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The Impact of Microbial Interactions on Ecosystem Function Intensifies Under Stress

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ABSTRACT

A major challenge in ecology is to understand how different species interact to determine ecosystem function, particularly in communities with large numbers of co-occurring species. We use a trait-based model of microbial litter decomposition to quantify how different taxa impact ecosystem function. Furthermore, we build a novel framework that highlights the interplay between taxon traits and environmental conditions, focusing on their combined influence on community interactions and ecosystem function. Our results suggest that the ecosystem impact of a taxon is driven by its resource acquisition traits and the community functional capacity, but that physiological stress amplifies the impact of both positive and negative interactions. Furthermore, net positive impacts on ecosystem function can arise even as microbes have negative pairwise interactions with other taxa. As communities shift in response to global climate change, our findings reveal the potential to predict the biogeochemical functioning of communities from taxon traits and interactions.

1 | Introduction

All ecosystems contain multiple organisms that contribute to emergent functioning. Consequently, a grand challenge in ecology is to predict how changes in community composition impact ecosystem function and how community structure–function relationships emerge from organism traits and responses to environmental change (Lavorel and Garnier 2002; Suding et al. 2008; Lennon et al. 2012; Waring et al. 2022). These questions of 'scaling' are particularly salient in both plant (Symstad et al. 1998; Kahmen et al. 2005) and microbial (Waldrop, Balser, and Firestone 2000; Wagg et al. 2014) communities, which are rich in genetic diversity and perform an array of ecosystem functions.

In communities with many co-occurring taxa, interactions between taxa with different traits influence community dynamics and ecosystem function. For example, organisms that compete for resources can have negative impacts on the growth of their neighbours (Foster and Bell 2012; Trinder, Brooker, and Robinson 2013; Allison et al. 2014). Conversely, organisms can facilitate the growth of neighbours directly, through exchange of resources or production of public goods (Schöb, Armas, and Pugnaire 2013; Bernabé et al. 2018; Wu et al. 2023), as well as indirectly, by suppressing a neighbour's competitor (Levine 1999). Such resource-based interactions have traditionally been evaluated across pairs of taxa (Thompson 1999; Gilman et al. 2010). However, pairwise interactions are difficult to measure in complex communities with many interacting taxa (Ponomarova and Patil 2015; Sanchez-Gorostiaga et al. 2019).

The magnitude and relevance of interactions may also vary with community composition. Communities may differ in average trait values that affect the ecological context in which different organisms interact (Wright et al. 2004). These community-average traits define the functional potential of a community and reflect the responses of co-occurring taxa to local environmental conditions (Muscarella and Uriarte 2016). As such, community-average traits represent a quantitative metric of the ecological context associated with a given community composition. Quantifying this 'community context' could aid in predicting the context dependency of how interactions impact ecosystem function, which has been a vexing problem in ecology (Chamberlain, Bronstein, and Rudgers 2014).

Microbial communities are relevant model systems for analysing the relationships between organism traits, community interactions and ecosystem function. In microbial communities, resource-based interactions can occur over the use of metabolically costly extracellular public goods (Özkaya et al. 2017; Smith and Schuster 2019). For example, microorganisms produce extracellular enzymes (hereafter referred to as 'exo-enzymes') to break down large organic polymers into smaller components that can be transported into the cell (Sinsabaugh, Antibus, and Linkins 1991; Allison and Vitousek 2004; Burns et al. 2013). In litter and soil, greater exo-enzyme production can increase rates of substrate degradation (Skujiņš and Burns 1976; Geisseler and Horwath 2009), which makes resources accessible to the community. However, the production of exo-enzymes varies across microbial taxa (Romaní et al. 2006; Ramin and Allison 2019), and cheating dynamics can also arise, such that function collapses when organisms use exo-enzyme products without paying the cost of production (Allison 2005; Allison et al. 2014; Abs, Leman, and Ferrière 2020).

Furthermore, environmental stress could affect the strength and ecosystem implications of microbial interactions. With global climate change, more frequent extreme events such as droughts and heat waves could increase physiological stress on microbes, thereby altering resource allocation and ecosystem function (Manzoni, Schimel, and Porporato 2012; Malik et al. 2020; Allison 2023). Still the consequences of climate change for resource-based interactions remain unclear, making it challenging to predict rates of organic matter decomposition and other processes.

To test how climate extremes might impact microbial interactions across varying community contexts, we used a microbiome simulator known as DEMENT (Decomposition Model of Enzymatic Traits; Allison 2012). The simulator represents diverse microbiomes with interactions involving exo-enzymes and their products. DEMENT's trait parameters are empirically derived, and its predictions of litter decomposition rates and enzyme distributions have been validated with empirical data (Allison 2012). Previously, DEMENT has served as a platform for in silico microbiome experiments, such as reciprocal transplants and climate manipulations (Allison and Goulden 2017; Wang and Allison 2022).

Using litter decomposition as an example ecosystem function, and drought as a climate extreme, we address three main questions: (1) What are the community- and ecosystem-scale impacts of taxa within different community contexts? (2) What is the relationship between taxon traits (e.g., exo-enzyme production, resource use and stress tolerance) and taxon impact? (3) Are there generalizable patterns in how interactions vary with drought stress and determine ecosystem function? Although we analyse microbial communities that decompose litter, these questions are relevant for any system in which ecosystem function emerges from a diversity of resource-based interactions within a community.

To address our research questions, we ran microbial exclusion experiments with the DEMENT simulator under ambient, moist and drought climate scenarios. We quantified interactions in these simulations using the 'taxon impact', or the change in a community- or ecosystem-scale metric when a specific taxon is excluded. Taxon impact is an integrative metric of how a focal taxon impacts an entire community (Amit and Bashan 2023; Sanchez et al. 2023). This approach allowed us to resolve the net impact of interactions at a scale and level of replication that would be difficult to achieve empirically.

2 | Methods and Materials

2.1 | Simulator Description

DEMENT is an individual- and trait-based simulator of organic matter decomposition that represents microbial interactions involving exo-enzymes and their products (Figure 1). The simulator is designed to represent the substantial complexity of environmental microbiomes while incorporating deterministic understanding of microbial exo-enzyme production, monomer uptake, and metabolism (Allison 2012). Previously, DEMENT has been applied to simulate microbial community responses to climate warming (Allison 2014), drought (Allison and Goulden 2017; Wang and Allison 2021), and microbiome transplantation along climatic gradients (Wang and Allison 2022). These applications—which are grounded in ecophysiological theory, conservation of mass and empirical comparison—lend confidence in DEMENT's performance and utility as a tool for virtual microbiome experiments.

DEMENT represents hypothetical microbial taxa defined by physiological traits, specifically the ability to produce exo-enzymes, take up monomers and resist drought-induced mortality. Distinct polymer substrate pools each have a fixed stoichiometry. Substrate pools are degraded via Michaelis–Menten kinetics, and hypothetical microbial taxa produce exo-enzymes which each degrade at least one substrate into a single monomer. Monomer uptake follows Michaelis–Menten kinetics with uptake rate proportional to a transporter-specific V_{max} parameter and taxon-specific biomass in each grid cell.

During simulations, microbial taxa produce exo-enzymes via both constitutive and inducible production, take up monomers, grow and maintain their cells, reproduce and eventually die. These processes are computed at a daily time step and depend on daily temperature and litter moisture. Furthermore, at the end of every time step, monomer concentrations in every grid cell are set equal to the grid-wide average, allowing taxa to access monomers that were produced in a different grid cell. In this way, community composition and function emerge through both the response of taxa to environmental conditions and through interactions between taxa over the production and consumption of shared resources.

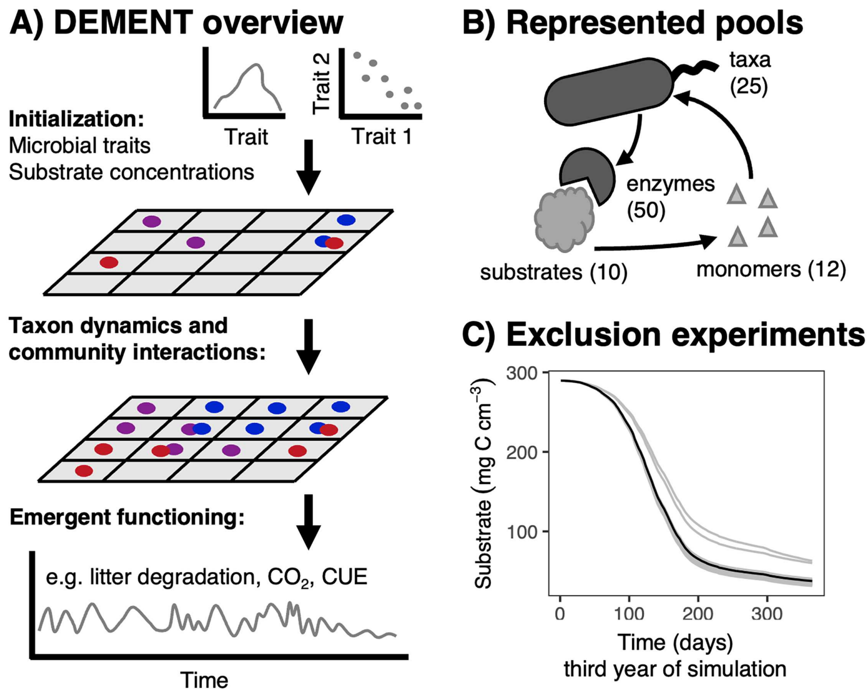

FIGURE 1 | Schematic of the DEMENT model and experimental design. (A) DEMENT is spatially explicit and represents microbial traits, taxon dynamics, community interactions and emergent functioning. (B) We modelled 10 substrates, 50 enzymes, 12 monomers (one for each substrate as well as two pools that represent inorganic nitrogen and phosphorus) and 25 microbial taxa. (C) To quantify taxon impacts on ecosystem function, we conducted exclusion experiments in which we removed a focal taxon from the initialization. The black line indicates a simulation with all taxa present. Grey lines indicate exclusion simulations without the focal taxon.

In plant litter, moisture limitation is an important physiological constraint on microbial growth and mortality (Manzoni, Schimel, and Porporato 2012; Malik et al. 2020). In the model, V_{max} values for exo-enzymes and uptake transporters are reduced at low water potential, limiting resource flows (Allison and Goulden 2017). The reduction in uptake V_{max} constrains uptake rates under dry conditions even though monomers are homogenised across the grid after each model iteration. Microbes can resist mortality from desiccation by allocating resources to osmolytes according to a randomly assigned osmolyte production trait that ranges between 0 and 1.0. Taxa with higher trait values have a lower sensitivity of mortality to desiccation but also pay higher respiratory costs for osmolyte production (Wang and Allison 2022).

DEMENT requires mass conservation and represents microbial growth as the balance between resource uptake and allocation to different processes. In this way, trade-offs among exo-enzyme production, monomer use and drought tolerance arise due to resource limitation. Because each of these processes involves metabolic costs, growth rates may decline as taxa allocate resources to more traits.

DEMENT is spatially explicit, and microbial taxa interact on a grid with absorbing boundaries, or edges that wrap around (Figure 1A). When initialising a simulation, substrates are homogeneously distributed across the grid, while microbial taxa are randomly distributed across the grid at equal frequencies. Here, we modelled litter decomposition dynamics on a 100×100 grid. We included 25 hypothetical microbial taxa, 50 exo-enzymes and 10 substrate pools to represent the composition of grass litter (Figure 1B and Table S1). Concentrations of substrates and densities of microbial taxa are initialised to represent approximately 1 mm^2 of litter surface area (Allison 2005).

We represented 25 taxa because this number allowed for degradation of all substrate types, and substrate degradation was not meaningfully different in simulations with greater richness (Figure S1). With fewer taxa, there was less overlap in trait combinations across the taxa and insufficient functional diversity to degrade all substrates (Figure S1). Although most leaf litter microbiomes contain far more than 25 microbial taxa, our simulations aim to represent the smaller subset of abundant taxa that physically interact over resources (Raynaud and Nunan 2014; van Tatenhove-Pel et al. 2021).

More detailed information about DEMENT parameters can be found in Table S2. Although we configured DEMENT to represent litter decomposition in a Mediterranean grassland, the model structure and parameterisation could be generalised to any microbiome with heterogeneity in resources, resource acquisition strategies and stress tolerance.

2.2 | Simulation Experiments

To quantify the impacts of different taxa on community dynamics and ecosystem function, we conducted exclusion experiments in which we removed a focal taxon from the initialisation. For communities of 25 taxa, we ran 26 simulations: one simulation of the entire community and 25 exclusion simulations (Figure 1C). All simulations were run for 3 years, during which substrate was replenished annually to represent litter inputs. Furthermore, at the beginning of each year, microbial taxa were re-initialised on the grid at their relative abundances from the end of the previous year. We treated the first 2 years of simulation as a model spin-up, quantifying responses in the third year of simulation as in Wang and Allison (2021). In this way, microbial community assembly dynamics were independent from initial conditions and determined by environmental conditions and interactions between community members on the grid.

To understand how taxon impacts varied under different community contexts and across a gradient of environmentally mediated physiological stress, we conducted exclusion experiments in 50 different microbial communities and three different climate forcings. This design resulted in 3900 total simulations (26 simulations × 50 communities × 3 climate forcings = 3900). Simulations were conducted in Python version 3.8.0 (Python Software Foundation, http://www.python.org). Code and data for simulations can be found at the Zenodo repository: https://doi.org/10.5281/zenodo.13684242 (Bertolet 2024).

2.3 | Microbial Community Context

We defined the community context of the 50 different microbial initialisations based on community-average trait values (Wright et al. 2004; Muscarella and Uriarte 2016). Specific traits included exo-enzyme production, monomer use and drought tolerance (Figure S2). We calculated community-average traits as the biomass-weighted average of all taxa in a community and used the taxon average biomass in the third year of the full community simulation to weight each taxon's contribution to the community-average value. These community-average traits constitute static, relative metrics to differentiate each community. That said, community-average traits do fluctuate at the daily time step and are sensitive to moisture and temperature conditions (Allison and Goulden 2017).

To quantify exo-enzyme production, we computed the taxon-specific costs of constitutive exo-enzyme production (mg C per mg biomass) and inducible exo-enzyme production (mg C per mg uptake) multiplied by the total number of exo-enzymes the taxon produces, as in Wang and Allison (2022). This quantity represents a relative exo-enzyme production metric, which ranged from 0 to 0.007 across all taxa. To quantify monomer use, we used the cost of transporter production multiplied by the total number of transporters, which ranged from 0.21 to 1.20 mg C per mg biomass. Lastly, to quantify drought tolerance, we used the costs of constitutive osmolyte production (mg C per mg biomass) and inducible osmolyte production (mg C per mg uptake). This quantity represents a relative drought tolerance metric which ranged from 0.010 to 0.10. We randomly and independently initialised the 50 different microbial communities, generating 1250 unique microbial taxa (25 taxa per community). Trait values for the 1250 microbial taxa can be found in the Figure S2.

2.4 | Climate Forcings

We conducted simulations under three different climate scenarios to explore the effects of physiological stress on the taxon impact on community dynamics and function. We used temperature and litter moisture data from a Mediterranean grassland site in Southern California as an 'ambient' climate scenario (Figure S3). We then constructed two additional climate forcing scenarios in which we varied litter water potential to create a gradient of moisture limitation and physiological stress. We constructed a 'drought' scenario by using a previously derived record of litter moisture used to represent the conditions of a desert site in Southern California (Wang and Allison 2022). Similarly, we constructed a 'moist' scenario using a soil moisture record derived to represent a subalpine site (Wang and Allison 2022). In both cases, we used the same temperature record as the ambient climate scenario and only considered how changes in moisture influenced the simulated community interactions and function. For each climate scenario, 1-year of temperature and moisture data were recycled for all 3 years of the simulation.

2.5 | Analysis of Model Output

For each focal taxon, we quantified the impact on ecosystem function using Equation (1):

$$\Delta S_i = S - S_i \tag{1}$$

where ΔS_i is the difference in total substrate degraded when focal taxon i is present, S is the total substrate degraded in the simulation with all 25 taxa present and S_i is the total substrate degraded in the simulation with focal taxon i excluded. A positive impact indicates that more substrate was degraded when taxon i was present, either through occupying additional niche space or through facilitative interactions with other taxa. A negative impact indicates that less substrate was degraded when present, evidence of exploitative interactions that decreased ecosystem function.

Additionally, as a measure of taxon impact on community dynamics, we quantified pairwise interactions between each focal taxon and all other taxa in the community (hereafter referred to as 'associate taxa') using Equation (2):

$$\Delta B_{ij} = B_j - B_{ij} \tag{2}$$

where ΔB_{ij} is the difference in average biomass of the associate taxon j when the focal taxon i is present, B_j is the average biomass of the associate taxon j in the simulation with all 25 taxa present, and B_{ij} is the average biomass of the associate taxon j in the simulation with the focal taxon i excluded. A positive taxon impact on the associate taxa biomass indicates that biomass of the associate j increased with focal taxon i present, and a negative impact indicates that the biomass of the associate j decreased when focal taxon i was present.

To determine how these impacts on community dynamics and ecosystem function varied across climate scenarios and community context, we used a two-way mixed model ANOVA, with climate scenario as a fixed effect, as the same 1250 taxa were subjected to three different climate scenarios, and community context as a random effect. Additionally, to understand system-specific patterns in taxon traits and ecosystem function, we analysed data from the climate scenarios separately and used multiple regression models to relate taxa traits to impacts on substrate degradation. Statistical analyses were conducted in R version 4.1.0 (R Core Team 2021), and code and data for statistical analyses can be found at the Zenodo repository: https://doi.org/10.5281/zenodo.13684242 (Bertolet 2024).

3 | Results

3.1 | Taxon Impacts in Different Communities and Under Different Climate Conditions

Across all simulations, we quantified the impacts of 1250 distinct microbial taxa in 50 different communities under three climate scenarios (Figure 2). As expected, we found that total substrate degradation varied significantly with both climate scenarios ($F_{1329.3}=110{,}109$, $p<0.05$) and community context ($F_{1200}=272.3$, $p<0.05$). Average total substrate degradation decreased from 286.7 ± 1.1 mg C cm^{-3} under moist conditions to 270.7 ± 10.9 mg C cm^{-3} under ambient conditions and 223.2.1 ± 24.2 mg C cm^{-3} under drought conditions (Figure 2A).

Taxon impact on substrate degradation varied significantly with climate scenario but not community context (climate effect: $F_{1329.3}=67.2$, $p<0.05$). Specifically, we found that decreasing moisture amplified taxon impacts on substrate degradation in both positive and negative directions, although the positive impacts were greater. Additionally, total substrate degradation increased with community-average enzyme production, such that communities with more enzyme producers degraded more substrate. However, taxon impacts under the drought scenario were significantly correlated with impacts under the ambient ($R^2=0.85$, $p<0.001$) and moist ($R^2=0.40$, $p<0.001$) climate scenarios, indicating similar directional effects of each taxon across the environmental conditions (Figure S4).

We also quantified all pairwise interactions, measured as the change in average biomass of an associate taxon when a focal taxon was excluded. Interestingly, we did not find differences in average taxon impact on associates across climate scenarios or communities (Figure 2C). Overall, negative pairwise interactions were more common than positive interactions, accounting for 66% ± 3.4% of all interactions.

3.2 | Relationships Between Taxon Traits and Ecosystem Function

Analysis of results within each climate scenario revealed that taxon impacts on substrate degradation were significantly related to taxon traits and community context (Figure 3). Here, we focus on data from two representative communities with low and high

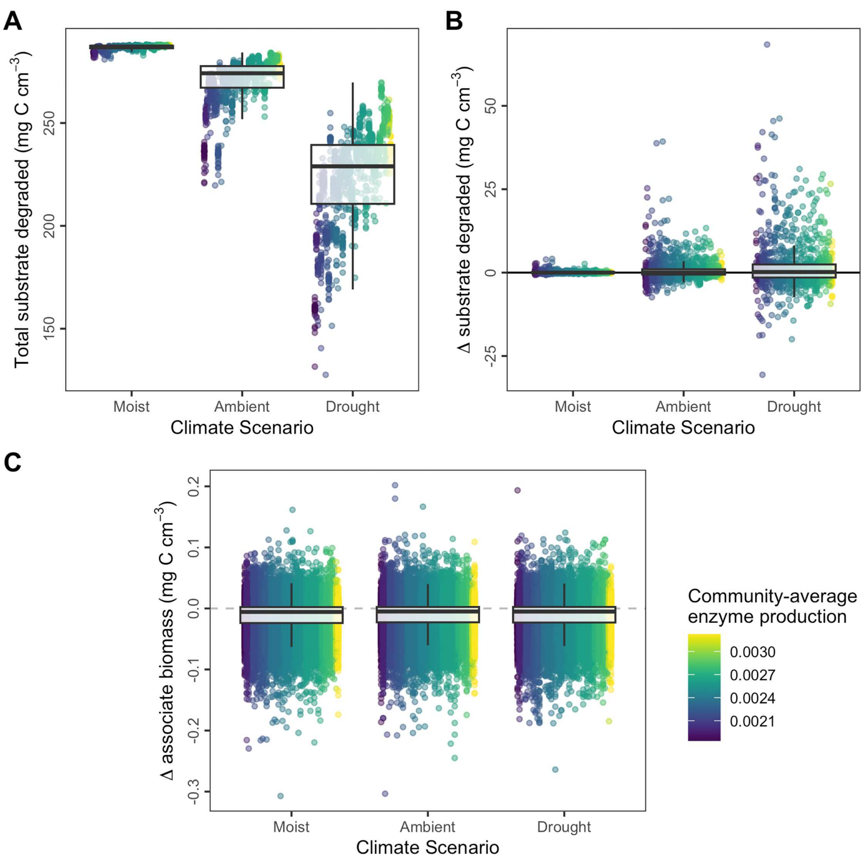

FIGURE 2 | (A) Total substrate degradation varied significantly with both climate scenario ($F_{251.88}=17{,}712$, $p<0.05$) and community context ($F_{251.88}=221.7$, $p<0.05$). Total substrate degradation decreased with drought and increased with community-average enzyme production. Points are ordered on the *x*-axis and coloured by community-average enzyme production. (B) Taxon impacts on ecosystem function, defined as the change in substrate degradation when a focal taxon is excluded. (C) Taxon impacts on community dynamics, defined as the pairwise change in average biomass of an associate taxon when a focal taxon is excluded.

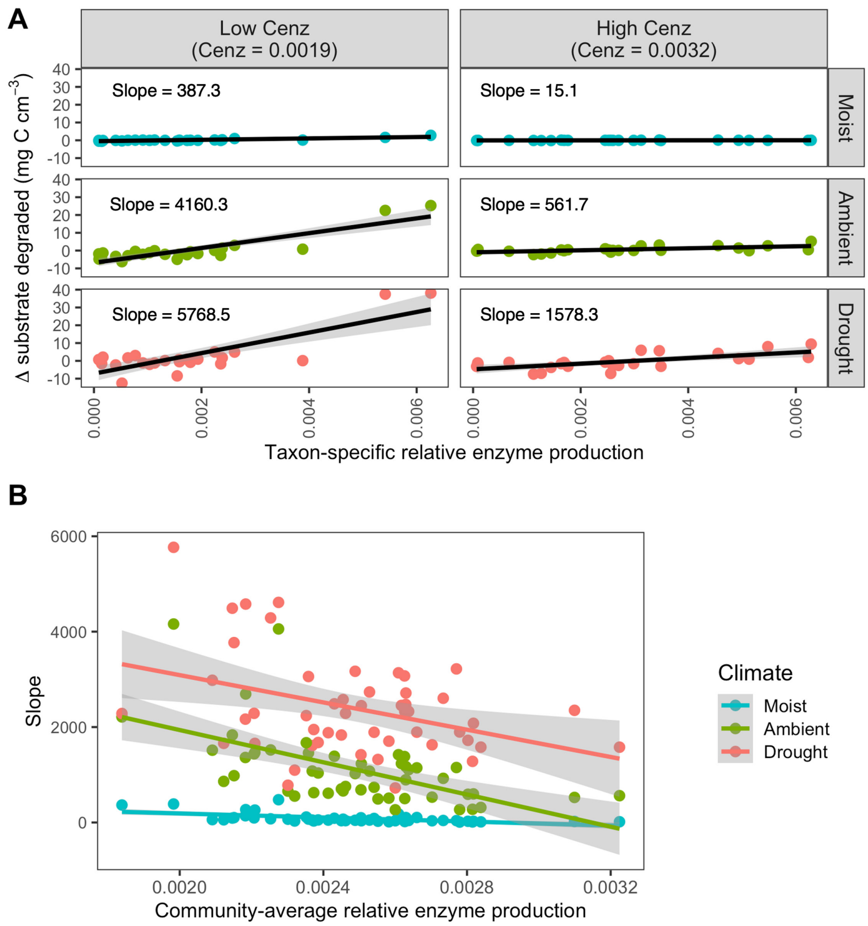

FIGURE 3 | (A) The impact of a focal taxon on substrate degradation is positively related to the taxon-specific relative enzyme production, but the relationship is mediated by community-average relative enzyme production (Cenz) and climate. Points are coloured by climate scenarios. Data are shown here for representative communities with low and high Cenz, but analyses were conducted for all 50 replicate communities. The black lines represent the predicted taxon impact from a linear regression that includes taxon-specific relative enzyme production, community-average relative enzyme production, climate conditions and their interaction (p-value < 0.001, $R^2 = 0.45$). (B) The relationship between the impact of a focal taxon on substrate degradation and taxon-specific relative enzyme production (i.e. the slope from Panel A) is negatively related to community-average relative enzyme production and mediated by climate conditions (multiple regression: p-value < 0.001, $R^2 = 0.70$).

community-average relative enzyme production (Figure 3A), but patterns were consistent across all communities (Table S3). Specifically, we found that taxon exo-enzyme production was positively related to the impact on substrate degradation, but the effect was mediated by the community-average exo-enzyme production and climate scenario. A multiple regression that included taxon exo-enzyme production, community-average exo-enzyme production, climate scenario and the interactions explained 45% of the variation in taxon impact (p-value < 0.001, $R^2 = 0.45$). Furthermore, within a given climate scenario, other microbial traits, such as monomer use and drought tolerance, were not significant in predicting taxon impacts on substrate degradation (Table S3).

Importantly, we found a significant negative interaction effect between taxon exo-enzyme production and community-average exo-enzyme production, indicating that the community functional capacity buffered the system against taxon loss (Figure 3B). The slope of the relationship between substrate degradation and taxon exo-enzyme production decreased with community-average exo-enzyme production and was mediated by climate (multiple regression across all climate scenarios: p-value < 0.001, $R^2 = 0.70$). Furthermore, the importance of the buffering capacity of the community exo-enzyme production (i.e., the slope) was highest under drought conditions and decreased in wetter scenarios (Figure 3B), indicating the greater influence of associate taxon interactions under drought conditions. Thus, enzyme-producing microbes substantially increased substrate degradation only in communities with low overall exo-enzyme production. In communities with high exo-enzyme production, other associate taxa also had high exo-enzyme production and were able to compensate for the loss of the focal taxon.

Further exploration of taxon impacts under all three climate scenarios revealed the importance of drought tolerance traits under stressful environmental conditions. Here, we focus on data from the drought climate scenario, and we use the ratio of exo-enzyme production to monomer use to visualise relationships between taxon traits and taxon impacts, with lower values of the ratio representing cheater strategies. In the drought climate scenario, taxa that were both drought tolerant and enzyme producers tended to have more positive impacts on substrate

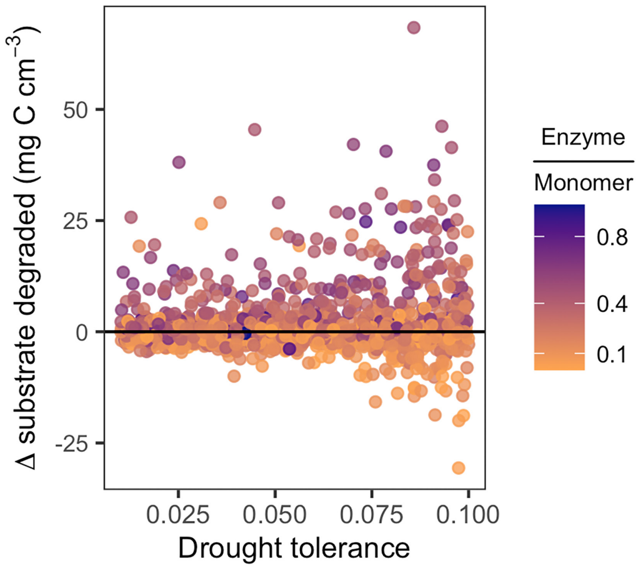

FIGURE 4 | Taxon impacts on substrate degradation in relation to drought tolerance. Points are coloured by taxon-specific exo-enzyme production relative to monomer use, with lower values representing cheating strategies. Data are shown from simulations under the drought climate scenario.

degradation (Figure 4). In contrast, taxa that were drought tolerant and cheaters tended to negatively influence substrate degradation (i.e., when cheaters were present, substrate degradation decreased). Interestingly, cheating microbes did not have meaningful negative impacts on ecosystem function under the ambient and moist climate scenarios (Figure S5). Instead, under moist conditions, community members always compensated for the loss of a taxon, irrespective of the traits of the excluded taxon.

There were exceptions to the general pattern that drought tolerance led to more amplified impacts of interactions. In some cases, a focal taxon with low drought tolerance (<0.05 relative drought tolerance) had meaningful positive impacts on substrate degradation, increasing the amount of substrate degraded by nearly 40 mg C cm^{-3} when present (Figure 4). These taxa had high exo-enzyme production (and high capacity to take up the corresponding monomers) in communities with low overall community exo-enzyme production. Thus, because the overall community was exo-enzyme limited, the presence of these taxa positively contributed to substrate degradation, despite their relatively low drought tolerance.

3.3 | A Generalisable Framework for Taxon Impacts on Community Dynamics and Ecosystem Function

Our simulations revealed three main outcomes for focal taxon impact on associate taxa biomass and substrate degradation (Figure 5). Taxa that had negative impacts on both associate biomass and substrate degradation functioned as cheaters (Figure 5A, lower left quadrant). Furthermore, taxa with positive impacts on substrate degradation were mainly enzyme producers. Some of these taxa facilitated associates' biomass (Figure 5A, upper right quadrant), but many enzyme-producing taxa had negative impacts on associate biomass (Figure 5A, lower right quadrant). In these cases, the focal taxon's enzymatic contribution to substrate degradation outweighed its negative impact on the biomass of other associate taxa. Thus, net positive effects on ecosystem function arose via both positive and negative pairwise interactions, and differential impacts on associate taxa did not necessarily alter ecosystem function.

4 | Discussion

As global change continues to affect all ecosystems, our study provides important mechanistic support for how physiology may mediate ecosystem responses from organismal to community scales. We used trait-based simulation of microbial-driven litter decomposition to quantify taxon impacts on community dynamics and ecosystem function, and we built a new framework for predicting the outcome of resource-based interactions (Figure 5B). Specifically, we show that resource acquisition traits influence whether a taxon's impact on ecosystem function is positive or negative, but net positive impacts can arise even if taxa have negative pairwise interactions. Furthermore, environmental stress amplifies taxon impacts on ecosystem function in both positive and negative directions, despite not influencing pairwise community interactions (Figure 2B).

In field studies, drought has significant impacts on microbial community composition and functioning. As gene expression and microbial abundances shift under drought (Schimel 2018), rates of decomposition and exo-enzyme production may decline (Allison et al. 2013; Qu et al. 2023). DEMENT simulator outputs largely agree with these observed trends, both here (Figure 2) and in prior studies (Wang and Allison 2021), lending support to the model's representation of microbial drought responses. Still, some of DEMENT's assumptions require further testing. For instance, monomer diffusion is likely slower under drought than assumed by DEMENT, which could cause the model to overestimate monomer sharing during dry periods. Most microbial activity occurs when monomer diffusion increases under wet conditions.

In our simulations, both drought and community context influenced the outcome of a focal taxon's presence and interactions. Cheating taxa had more negative impacts on substrate degradation under drought conditions, while exo-enzyme producers had more positive impacts under the same stressful conditions (Figure 5). Our results thus suggest that the cost of investment in stress tolerance amplifies the impact of resource-based interactions on ecosystem function, even as stress does not influence patterns in pairwise community interactions (Figure 2C).

Context dependency of microbial interactions and function has been previously observed in laboratory experiments with microbial consortia (de Muinck et al. 2013; Chevrette et al. 2022) and is often viewed as a challenge for predicting ecosystem function from microbial traits (Sanchez-Gorostiaga et al. 2019). Physiological stress due to abiotic environmental conditions may also contribute to the context dependency of ecosystem function (Schimel, Balser, and Wallenstein 2007; Hawlena and Schmitz 2010). Yet, we found that the taxon impact on substrate

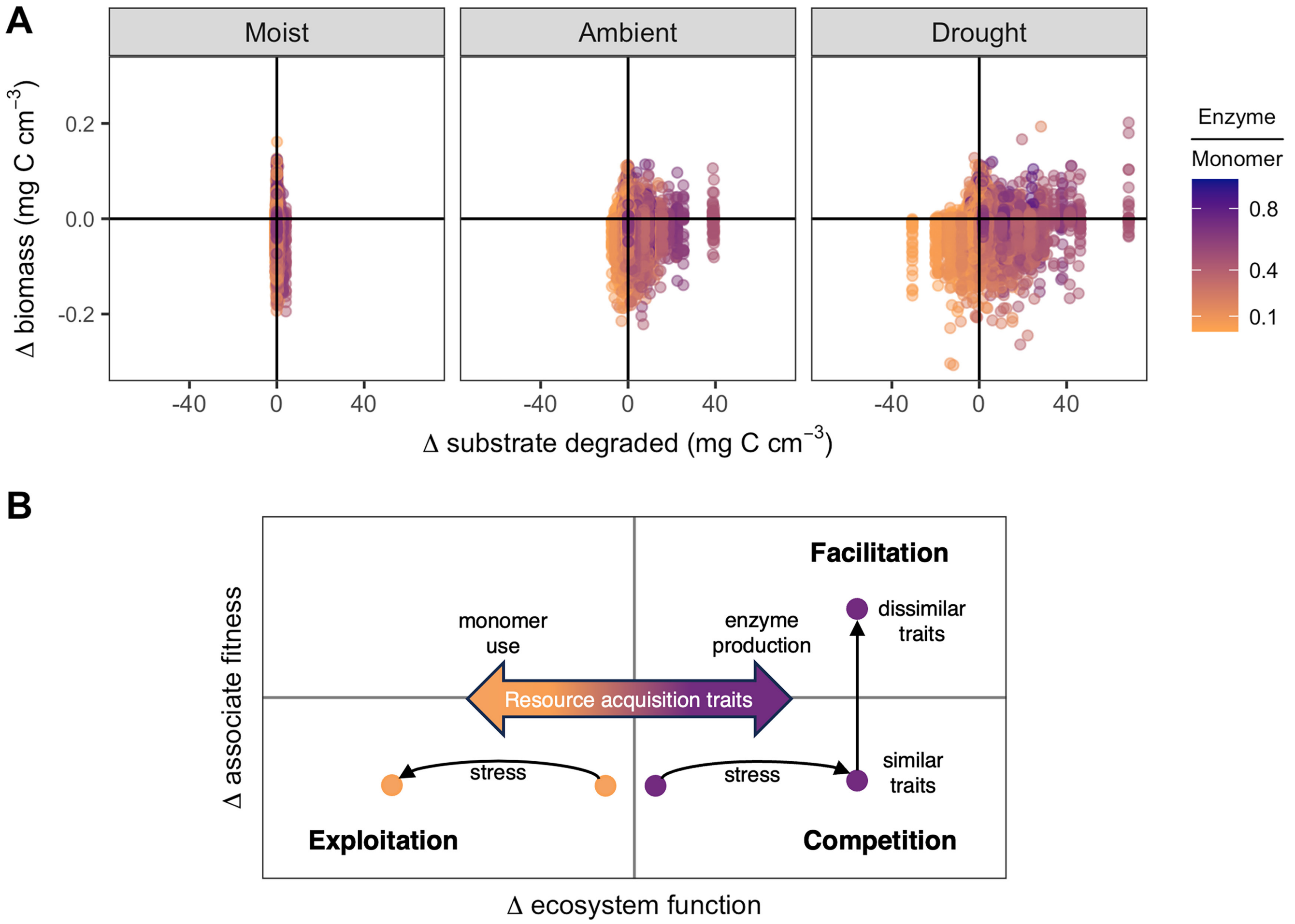

FIGURE 5 | (A) Focal taxon impacts on associate biomass and substrate degradation. Points are coloured by taxon-specific exo-enzyme production relative to monomer use, with lower values representing cheating strategies. (B) A generalisable framework for predicting taxon impacts on community dynamics and ecosystem function. Traits associated with resource acquisition determine whether impacts on ecosystem function will be positive or negative, but environmental stress amplifies the impact on ecosystem function in both positive and negative directions. In our simulations, under low environmental stress, focal taxa did not have meaningful impacts on substrate degradation regardless of taxon traits. When environmental stress was high, taxa that invested in greater enzyme production had more positive impacts on resource degradation. Trait dissimilarity between the focal taxon and the associate taxa determines whether exclusion of the focal taxon will lead to positive or negative impacts on the associate's fitness (y-axis position). Analysis of our data showed that, when a focal taxon had high positive impacts on substrate degradation, similar taxa tended to have competitive interactions and dissimilar taxa tended to have facilitative interactions. Furthermore, there were very few focal taxa that had negative impacts on substrate degradation and positive impacts on associate taxa (upper left quadrant) because positive impacts on associates require higher rates of enzyme production by the focal taxon.

degradation was predictable based on community context as defined by exo-enzyme production. In DEMENT, exo-enzymes are directly related to the community capacity for substrate degradation through Michaelis–Menten kinetics. Specifically, in communities with low average exo-enzyme production, enzyme producers had large positive impacts on substrate degradation (Figure 3). Conversely, if the community had high enzyme capacity, loss of an enzyme producer had little effect on ecosystem function.

Similarly, we found that cheating taxa did not substantially negatively influence ecosystem function in communities with high functional capacity. Other studies have found that cheating can reduce substrate degradation rates (Allison 2005; Allison et al. 2014; Kaiser et al. 2015), but our analysis shows that a community context with high enzyme production can mitigate these impacts. Recent work using laboratory cultures has also found that cheating interactions are diminished in more diverse communities (O'Brien, Culbert, and Barraclough 2022) due to the higher likelihood of including species that outcompete and suppress cheaters.

Relationships between taxon traits and community context offer promise for predicting ecosystem functions in communities with many co-occurring taxa. In communities with high functional capacity, ecosystem function should be robust to the addition and subtraction of taxa, even those taxa with extreme trait values. This robustness is supported by empirical observations, which often find high resilience of microbial functions to changes in community composition (Waldrop, Balser, and Firestone 2000; Bell et al. 2005). However, our results also suggest that, in communities with low functional capacities, changes in composition will have large impacts on function. In accordance with this prediction, biomass of an inoculated *E. coli* invader was higher in microbial communities with lower substrate use capacity (Mallon et al. 2015). When environmental stress was greater in our simulations, the impact of a focal taxa was amplified, likely due to the trade-off between resource acquisition and stress tolerance traits inherent in DEMENT (Allison and Goulden 2017).

Additionally, we found that net positive impacts on ecosystem function can arise even if taxa have negative pairwise interactions with each other. There were many cases in which focal taxa had negative impacts on associate taxa biomass but positive impacts on ecosystem function (Figure 5A, lower right quadrant). Laboratory experiments of culturable microorganisms often observe competitive pairwise interactions (Foster and Bell 2012), and while there is substantial debate on the ubiquity of competitive versus facilitative interactions (Mee et al. 2014; Kehe et al. 2021), our results suggest that negative interactions in a community do not necessarily imply negative impacts on ecosystem function. Specifically, we found that the presence of a focal taxon could have a negative impact on an associate taxon's biomass and a positive effect on substrate degradation when both taxa were enzyme producers (Figure 5B). Thus, system-specific understanding of the mechanism of interactions should allow for understanding of the scaling between community interactions and ecosystem function.

One notable assumption of our model is that traits, such as enzyme and osmolyte production, vary among taxa. Therefore, shifts in community-average traits are largely driven by changes in the abundance of taxa rather than physiological acclimation within taxa. Although the model represents inducible enzyme production, more sophisticated up- or down-regulation of enzyme production might reduce the strength of interactions among taxa. However, metabolic costs of regulation could reduce the viability and ecological relevance of strategies with high physiological plasticity (Kalisky, Dekel, and Alon 2007).

The interaction mechanisms and ecosystem consequences simulated by DEMENT can help generate hypotheses about microbial interactions that may be occurring in the real world. There is some evidence from laboratory consortium studies that positive bacterial interactions strengthen with increasing stress from toxicity (Piccardi, Vessman, and Mitri 2019), consistent with our model simulations of drought stress. Although both positive and negative taxon impacts on substrate degradation increased with drought, the positive impacts were more pronounced. Validating these presence-impact results with 25 microbial taxa in the field would be a challenge, but it might be possible to design exclusion experiments to test our model predictions in the laboratory, perhaps with a smaller number of taxa. For instance, our simulation design could be replicated using a complex substrate in liquid media hosting synthetic communities of bacteria in microplate wells.

The patterns we observed may apply to other communities in which interactions are resource-based and taxon traits include trade-offs between stress tolerance, resource acquisition and growth. For example, in many savanna ecosystems, tree species can facilitate understory grass productivity via hydraulic lift, the process by which soil water is moved upwards through the roots of plants (Caldwell, Dawson, and Richards 1998). Assuming that water is important for plant fitness, we would predict that interactions become more pronounced during stress, but that the impact of interactions on neighbour fitness and primary productivity is dependent on water use efficiency and drought tolerance. Indeed, studies on hydraulic lift have documented both facilitative (Prieto et al. 2011; Yu and D'Odorico 2015) and competitive (Ludwig et al. 2004) interactions and have highlighted the context dependency of hydraulic lift interactions.

In conclusion, our results provide new insight on how resource-based interactions might influence community dynamics and ecosystem function under changing environmental conditions. Our results suggest that shifts in the community composition of low functioning communities may have impacts on ecosystem function, and that these impacts may intensify under drought stress. As communities respond to global climate change, quantifying taxa traits, resource-based interactions and environmental stress can allow for robust understanding and prediction of ecosystem responses.

Author Contributions

B.L.B. and S.D.A. conceived of the presented idea. B.L.B. conducted model simulations and analysed data with input and technical guidance from L.C.R., J.M.M., A.F. and S.D.A. B.L.B. wrote the initial manuscript draft. All authors contributed to data interpretation, provided written feedback and approved the final version.

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Data Availability Statement

All data and code are currently publicly available at the Zenodo repository: https://doi.org/10.5281/zenodo.13684242.

Peer Review

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Supporting Information

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