Changes in species interactions amplify the temperature dependence of microbial community respiration

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The sensitivity of microbial community respiration to temperature is crucial for understanding the effects of climate change on the carbon cycle[1,2]. However, large uncertainties about the magnitude of this response exist, owing to limited mechanistic understanding of how the thermal sensitivity of respiratory flux emerges in complex microbial communities[3,4]. Here, we develop a mathematical model that predicts how the direction and strength of species interactions affects the temperature sensitivity of microbial community respiration. Our theory predicts that temperature sensitivity is amplified as species interactions become more positive (e.g., move from competition to facilitation), because warmer temperatures disproportionately increase the positive feedbacks between the temperature-sensitivities of species-level metabolic and biomass accumulation rates. Consistent with our predictions, we found that the temperature sensitivity of respiration in laboratory bacterial communities that had a one-month period of 'adaptation' was 60% higher than communities assembled *de novo* from the same strains with no adaptation period due to the establishment of facilitation between strains through cross-feeding in the adapted communities. Our findings demonstrate that rapid changes in the direction and strength of species interactions can profoundly change the response of microbial community functioning to temperature fluctuations.

Empirical data show that ecosystem-level respiration generally follows an exponential-like relationship with temperature[5], raising concerns that future warming will increase carbon emissions from the biosphere and accelerate rates of global warming[1,6–8]. A major component of this thermal response is driven by the microbial components of the ecosystem[1,2]. Indeed, microbes are a dominant component of the earth's total biomass[9], and by degrading the organic carbon from primary and secondary production contribute significantly to carbon cycling. For example, bacterial contributions to ecosystem respiration have been estimated to be >50% in some ocean regions[2,3]. Consequently, even small differences in the thermal sensitivity of microbial community respiration could have major impacts on projections of future global warming[3,10].Yet, the response of microbial community respiration to temperature represents a critical uncertainty in climate-carbon cycle projections for the next century, and an important but unresolved question in microbial ecology[1,4,11].

Current models of the temperature responses of multispecies ecosystems typically assume that thermal responses can be scaled up from the individual to community- or ecosystem-level by a simple addition of the temperature responses of component taxa[10,12–15]. These models focus only on the direct effect of temperature on individual metabolism, ignoring the effects of species interactions which could alter the amount and distribution of biomass within ecosystems, affecting total ecosystem respiration and its thermal sensitivity[16,17]. Thus, current models are unlikely to be an accurate representation of the processes that contribute to the temperature sensitivity of respiration in natural ecosystems, where species interactions are critical for shaping the structure and dynamics of complex communities[18–20], particularly in response to changes in the abiotic environment[21].

In microbial communities in particular, where demographic processes and population turnover occur over short timescales, temperature dependence of community respiration more likely reflects the impacts of temperature both directly on individual metabolism, and indirectly through species' interaction-driven biomass dynamics. Microbial taxa interact in numerous ways, ranging from competition for limiting abiotic resources, to facilitation, typically through cross-feeding on metabolic by-products[22–24]. Because key microbial metabolic traits are temperature-sensitive, as temperatures change these interactions inevitably result in shifts in biomass dynamics, and thus community respiration[25]. For example, widespread facilitation may amplify the effects of temperature by creating a positive feedback loop due to enhanced metabolic and growth rates in warmer conditions. Conversely, if weak or neutral interactions dominate, such as when species partition resource use, the species' population biomasses should become relatively decoupled, and the response of community respiration to temperature should emerge through the simple addition of the thermal responses of individual taxa. In general, when interactions are strong, feedbacks between populations should be greater, amplifying the (positive or negative) effects of temperature across the whole system.

We investigated the role of biotic interactions in the temperature dependence of community metabolism by combining theory with laboratory experiments. In both, we focus on the stages of community growth before populations reach carrying capacity. This is because transient population

dynamics are important to the respiratory flux of microbial communities for two key reasons. First, in natural systems the bulk of respiratory flux occurs when resource availably is high (e.g., spring blooms in aquatic systems [26] and autumn litter fall in soils[27]) during which growth is near-exponential, making short-term population responses important. Second, the frequent environmental perturbations and immigration events that microbial communities experience mean that they are constantly kept away from true equilibrium over long time-scales.

We first developed a mathematical model to explore the effects of species interactions on the thermal response of community-level (henceforth, synonymous with "ecosystem-level") respiration (Fig 1). Consider a community comprising of N interacting species. Within this system, the total temperature (T)-dependent respiration rate ($R_{eco}(T)$) depends on the sum of contributions of each population's total respiration, which in turn can be expressed as the product of mass-specific respiration ($R_i(T)$) and biomass ($C_i(T)$) of each population:

$$R_{eco}(T) = \sum_{i=0}^{N} R_i(T)C_i(T)\,. \qquad (1)$$

This equation indicates that temperature affects community respiration by changing mass-specific respiration of individual populations, by changing their biomasses, or both (Fig 1a). Next, we derive the thermal sensitivity of $R_{eco}(T)$ (the magnitude of change of community respiration to a unit change in temperature in log-scale), which we denote by an apparent activation energy, E_{eco} (see Methods):

$$E_{eco} = \frac{\sum_{i=0}^{N} R_i(T)C_i(T)\left(E_{R,i}+E_{C,i}\right)}{\sum_{i=0}^{N} R_i(T)C_i(T)}\,, \qquad (2)$$

where $E_{R,i}$ and $E_{C,i}$ are the thermal sensitivities (apparent activation energies) of mass-specific respiration and biomass dynamics of the ith species' population, respectively. Eq 2 shows that E_{eco} is given by the average thermal sensitivities of biomass dynamics and respiration across all species (strains) in the system, weighted by each species' total respiratory output, $R_i(T)C_i(T)$. Note that Eq 2 also contains temperature dependent terms reflecting the effects of biomass dynamics, which results in a non-exponential thermal response of total ecosystem respiration (Fig. 1b). Next, we consider how E_{eco} (Eq 2) is affected by interspecific interactions. Assuming interactions do not affect species' mass-specific respiration rate R_i (i.e., a single strain' cell will have roughly the same respiration rate in the presence or absence of interactions), we focus on how they affect the biomass terms (C_i's and $E_{C,i}$'s) in Eq 2. We show that the thermal sensitivity of community-level respiration can be partitioned as (see Methods)

$$E_{eco} \approx \overline{a}\gamma + N\mathrm{Cov}\left(w_i(\overline{a}), \left(E_{R,i} + \omega_i\right)\right) + \left(\overline{E_R} + \overline{\omega}\right), \qquad (3)$$

where $\overline{a}$ is the average of the interaction coefficients between all species pairs (a_{ij}'s), $\gamma = \frac{d\overline{r}}{dT}\frac{(N-1)\overline{C_0}t^2}{2}$ is the average thermal sensitivity of time (t)-dependent biomass across all populations (driven by temperature-dependent changes in average population growth rate $\overline{r}$), $w_i(\overline{a}) = \frac{R_iC_i(\overline{a})}{\sum_{i=0}^{N} R_iC_i(\overline{a})}$ is the weighting of the ith species' contribution (its normalised respiratory output), and $\omega_i = \frac{dr_i}{dT}\left(t + \frac{t^2 a_{ii}C_{0,i}}{2}\right)$ is the thermal sensitivity of its biomass at time t. The dependence of these weights on $\overline{a}$ arises through the effects of species interactions on population biomasses ($C_i(\overline{a})$).

Equation 3 shows that the thermal sensitivity of community respiration is determined by three components: (i) the effect of averaged interspecies interactions ($\overline{a}\gamma$), (ii) the covariation between species' responses to interactions (via the weighting terms) and their thermal sensitivities $\left(N\mathrm{Cov}\left(w_i(\overline{a}), E_{R,i} + \omega_i\right)\right)$ and (iii) the average thermal sensitivities of respiration and biomass growth (not accounting for interactions) across species in the community $\left(\overline{E_R} + \overline{\omega}\right)$. When interactions are on average neutral ($\overline{a} = 0$) the first of these terms is zero and community sensitivity is dependent

only on internal factors affecting species' population growth (growth rates and intra-specific interactions in the ω and covariance term). When interactions are non-neutral $(\overline{a} \neq 0)$ they will either amplify or dampen the sensitivity of community respiration relative to this neutral case (Fig 1b). More facilitatory (positive) interactions will increase (amplify) thermal sensitivity, while competitive interactions will result in a reduction (dampening) in sensitivity (including intransitive competition; see Methods). In general, stronger interactions (i.e. greater absolute values of $\overline{a}$) will result in greater changes in community-level sensitivity. This amplification or dampening happens because interactions modulate the rate of change in biomass with temperature across the community (altered rates of biomass accumulation), captured by the γ term.

In addition to this direct effect, interactions can also alter community sensitivity through the covariance term in Eq 3, which occurs when species whose biomass is strongly affected by the interactions (i.e. those with more extreme $w_i(\overline{a})$ values) also tend to have higher temperature sensitivities of respiration and biomass accumulation $(E_{R,i} + \omega_i)$). Though there is no empirical evidence of such relationships, it is feasible that these patterns exist in nature. For example, in microbial communities it is possible that temperature and resource specialism are correlated such that species with wide thermal niches (thermal sensitivities) also tend to be more general in their resource use (and thus are more affected by competition imposing a negative covariance structure). The relative effect of interactions through this covariance term will depend on the correlation between these two factors as well as the size of their variation across the community (i.e. greater variation in thermal sensitivity allows for more bias towards high sensitivity values).

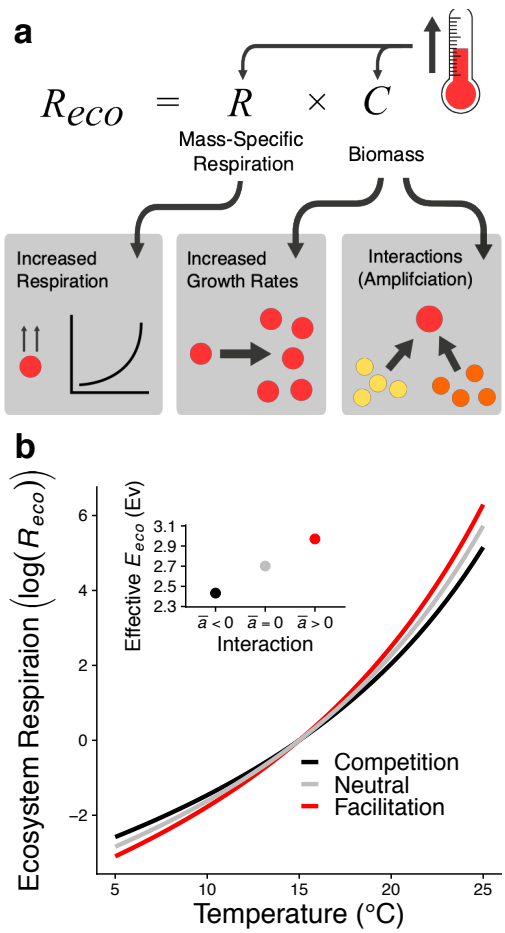

Fig 1. Changes in biotic interactions alter the temperature sensitivity of microbial community respiration. a) Temperature can act on community-level respiration either by affecting individual metabolism directly (increasing respiration), or the amount of biomass, which is determined by the effects of temperature on growth rates and interactions between species. b) Prediction of the relationship between temperature and community respiration under different interaction structures. Respiration

becomes more sensitive to temperature change as interactions become more positive. Main plot shows community respiration, log(R_{eco}) normalised to a common T_{ref} (15°C) at three levels of interaction strength across the community. Note that the curves are nonlinear in log scale because the thermal sensitivity of community respiration (the slope of log(R_{eco}) versus temperature) is itself temperature-dependent (Eq 2) due to the nonlinear change in biomass dynamics with temperature as explained in the main text. Inset plot shows the resultant effective thermal sensitivity E_{eco} measured at T_{ref}. See methods for parameters used to generate predictions.

We tested these theoretical predictions using experiments with aerobic heterotrophic bacteria. To investigate how changes in interaction structure (e.g., from competitive to facilitatory) affect the temperature sensitivity of community respiration, we assembled replicated communities of 8 bacterial taxa isolated from geothermal streams in Iceland by incubating them together in a minimal, single carbon source media (M9 + glucose) at ambient temperature (20°C) through several serial transfers (~100 generations). These allowed us to (a) use a diverse array of natural isolates that vary considerably in their thermal physiology; and (b) exploit the tendency of bacterial taxa to increase facilitation by cross-feeding (exchanging metabolic by-products) when subject to resource limitation over time, producing replicated communities with the same taxa but different interaction structures[28–30]. We henceforth refer to these as 'adapted' communities. For comparison, we also assembled replicated communities using the same ancestral taxa, but incubating them for a much shorter period constraining their capacity for adaptation (see Methods) ('de novo communities').

In all adapted communities, biomass dynamics stabilised after 16 days (7 transfers, ~50 generations), with 5 of the 8 taxa from the original taxon pool persisting at a relatively stable total abundance. At the end of the experiment, after 30 days (14 transfers, ~100 generations), we re-isolated the taxa from each of the replicated assembled communities. We first assessed whether community adaptation affected the thermal response of respiration for each of the 5 taxa along a broad temperature gradient (15-35°C), for populations from both the de novo and the adapted communities. We found no significant difference in any of the parameters of the temperature response of respiration between the ancestral isolates and the same taxa isolated from the adapted communities (Fig. 2a, Extended data Fig. 1, Table 4), showing that the population-level temperature response remained unchanged following adaptation.

Based on our theory, we predicted that the thermal sensitivity of total community respiration should be higher in the adapted communities where facilitatory interactions were expected to have become more prevalent, compared to those incubated for a much shorter period (2 days; hereafter termed 'de novo' communities). As we expected metabolic facilitation (i.e. the exchange of metabolic by-products between populations) to be the main mechanism for any change in interaction structure, we performed the community respiration assays in both M9+glucose and "spent" media (obtained by allowing communities to grow until all the initial glucose was depleted and only metabolic by-products remained, see Methods). If an increase in metabolic facilitation was the main mechanism for changes in species interactions, then we expected to see an amplification of the thermal sensitivity of respiration in the adapted communities in the spent media, because the taxa that comprise these communities will have adapted to persisting on the metabolic by-products of their conspecifics whereas the de novo assembled communities will not. By contrast, in the M9+glucose media, populations will be able to independently access glucose, free from exploitative or interference competition (as the assays were carried out at low densities in the exponential phase of growth) leading competitive interactions. When interactions are weak our theory predicts a relatively small amplification effect, and we therefore anticipate comparable temperature sensitivities between the population- and community level in both de novo and adapted treatments.

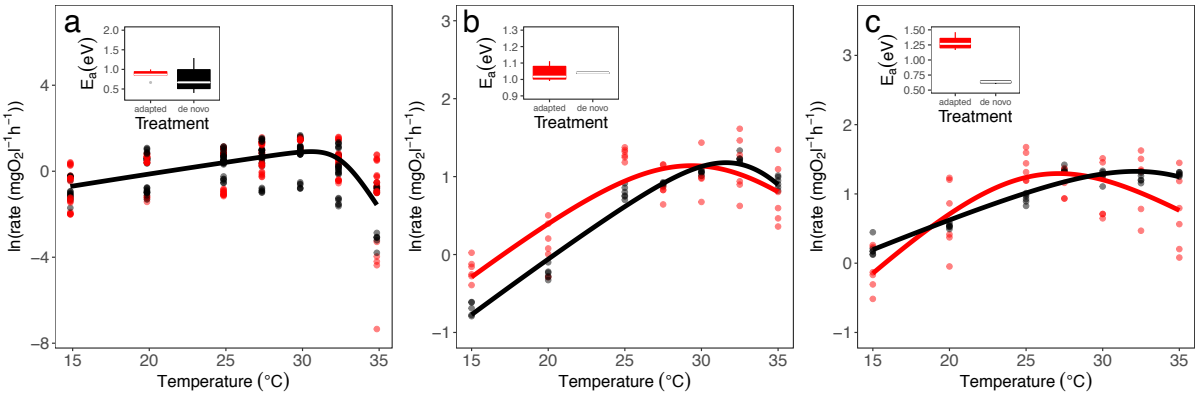

Fig 2. Microbial facilitation amplifies the temperature sensitivity of community respiration following community adaptation. Temperature dependence of respiration at the population (a) and community level in (b) M9+glucose and spent media (c). Colours denote whether populations or communities are from the adapted (red) or de novo community isolates (black). Inset plots show the distribution of thermal sensitivities (*E,* activation energy) for each treatment where box plots depict the median (centre line) and the first and third quartiles (lower and upper bounds). Whiskers extend to 1.5 times the interquartile range (the distance between the first and third quartiles). The solid lines represent the average temperature sensitivity estimated by fitting the Sharpe-Schoolfield equation using non-linear mixed effects models (see Methods).

Consistent with these predictions, we found that the average temperature sensitivity of respiration was statistically indistinguishable between the de novo and adapted communities measured in M9+glucose (Fig. 2b, Extended data Table 5). Furthermore, the apparent activation energy of respiration at the population- and community-levels in the M9+glucose media (where interactions are expected to be weak) were indistinguishable (species = 1.01 eV ± 0.19, community = 1.04 eV ± 0.17) as predicted by Eq 3 for near neutral interactions. However, when we quantified the temperature response of community respiration in spent media, as expected from the theory, we found a marked increase in the thermal sensitivity of respiration, compared to that of de novo communities (Fig. 2c, Extended data Table 5) and the activation energy of the assembled community in the spent media was 40% higher (1.4 eV ± 0.40) than the average population-level activation energy. To eliminate the possibility that the observed amplification of community respiration was driven by changes in per-capita metabolic rates of the strains instead of interaction-driven biomass dynamics, we compared the thermal sensitivity of per capita respiration (mg O_2 L^{-1} h^{-1} $cell^{-1}$) and biomass accumulation (see SI) between the de novo and adapted communities. We found that the thermal sensitivity of per-capita respiration was indeed statistically indistinguishable between the de novo and adapted communities (Extended data Fig. 2, Table 6), while that of biomass accumulation was significantly higher in the latter (Extended data Fig. 3, Table 7). These empirical results are consistent with our theoretical prediction that positive interactions result in population dynamical feedbacks that ultimately amplify the temperature sensitivity of community respiration via changes in biomass dynamics.

Having established that the temperature sensitivity of respiration was markedly higher in the adapted communities, we next quantified the strength and direction of interactions among the five taxa in the adapted and de novo assembled communities to confirm that interactions had become more facilitatory (or less competitive). First, we looked at how the asymptotic biomasses of the communities and the individual taxa (i.e. carrying capacity, *K*) changed following adaptation. If interactions had become more facilitatory, we expected to see higher biomass attained in these communities due to more efficient use of limiting resources. When each taxon was grown in monoculture on the M9+glucose media for 72 h at 20°C, we saw no statistically significant effect of treatment on *K* before and after adaptation (P = 0.56, Extended data Fig 1, Table 1). However, when the same test was performed with multi-species communities, *K* was higher in the assembled community (Fig. 3a, M9 +glucose media, Extended data Table 2). To further investigate these effects, we repeated the experiment, but this time, incubated the communities in spent media. We found that the adapted community reached higher a *K* compared to the de novo assembled community on the spent media (Fig 3a, Extended data Table 2). Furthermore, the *K* attained by the adapted community in the spent media was even higher than it

attained in the M9+glucose media. Altogether these results suggest that the adapted communities were better able to exploit the available resources either in the form of M9+glucose or the cross-feeding on each other's metabolic by-products.

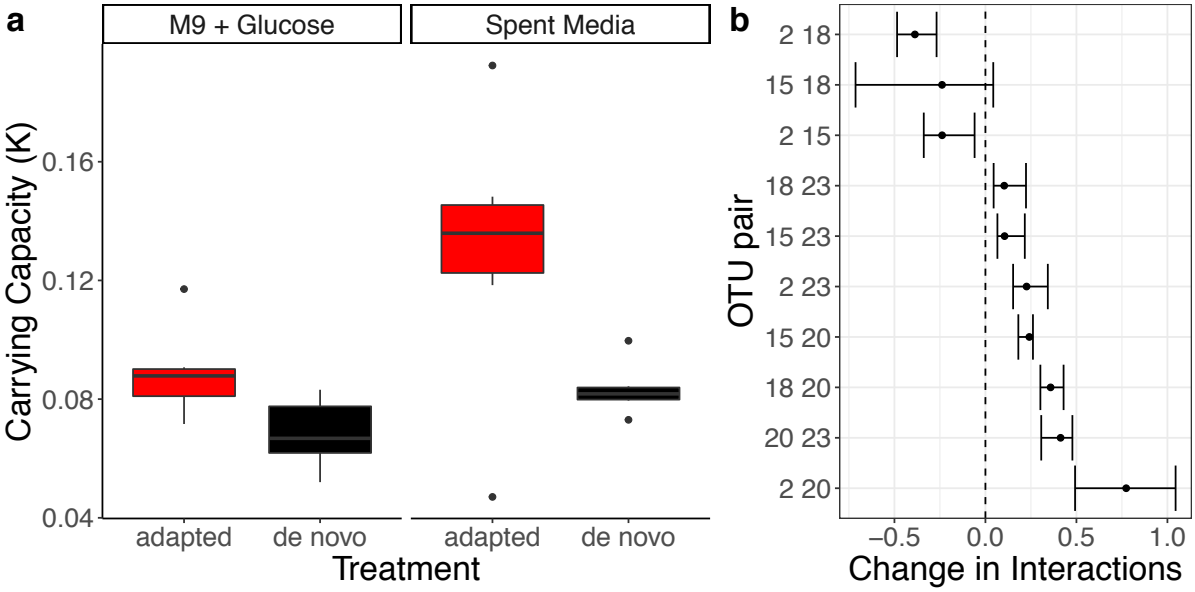

Fig 3. Emergence of facilitation in assembled microbial communities. (a) Carrying capacity of the adapted and de novo assembled communities grown in either M9+glucose or spent media for 72 h at 20°C (Extended data Table 2). (b) Change in interaction strength between pairwise combinations of taxa from the de novo to adapted communities in the M9+glucose. Each row shows the average and 95% bootstrapped confidence intervals of the estimated change in interactions for each pair. Negative values indicate interactions have become more competitive while positive values indicate that interactions have become more facilitatory. The interactions become predominantly more facilitatory (70% of the cases), with $\overline{a}$ changing from -0.07 in the de novo to 0.065 in the adapted communities.

Next, to establish that the observed increase in asymptotic biomass of adapted relative to de novo communities is indeed driven by a shift towards facilitative interactions, we performed an additional laboratory experiment to quantify the change in the direction and magnitude of the pairwise interactions after adaptation. We first grew isolates of each taxon before and after adaptation for up to 72 h (depending upon when they reached carrying capacity) at 20°C in M9+glucose and the spent media, as well as all possible pairwise combinations of taxa. We then estimated pairwise interaction strengths using a measure based on the comparison of growth rates in mono- versus bi-culture, combined with bootstrapping to determine statistical significance (see Methods). When grown on M9+glucose media, interactions became predominantly positive (facilitatory) following adaptation (Fig. 3b). When the same experiment was attempted in the spent media, most of the mono- and bi-cultures either did not grow or went extinct, despite the whole communities being able to coexist under these conditions. This indicates that, as expected, the community context was required for these populations to be able to utilize the spent media. This point can be made more exact by considering the Lotka-Volterra equations (see Methods). The experiments indicate that the population growth of monocultures in spent media was negative, such that growth plus the effects of density dependence were negative, i.e., $r_i - a_{ii}C_i < 0$. The joint population growth is still negative in bi-culture because the effect of positive pairwise interactions is still not enough to allow persistence. In contrast, the whole community's growth is positive where all interspecies interactions are present, i.e., $r_i - a_{ii}C_i + N\overline{a}\overline{C} > 0$. Taking both these constraints, it follows that the net effect of interactions must be positive to outweigh the negative intrinsic growth rates and that $\overline{a} > 0$ in the assembled communities, consistent with our estimates of the pairwise interaction coefficients.

We also tested the possibility that a change in the interaction structure favoring populations with higher thermal sensitivity (i.e. an increase in the covariance term in Eq. 3) was responsible for the

amplification of community respiration by looking at the relationship between the population level thermal sensitivity values and the estimated interaction coefficients. We found no relationship between the two either before or after adaptation indicating that the covariance term contributed relatively little to the overall community sensitivity (Extended data Figure 7). Altogether, these results provide strong evidence that a change in pairwise interactions that drove the amplification of ecosystem respiration in the experiments.

Overall, our results suggest that in general, nonlinear species interactions drive changes in the thermal sensitivity of microbial community respiration through their effects on the species' biomass dynamics. This change occurs in a predictable way, allowing characterisation of the relationship between the average interaction strength in the community and the thermal sensitivity of respiration. That changes in the nature (direction and strength) of microbial species interactions can so profoundly alter the temperature sensitivity of community-level respiration has far-reaching implications given the significant contributions that microbial communities make to overall ecosystem functioning across both aquatic and terrestrial realms. Indeed, microbial communities tend to be biased towards either competitive or facilitatory interactions across space[24], or over time (especially, during assembly[19,29]), which means that they can either dampen or amplify the effects of temperature change on their carbon cycling services. For example, changes in interaction structure over time due to longer-term assembly and turnover dynamics could mean that the same microbial community could switch between states that dampen (when competition dominates, at early stages of community assembly) and amplify (with facilitation dominates, in later states of community assembly) the sensitivity of ecosystem functioning to temperature change. In particular, microbe-mediated decomposition of organic matter, which is a key component of CO_2 and CH_4 fluxes in the carbon cycle, depends on facilitation among diverse consortia of prokaryotes. Our finding that facilitation among microbes amplifies the temperature sensitivity of community metabolism may help explain the relatively high thermal sensitivity seen in microbe-dominated methane-decomposing communities[31].

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Data Availability

All data is available to download in the git repository at https://github.com/CleggTom/TemperatureAmplification.

Code Availability

Code used for analysis of lab experiments is available to download from the git repository at https://github.com/CleggTom/TemperatureAmplification

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Author Contributions: G.Y-D and S.P. conceived the study; F.G. and G.Y-D designed the lab experiments; F.G., R.W. and D.B.O carried out the lab experiments, T.C and S.P derived and analysed the theoretical model; all authors conducted the analysis of the experimental data and wrote the manuscript.

Competing interests The authors declare no competing interests

Additional Information

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