litter decay, the genotypes are defined by only two traits: cellulase production rate and cellulose-monomer uptake rate. These traits are linked by a positive relationship, whereby higher cellulase producers take up cellulose monomers more rapidly. Without this relationship, resource sharing would counter-select cellulase producers due to cheating. The slope of this relationship is determined by what we call the “uptake scalar.” Only cellulase production can mutate within a specified range, and the cellulose-monomer uptake rate adjusts according to the uptake scalar. In our control run, cellulase production rates ranged between 1.5×10^{-5} and $1.5 \times 10^{-4} \text{ mg C mg}^{-1} \text{ day}^{-1}$ (Wang and Allison 2021), distributed across 11 equal intervals corresponding to 11 genotypes. All the genotypes are bacterial with an initial biomass of 1 mg cm^{-3} . Thus, at the start of the control simulation, there were 11 genotypes and 11 mg cm^{-3} of leaf substrate per grid box.

2.3 | Litter Chemistry Shift

To simulate selection driven by a shift in litter chemistry, we ran the model to obtain genotypes adapted first to a cellulose-rich litter for 1000 years. We chose 1000 years because the modelled community takes 40–500 years to reach equilibrium and is robust to small perturbations of parameters. Then we changed the input to a cellulose-poor litter for another 100 years (Figure 2) to simulate the response of microbes during a long period consistent with a change in litter chemistry on the time scale of global change. The quality shift mimics the shift from a grassland to a shrubland as observed in the Southwest of the United States (Petrie et al. 2015). We used the litter composition from Allison (2012) for cellulose-poor litter.

2.4 | Mutation, Short- Vs. Long-Range Dispersal

The only trait assumed to adapt to litter change is cellulase production as observed empirically in response to change in cellulose availability (Acharya and Chaudhary 2012; Bhati and Sharma 2021; Gupta et al. 2020). We performed two simulations, termed mutation and dispersal treatments, where the adaptive process over the entire 1100 years of simulation is driven by either mutation or dispersal alone. In the mutation treatment, every time there is a division, the offspring either carries a different trait value than the parent (with a probability p_{mut}) or keeps the same trait (with probability $1-p_{mut}$). When different, the new trait value is set to one level of cellulase production above or one below with the same probability. In the dispersal treatment, a microbial individual outside of the grid (a disperser) enters the grid with the same probability p_{disp} anywhere in the grid and takes on the mass of the individual it replaces for mass conservation. If dispersal is 100% 'short-range', the disperser's trait value is sampled from the current population trait distribution within the grid. If the dispersal is 'long-range', the disperser's trait value can be anywhere in the whole range. In other words, if the dispersal is 100% long-range, mutation and dispersal will explore the same trait space, but they differ in magnitude: mutation can only reach adjacent trait values, whereas dispersal can introduce trait values from anywhere in the trait space. For p_{mut} , we took the empirical value of

0.02 mutations per division (Yang et al. 2023), which corresponds to 42 mutations on the grid per day out of 101,376 ($11 \times 96 \times 96$) individuals initially. For p_{disp} , we used the same value as p_{mut} . We also compared an empirical value of 1000 dispersers $\text{cm}^{-2}\text{day}^{-1}$, which corresponds to ~ 18 dispersers on the grid per day given that our grid contains 96×96 grid boxes of 10^{-9}cm^3 each and two surfaces (above and below; $96 \times 96 \times 10^{-6} \times 2 = 0.018\text{cm}^2$ of surface receiving dispersers) (Barbour et al. 2023).

2.5 | Quantification of Adaptation

To test the hypothesis that mutation results in faster mass loss than dispersal, we checked if litter mass loss at the end of the simulation after the litter chemistry change (over the days 1 to 100 of year 1100) was greater with mutation than dispersal (Figure 2b).

3 | Results

3.1 | Mutation Leads to Faster Litter Decomposition Than Short-Range Dispersal

We found that the litter mass loss was 12.7% higher in populations with mutations on the last day of the litter chemistry change simulation (Figure 3b), consistent with our hypothesis. This pattern stabilised at year 1040, while the population stabilised at year 1005 in the dispersal treatment, and at year 1040 in the mutation treatment (Figure S1). Full adaptation occurs also when mutations are allowed either only pre-litter change or only post-litter change (Figure S2).

3.2 | With Mutation, Extinct Genotypes Reappear, but Not With Dispersal

To determine why there is faster litter mass loss after 100 years of altered litter chemistry with mutation compared to short-range dispersal, we examined the population composition over time before and after litter change (Figure 4). Before litter change, cellulose-rich litter selected for intermediate cellulase production

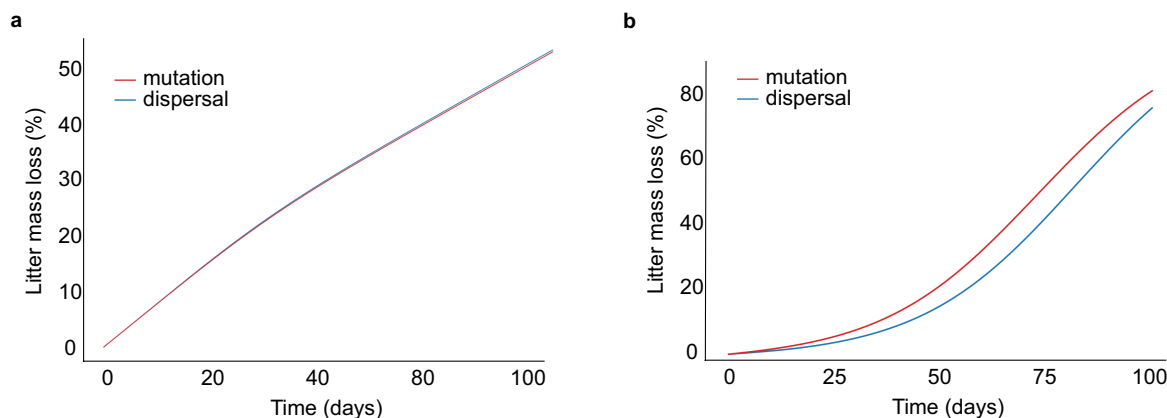


FIGURE 3 | Litter mass loss from day 1 to 100 of (a) year 1000 (end of the period prior to litter change), (b) year 1100 (end of the period post-litter change) for populations with mutation (red) and dispersal (blue). Pre-litter change, the litter mass loss curves for dispersal and mutation overlap. Dispersal is 100% short-range and the dispersal and mutation rates are equal (42 dispersers or mutants per grid per day). The number of genotypes is 11 and the uptake scalar is equal to 0.05.

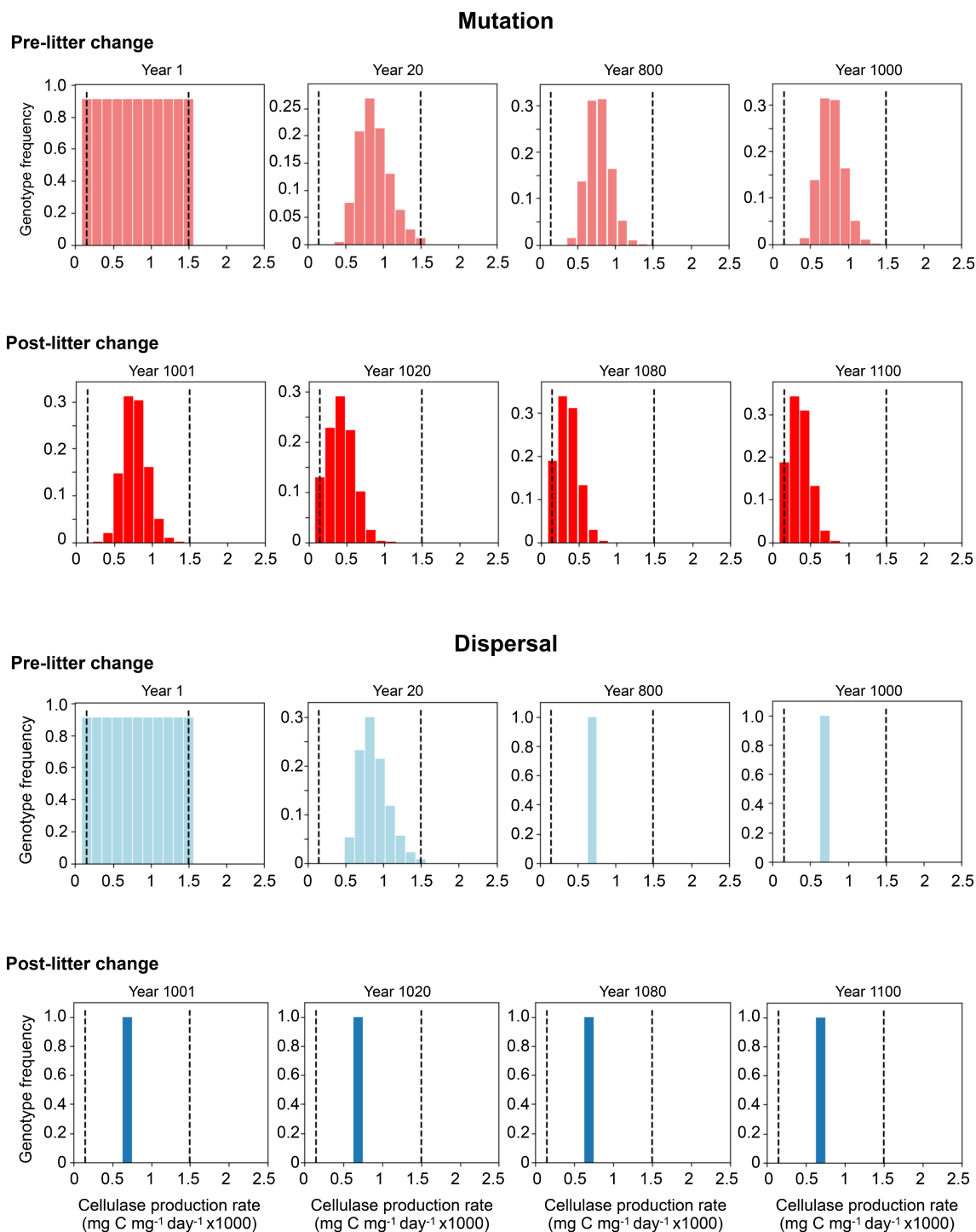


FIGURE 4 | Distribution of genotypes per cellulase production rate with the mutation (2 first rows in red) and dispersal (2 last rows in blue) treatments for years 1, 20, 800 and 1000 (pre-litter change in light colour), and for years 1001, 1020, 1080 and 1100 (post-litter change in dark colour). Same parameter values as in Figure 3.

rates ($6.9 \times 10^{-5} \text{ mg C mg}^{-1} \text{ day}^{-1}$ on average, compared to the initial range of 1.5×10^{-5} and $1.5 \times 10^{-4} \text{ mg C mg}^{-1} \text{ day}^{-1}$) in both the mutation and dispersal treatments. Interestingly, the two treatments resulted in distinct equilibrium population compositions: most genotypes remained present even if in low abundance in the mutation treatment, whereas only one genotype persisted in the dispersal treatment. This disparity did not impact population-averaged cellulase production and litter decay

(Figure 3a), but it explains why full adaptation occurs when the post-litter change dispersal treatment is preceded by the pre-litter change mutation treatment (Figure S2). After the litter chemistry change, the population composition stabilised after 40 years but differed significantly between the mutation and dispersal treatments. In the mutation treatment, all the genotypes were still present, yet with the strongest selection for genotypes 2 and 3, which are lower cellulase producers. Conversely, only

the highest cellulose producer, genotype 5, was present in the dispersal treatment. This difference arose because short-range dispersal introduced only the genotypes that were present in the population, and consequently did not allow the reappearance of the extinct low cellulase-producing genotypes that were counter-selected in cellulose-rich litter.

3.3 | Robustness of the Results

To determine the robustness of our findings regarding greater mass loss with mutation, we conducted simulations across three values for the initial number of genotypes (5, 11, 17) and three values of the scalar that dictates the slope of the relationship between the cellulase production rate and the cellulose-monomer uptake rate: 0.04, 0.05, and 0.06 day⁻¹. The higher mass loss with mutation is a robust result, with mass loss being 2%–13% greater for mutation than dispersal across all sensitivity experiments. The difference in litter mass loss between the mutation and dispersal treatments increased both with increasing number of genotypes and uptake scalar (Figure 5). The strongest sensitivity of the litter mass loss amplification with mutation vs. dispersal was to the number of genotypes. Decreasing the number of initial genotypes to 5 reduced the adaptation difference between mutation and dispersal because the highest cellulase producer in the 5-genotypes population was then genotype 4, which was less adapted to cellulose-rich litter, but better adapted to cellulose-poor litter than genotype 5 selected in the 11-genotypes population. The mutation treatment illustrates how selection is suboptimal in the 5-genotypes population because the genotype distribution is cut off, meaning that if taxa with higher index values were present in the initial community, they would be selected (Figures S3 and S4). The difference between the mutation and dispersal treatments also increases with increasing uptake scalar because a stronger cellulase producer is selected before litter change when the uptake scalar increases (genotype 5 instead of genotype 4). Stronger cellulase producers are selected when the uptake scalar is high (Figure S4), because increasing

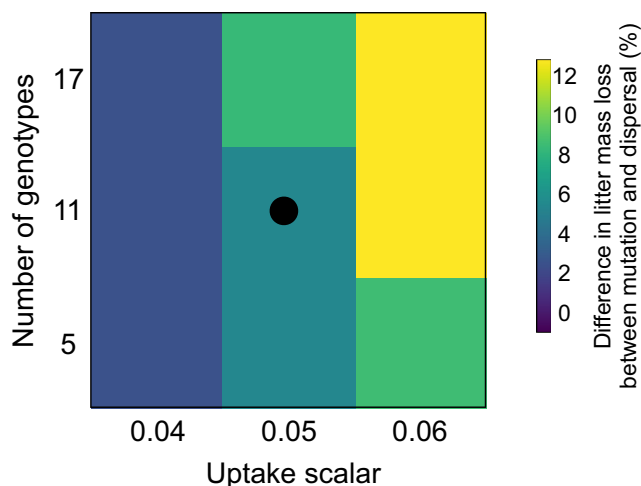


FIGURE 5 | Sensitivity analysis to the uptake scalar (x axis) and the number of genotypes (y axis). The colour represents the difference in litter mass loss between mutation and dispersal. Other parameters have the same values as in Figure 3. The dot corresponds to the control run.

the uptake scalar increases the benefit: cost ratio of producing cellulase.

3.4 | Long-Range Dispersal and Empirical Rate

We assessed the impact of short- vs. long-range dispersal, with scenarios ranging from 100% short-range—where all dispersers originated from the current population composition—to 100% long-range, where dispersers represented the full spectrum of cellulase producers (Figure 6, top row). The significant differences in litter mass loss between the mutation and dispersal treatments vanished when dispersal was entirely long-range because 100% long-range dispersal can restore any genotype that became extinct before an environmental change. The functional distinctions between the mutation and dispersal treatments re-emerged when no more than 0.001% of the dispersal was long-range. These results remained largely unchanged when we reduced the dispersal rate to 18 cells per grid per day (Figure 6, bottom row). Dividing the dispersal rate by two does not make a difference over a 100-year timescale.

4 | Discussion

To test the relative importance of mutation versus dispersal in controlling microbial adaptation to litter chemistry change, we ran simulations with a spatially explicit model that resolves microbial functional diversity in an idealised manner by assuming that the only functional difference between genotypes is from cellulase production and cellulose-monomer uptake rates. We found, as hypothesized, that adaptation through mutation can be more effective in the long term for adjusting to new conditions, outperforming short-range dispersal between 2% and 12.7% in terms of new litter decay, when long-range dispersal was smaller than 0.001%. Our findings reveal the potential significance of mutations in the functional response of microbiomes to global change. This result is consistent with an empirical study by Chase, Weihe, and Martiny (2021) that quantified the amount and rate of selected mutations in field soil microbial communities. They observed mutations converging based on climate within relatively short timescales (18 months) and associated with traits such as cellulose degradation, xylan degradation, and biofilm formation.

We found that the difference in adaptive capacity between mutation and dispersal vanished when long-range dispersal exceeded 0.001%. A long-range dispersal of 0.001% means that a disperser introduces a new trait value to the local community every 24 days per mm². Although data are sparse, such low rates of long-range dispersal may be relevant in the field. Walters et al. (2022) tested various vectors of dispersal—including wind, vegetation, and soil—and found that most dispersal originated from local vegetation. Even a few meters away from other vegetation types, dispersers were still predominantly coming from their own vegetation type. Additionally, in this study, dispersers were collected on glass, which does not test their capacity to establish in the local microbial community. Establishment might be easier in the model than in nature, where factors such as priority effects, seasonality, predation, and genotype/species drift complicate the process (Barbour and Martiny 2024). In

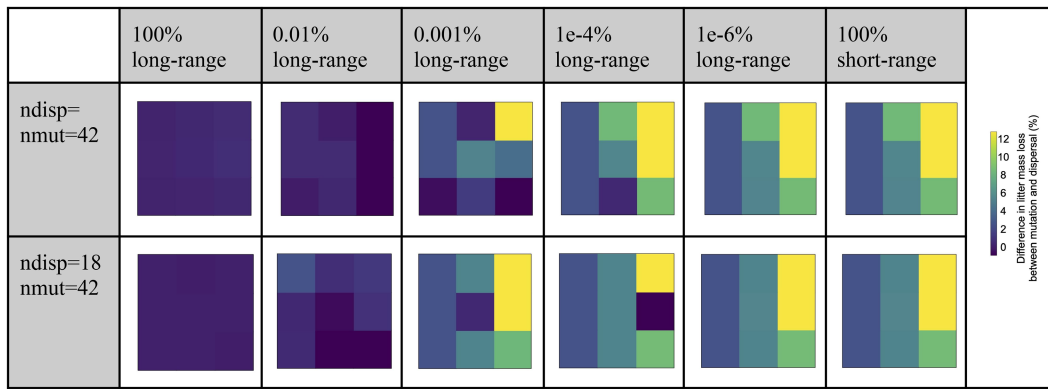


FIGURE 6 | Difference in litter mass loss between the mutation and dispersal treatments for different levels of long-range dispersal (columns). Top row: Equal probability of mutation and dispersal; Bottom row: Empirical rate of dispersal. In each density plot, the three rows correspond to the same three values for the number of genotypes (5, 11, 17), and the three columns correspond to the same three values of the uptake scalar (0.04, 0.05, 0.06) as shown in Figure 5.

summary, long-range dispersal and establishment might be rare compared to short-range dispersal and mutations.

Additional studies could examine the interactions between different adaptive mechanisms. Previous work, both theoretical and empirical, has presented conflicting views on whether standing diversity impedes (Brockhurst et al. 2007; Johansson 2008; de Mazancourt, Johnson, and Barraclough 2008) or facilitates (Blazanin and Turner 2021) evolution by mutation. No study has yet examined the effect of the interaction between dispersal and mutation. Conducting such research using a model would be much easier than doing so empirically. We could use the model from this study, activate both mutations and dispersers, and compare the adaptive trajectory to the one we have presented. Empirically, one could combine the experimental designs of Chase, Weihe, and Martiny (2021) and Walters et al. (2022) with whole communities and isolated strains, using mechanical barriers to manipulate dispersal.

Our study involved the evolution of two correlated traits. To begin scaling up to the ecosystem level, the next step would be to predict the effects of mutation at the community level by investigating the co-evolution of multiple independent traits. For instance, the adaptation of osmolyte production could be studied in conjunction with cellulase production in response to changes in both moisture conditions and litter chemistry. Additionally, once we gain a thorough understanding of the adaptive mechanisms at the population level, we could expand our focus to the community level by integrating multiple co-evolving functional groups. These groups would differ in the values of all microbial traits, allowing us to observe the consequences of trait adaptation at both the population and community levels. Validation could be achieved using metatranscriptomics and metabolomics data, which capture functions at the community level (Malik et al. 2020).

In conclusion, the importance of distinguishing between different adaptive mechanisms and their functional outcomes cannot be overstated from a biogeochemical perspective. While analytical models benefit from simplicity to ensure solvability, our study challenges the notion that predictions of adaptation can be mechanism-agnostic (Abs et al. 2022; Gibert et al. 2022, 2023;

Han et al. 2023). Our findings particularly caution against this assumption in the context of short-range dispersal, where we observed that mutation led to significantly different functional responses, even 100 years after an environmental change. Thus, our study underscores the need to carefully consider the properties of a system, in particular the source of dispersal, having in mind that those properties might change with seasons or disturbances (Barbour et al. 2023), before equating the impact of different adaptation mechanisms.

Author Contributions

Elsa Abs: conceptualization (lead), investigation (lead), supervision (lead), validation (equal), writing – original draft (lead), writing – review & editing (lead). **David Coulette:** model development (lead), investigation (equal), validation (equal), writing – review and editing (equal). **Philippe Ciais:** writing – review and editing (equal). **Steven D. Allison:** validation (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The DEMENTpy model is coded with Python, and the statistical analyses and plots were generated with Python, and are available here: [10.5281/zenodo.11210624](https://doi.org/10.5281/zenodo.11210624).

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14530>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.