Climate Change Factors Interactively Shift Peatland Functional Microbial Composition in an Ecosystem Warming Experiment

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Microbes both affect the global carbon cycle that influences climate change, and are in turn influenced by environmental change. Here, we address how this happens using data from a long-term whole-ecosystem warming experiment at a boreal peatland to answer how temperature and CO_2 jointly influence communities of abundant, diverse, yet poorly understood non-fungi microbial Eukaryotes (protists). These microbes influence ecosystem function directly through photosynthesis and respiration, and indirectly, through predation on decomposers (bacteria, fungi). Using a combination of high-throughput fluid imaging and 18S amplicon sequencing, we report large climate-induced, community-wide shifts in the community functional composition of these microbes (size, shape, metabolism) that could alter overall function in peatlands. Importantly, we demonstrate a taxonomic convergence but a functional divergence in response to warming and elevated CO_2 but most environmental responses are contingent on organismal size, such that warming effects on functional composition are reversed by elevated CO_2 and amplified in larger microbes but not smaller ones. These findings show how the interactive effects of warming and rising CO_2 could alter the structure and function of peatland microbial food webs — a fragile ecosystem that stores 25% of terrestrial carbon and is increasingly threatened by human exploitation.

climate change | microbial diversity | community ecology | functional traits
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Introduction

Greenhouse gas emissions set the pace of climate change (1) and most ecosystems on Earth influence this process by serving as carbon (C) sources or sinks (2). Overall, terrestrial ecosystems mitigate ≈30 % of anthropogenic CO_2 emissions (3, 4). The predominant terrestrial carbon sink — peatlands — store 100% more carbon than all forests while covering less than 3% of the globe (5–8). *Sphagnum* mosses dominate peatlands (9) and are responsible for most C sequestration in the form of recalcitrant peat (10). They harbor diverse communities of single-celled (*i.e.,* bacteria, archaea, protists) and multi-celled (*i.e.,* fungi, metazoa) organisms (11) that influence C cycling directly (12, 13), through respiration of $\approx 100\ \mathrm{Pg \cdot C \cdot yr^{-1}}$ in soils alone (14, 15), and indirectly, by supplying nitrogen needed for *Sphagnum* moss growth (16–18), converting methane into CO_2 necessary for photosynthesis (19–21), providing stress tolerance to the host mosses (22, 23), and assisting in host-pathogen defense (24). How ecological interactions with other members of the moss-associated community modulate the effects of these microbes on peatland C cycling (25–27), is poorly understood. Predation by metazoans plays a prominent role in peatland C cycling (28), so it is likely to also impact microbial communities. Unicellular Eukaryotes collectively known as protists store 2× more C globally than all animals combined (29, 30), contribute to C cycling through mixotrophic metabolism (31), and also serve as one of the principal biological controls on microbial respiration and photosynthesis through predation and competition (32–34). Protists also directly influence plant growth and health through their effects on the rhizosphere (32, 35, 36) and phyllosphere (37, 38) — thus indirectly modulating plant growth through their effects on beneficial microorganisms (39, 40). In turn, climate effects can induce changes in moss microhabitat that affectpredation, resource acquisition, and life cycles of associated protists(31).

But how the structured and function of protist communities may respond to climate change in peatlands, is not known. Simple protist functional traits — *i.e.*, characteristics controlling how organisms respond to the environment or affect ecosystem properties (41) — such as cell size, cell shape, and cellular contents can be used to predict warming effects on protist communities and ecosystem function because of underlying links to metabolism and respiration rates is unknown (42). By quantifying changes in functional traits of these protist communities, in addition to changes in abundances, biomass and composition, we can infer changes in their ecological function and impacts in peatland C cycling. For example, metabolic demand and total respiration rates increase with increasing temperature, favoring smaller organisms (43, 44) with a shape (long and slim) that maximizes energy intake and minimizes energetic costs (45, 46). Increased metabolic demands can impact resource acquisition strategies (e.g., increased heterotrophy over autotrophy) (47–50), resulting in measurable changes in cellular optical properties such as red/green color ratio or the heterogeneity of gray-scale values, which have been linked to cellular contents and cell viability (51, 52). Consequently, changes in functional composition could alter net C fluxes and other elements within peatlands (53–56).

Here, we address how peatland protist communities —— op-

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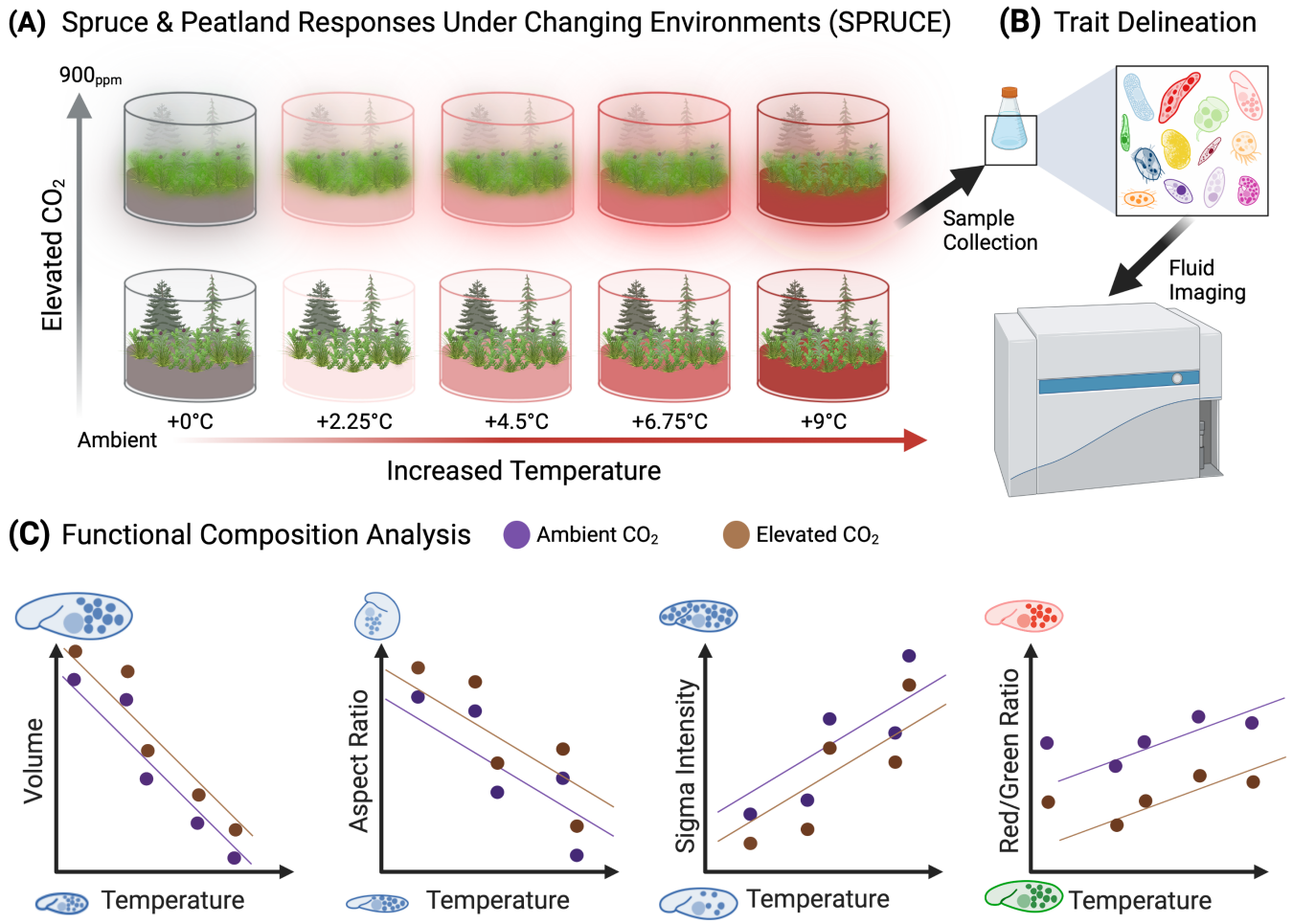

Fig. 1. (A) Samples were collected in a 2-factorial mesocosm design in boreal peatlands with variation in temperature (+0, +2.25, +4.5, +6.75, +9℃) and CO_2 (+0 PPM, +450 PPM) concentrations. Protist samples were collected from the upper peat layer within each treatment and processed *ex situ*. (B) After incubation (24 hours in climate-controlled growth chambers, Carolina protist liquid media, 22℃ and 65% humidity), samples were analyzed via fluid imaging to quantify abundances across treatments and physical and optical functional traits. (C) Functional composition data hypothesized on first-principles of metabolic and ecological theory. We anticipate decreases in size (e.g., volume), shape (e.g., aspect ratio), and cellular contents (e.g., sigma intensity) under warming, with an increase in red/green ratio (e.g., photosynthesis). Under elevated CO_2 we expect larger cell volumes, more roundedness, increased cellular activity, and lower red/green ratios.

erationally defined here as the community of all non-fungal Eukaryotes —— change in novel climates. We quantify shifts in abundance, biomass, taxonomic composition, and functional trait composition in a peatland long-term whole-ecosystem experiment with temperature and CO_2 manipulations of living moss and superficial peat: the SPRUCE long-term whole-ecosystem warming experimental site (57) (Fig. 1A). We quantified protist abundance, biomass, and community functional traits through fluid imaging and used 18S rRNA gene sequencing to infer mechanisms of change in observed protist community functional trait composition (e.g., through taxonomic shifts or plasticity). We test the hypotheses that increasing temperatures lead to: (1) a decrease in protists' body size — i.e., the temperature-size rule (43, 45), (2) an increase in surface-to-volume ratio (aspect ratio), as protists optimize shape to increase energy uptake (surface) and reduce metabolic costs (volume) (58), (3) an increase in cellular optical heterogeneity (or cellular "contents"), as temperature-induced increased metabolic rates requires more cellular machinery (59), and (4) increased heterotrophy (increased red/green ratios) to keep up with metabolic demands. Additionally, we expect elevated CO_2 to result in an increase in total community biomass (60, 61) as more CO_2 fuels photosynthesis at the base of the food web.

This CO_2 driven increase in energy availability at the base of the microbial food web should also result in: 1) an increase in protist volume in response to more energy availability (Fig. 1C), 2) an increase in aspect-ratio as increased available energy releases cells from shape metabolic constraints, 3) an increase in sigma-intensity, due to increased production of cellular machinery to process available energy, and 4) an increase in autotrophy (measured as decreases in the red/green ratio of cells) relative to heterotrophy (43, 62, 63). We show that warming and CO_2 have significant, negative interactive effects, on the taxonomic and functional composition of peatland protist communities that is in turn dependent on organismal size and could result in important consequences for C cycling in peatlands.

Materials and Methods

A. Study Site and Field Sampling. The study site is within the S1-Bog of the Marcell Experimental Forest (47° 30.4760′ N, 93° 27.1620′ W; 418 m above mean sea level), MN, USA. It sits on the southern edge of the temperate boreal forest range in North America, with a sub-humid continental climate. The S1-Bog — above a water table with marginal groundwater influence — consists of an ombrotrophic peatland dominated by a forest canopy of black spruce (*Picea mariana*) and tamarack (*Larix laricinia*). Understory plants are mixture of ericaceous scrubs, herbaceous sedges and grasses, and a bryophyte layer dominated by *Sphagnum* spp. mosses. Mosses are distributed in hollows (*S. angustifolium* & *S. fallax*) and in drier hummocks (*S. divinum* previously called *S. magellanicum* and *S. fuscum*). Other bryophytes include feather mosses (*Pleurozium* spp.) and haircap mosses (*Polytrichum* spp.). For further description of the site and below-ground peat profile, see (64) and (65).

The *P. mariana–Sphagnum* spp. raised bog experimental ecosystem consists of open-top chambers 12m in diameter in a factorial design of ambient +0 ppm and +450 ppm CO_2 treatments across ambient (+0, +2.25, +4.5, +6.75, +9°C soil (initiated June 2014) and air (initiated June 2015) warming treatments (Fig. 1; (64)). We collected superficial samples (1-5 cm) from SPRUCE containing living plant tissue and superficial peat from two sub-plot locations. We placed the samples in individual sterile bags and over-night shipped them to Durham, NC for imaging of protist communities while additional samples were flash-frozen and over-night shipped to Oak Ridge, TN for DNA extraction and 18S amplicon sequencing. Upon reception of samples for imaging, we removed the material from sterile bags and transferred samples to Carolina protist media (Liquid Protozoan Nutrient Concentrate; 13-2350) through glass funnels. We collected the discharge from the funnels in 250 ml glass jars and kept the cultures at 22°C and 65% humidity for 24 hours before fluid imaging.

B. Density and Biomass. Protist wer operationally defined in this study as all non-fungal unicellular Eukaryotes. Their densities were estimated as simple counts ($\hat{E}$) of the number of imaged particles per volume analyzed using fluid imaging with a FlowCAM (Yokagawa Fluid Imaging, USA) of 6 mL water samples from incubated jars at 10× magnification. This estimate accounts for the FlowCam efficiency, which screens roughly 75% of the sampled volume. Biomass was estimated using efficiency-corrected measurements of total protist volume (see supplementary materials).

C. Trait Measurements. We quantified functional traits (Table S1) by manually curating the ensuing cell images in Visual Spreadsheet software program (Yokagawa Fluid Imaging, USA), discarding all non-protist images, and retaining only high-quality protist images for trait quantification. All protist images (n = 211,039), regardless of quality, were kept for abundance estimations). To test our hypotheses about size, shape, cellular contents, and energy acquisition mode, we selected four traits (volume, aspect ratio, sigma intensity, red/green ratio) representing these functional trait categories from a larger set of 37 physical and optical functional traits of possible proxies by eliminating highly correlated and co-linear traits (see supplementary materials; Table S1, Fig. S1A). Further, (42) found these four traits to be significantly correlated with temperature performance curves (TPCs) of protists and their metabolic functioning.

D. Analyses. We tested the effects of temperature and CO_2 levels on the abundance and biomass of the protist communities with generalized additive models (GAMs) and used generalized linear models (GLMs) to test for effect on the traits. To test hypotheses 1-4, we first clustered individual cellular observations into size classes based upon the natural log of protists' geodesic length (e.g., longest axis) using Gaussian finite mixture modelling with the R package *mclust* (66). We chose length as it was less correlated with the traits of interest and would reduce co-linearity in our models between the size class cluster and the functional traits (Fig. S2). We selected an optimal set of five size classes with a Gaussian mixture model and Bayesian Information Criterion (BIC) (Fig. S3). We then ran GLMs for each functional trait against size class (factor), temperature (continuous), and carbon dioxide level (factor). Associated Pearson correlation coefficients and p-values were obtained via the *ggpubr* R package (67) and are reported for each size class (Fig. S4). Additionally, we examined changes across environments in the estimated abundance and biomass (grams) of the community per size class with GAMs (k = 5) using the R package *mgcv* (68), reporting associated Pearson correlations and p-values for each size class (Fig. S5).

E. Amplicon Sequencing. To understand the possible mechanisms behind observed changes in abundance, biomass and functional traits, we extracted genomic DNA from our samples with the DNeasy 96 Plant Kit (Qiagen) and amplified the V4 region of the 18S rRNA gene following (69). Samples were multiplexed, pooled and sequenced on an Illumina MiSeq instrument with paired end kit (2 x 251). We processed protist sequences with the QIIME 2 v 2021.2 platform. Paired sequences were demultiplexed with the plugin demux, quality filtered (denoised, dereplicated, chimera filtered and pair-end merged), and processed in Sequence Variants (SVs) with the dada2 plugin (70). Taxonomy followed the Pr2 (18S) database (71) and sequences assigned as "bacteria" or Embryophyceae were removed. We used sequence variants to calculate alpha diversity as counts and the Shannon diversity (calculated beta diversity) and compositional dissimilarity, or Bray-Curtis distance, with the phyloseq package (72).

Results

Experimental manipulations of temperature and CO_2 levels induced an 80-fold change in total observed protist abundance (F = 2.2554; p = 0.02244, Fig. S5A) and in biomass (F = 2.2504; p = 0.02273, Fig. S5B) across treatments (Fig.

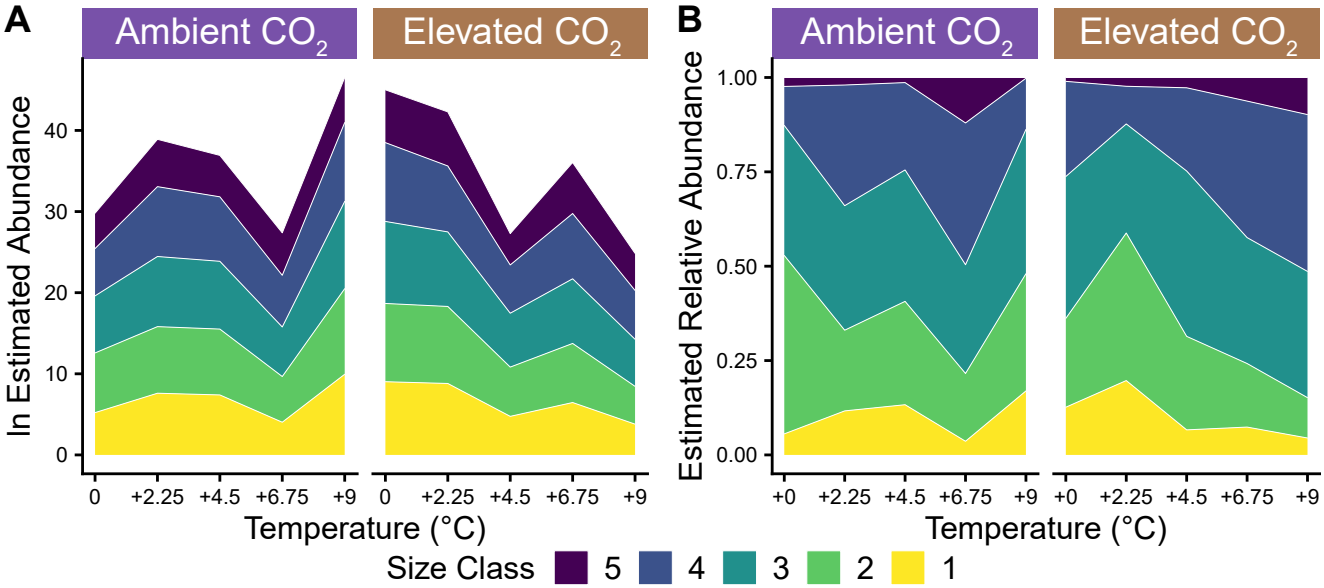

Fig. 2. Estimated protist abundances. (A) Estimated total abundance data on the natural log scale for size classes across temperatures under ambient and elevated CO_2 treatments. Data indicates that abundances increase across size classes with temperature under ambient CO_2 levels but decreases under elevated CO2 levels. (B) Relative abundance of size classes by CO_2 treatment calculated from total estimated abundance (A) across temperatures. Results show that different size classes respond differentially to environmental treatments. Size Class 1: 12.43 μm - 17.07 μm; Size Class 2: 17.07 μm - 20.68 μm; Size Class 3: 20.68 μm - 28.24 μm; Size Class 4: 28.24 μm - 59.74μm; Size Class 5: 59.74 μm - 526.43 μm.

2A), as well as a shift in the relative dominance of size classes (Fig. 2B). Across all body size classes, protist abundance and biomass increased with temperature under ambient CO_2 (Fig. 2A). This trend reversed under elevated CO_2, with major declines in biomass and abundance across size classes (Fig. 2A). The proportion of abundance within size classes remained relatively consistent with increasing temperature under ambient CO_2 conditions; however, under elevated CO_2 conditions, the relative proportion of larger protists increased at the expense of the two smallest size classes (Fig. 2B).

A three-way interaction between temperature, CO_2 concentration, and size class drove significant changes in the functional trait composition of protist communities (Fig. 3): size (F = 4,007; $p \ll 2.2x10^{-16}$); shape (F = 13,204; $p \ll 2.2 \times 10^{-16}$); cellular contents (F = 789.05; p $\ll 2.2x10^{-16}$); and energy acquisition (F = 657.15; p $\ll 2.2x10^{-16}$). The magnitude of the change was driven by the CO_2 treatment, with elevated CO_2 rates of change outpacing that of ambient CO_2 by up to a factor of 25 (Fig. 3). Under ambient CO_2, protists were smaller (Figs. 3A, S6), less round (Figs. 3B, S7), showed more cellular contents (Figs. 3C, S8), and became redder (more heterotrophic) at lower levels of warming but greener (more autotrophic) at higher levels of warming (Fig. 3D, Fig. S9). Conversely, protists under elevated CO_2 were larger (Fig. 3A, S6), rounder (Fig. 3B, S7), had fewer cellular contents (Fig. 3C, S8), and got redder (Fig. 3D, S9). Thus, with the exception of the two smallest size classes for red/green ratio, protists displayed inverse patterns for all traits in response to increasing temperature under ambient and elevated CO_2 levels.

Some of these functional responses are at least in part mediated by protist size, as protist volumes rate of change with warming was strongly size-dependent (Fig. S10A, ($0.014 < p < 0.066$), c.f. (44)); larger size classes responded more strongly to temperature than smaller ones. While the rates of change in all traits display interesting non-linear size-dependency, we found weaker support for allometry in shape, cellular contents, and energy acquisition (Fig. S10B-D).

Observed changes in community functional trait values could be the result of plastic change across all or most protists in the community, or taxonomic compositional shifts that led to communities whose functional traits differed from the original ones. Amplicon sequencing results show that important taxonomic shifts (Fig. 5A) underlie the observed changes in functional traits (Fig. 4). Increasing temperature leads to a decrease in the diversity of microbial communities (Fig. 5B,C) — consistent with multiple studies across biomes that find climate change decreases diversity of species across scales (73–75). Importantly, temperature interacts with CO_2 such that the effects of CO_2 treatment decrease at warmer temperatures, leading to a near convergence in the taxonomic compositional similarity between ambient and elevated CO_2 as Bray-Curtis dissimilarity decreases rapidly (Fig. 5D), despite a dramatic divergence in functional traits (Fig. 2).

Discussion

Understanding how moss-associated microbial communities change with temperature and CO_2 concentrations is vital for predicting how peatland ecosystems will respond to climate change (7, 76, 77) and alter the global C cycle (78–80). Here we find strong evidence of changes in the abundance, biomass, functional traits, and composition of important but poorly understood members of peatland microbial communities. These changes are driven by an interaction

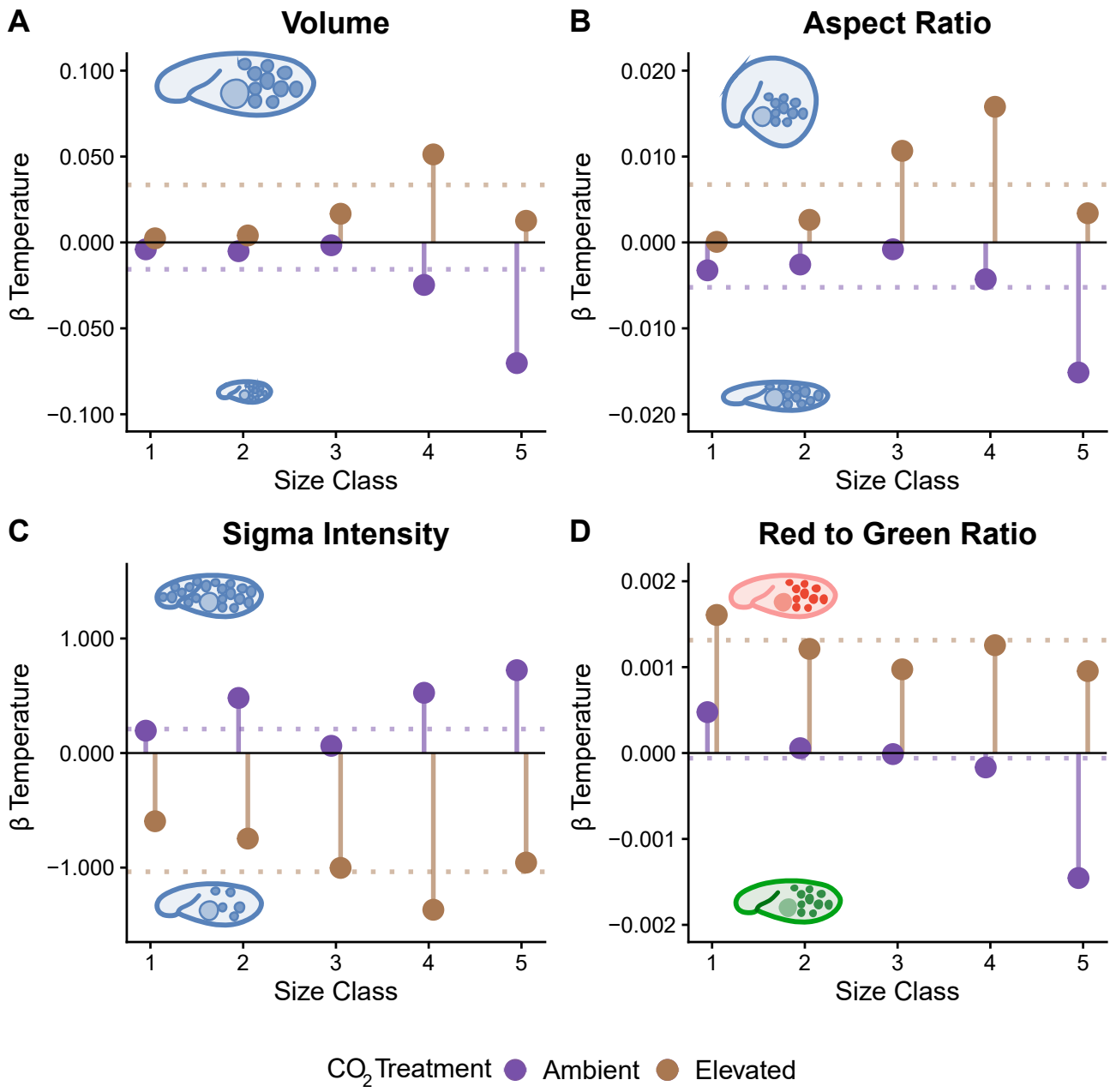

Fig. 3. Rate of change across temperatures (β or slope) for functional traits by protist size class and CO_2 treatments (lollipops). Slopes were calculated from GLMs. Mean slope across size classes displayed as dashed line. Positive slope values indicate: (A, Volume) increasing size; (B, Aspect Ratio) higher symmetry and roundedness (shape); (C, Sigma Intensity) higher optical heterogeneity; and (D, Red/Green ratio) increasing redness and/or decreasing greenness.

between warming and CO_2 concentration (Figs. 2-4). We show that peatland protist communities are sensitive to climate change, and under ambient CO_2 match our expectations based upon metabolic theory — getting smaller, less round, more active, and more heterotrophic. However, these trends are reversed by elevated CO_2 concentrations (Fig. 3), and the magnitude and direction of these changes are driven by non-linear size-dependence (Fig. S10). While protist communities converge in taxonomic composition between ambient and elevated CO_2 levels as temperature rises, they diverge in functional trait composition, suggesting important but yet unknown effects on peatland function with environmental change.

Protist reductions in volume (Figs. 3A, S6) and roundedness (Fig. 3B, Fig. S7) observed under ambient CO_2 and elevated temperatures was predicted from metabolic theory, and this suggests that we can anticipate complex temperature responses in natural and intricate microbial communities based on first principles. For example, temperature selects for smaller organisms and/or organisms with larger surface-to-volume ratio that can meet higher metabolic demands while conserving resources as metabolism costs increase at higher temperatures (81). This negative relationship between size and temperature —the "temperature-size rule" (43, 45)—is

well documented for both single-celled (43) and multi-celled organisms (82–84), but was so far thought to be a plastic response.

Here, we show that the temperature-size rule can result from community composition shifts that select for smaller organisms (Fig 3). Similarly, shape shifts (e.g., a decrease in roundedness with temperature) likely results from selection to conserve energy by simultaneously reducing volume (which increases metabolic costs), and increasing surface (which increases resource acquisition) (85). Changes in protist shape and size have multiple ecological consequences, including population dynamics and ecological interactions within communities (34, 42, 86), as well as total respiration, which decreases with volume (87). Shifts in size and shape can occur quite rapidly and can be as dramatic as 50% or more (62, 88). Likely, species that cannot rapidly respond to temperatures are replaced by those that can, leading to high species turnover (Fig. 4).

Counter to our hypothesis, we report surprising reversals in functional trait change with temperature between CO_2 treatments (Figs. 3, 4, S6-S9) suggesting that joint temperature and CO_2 impacts in microbial food webs may be more com-

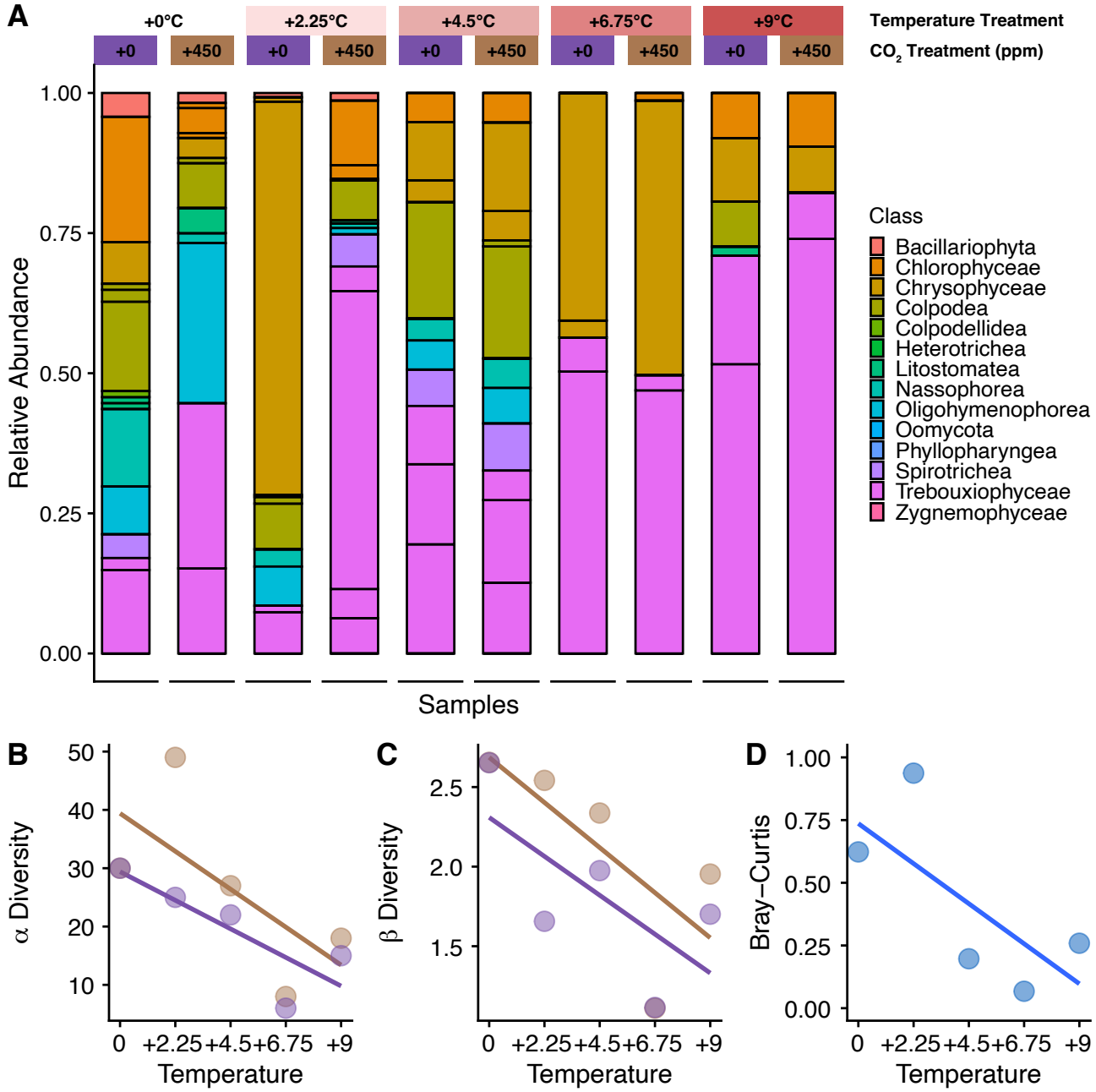

Fig. 4. Change in (A) protist Order relative composition (colored by Class) and (B, C) diversity of protist community across temperatures and CO_2 treatments. (A) Protists' Order composition (colored by Class) shifts both with temperature increase and within CO_2 treatment, with a decrease in (B) total species composition and (C) species diversity at higher temperatures. (D) Species composition becomes more homogeneous—lower Bray-Curtis distance—between CO_2 treatments at higher temperatures, indicating an interactive effect (pearson's correlation = -0.71).

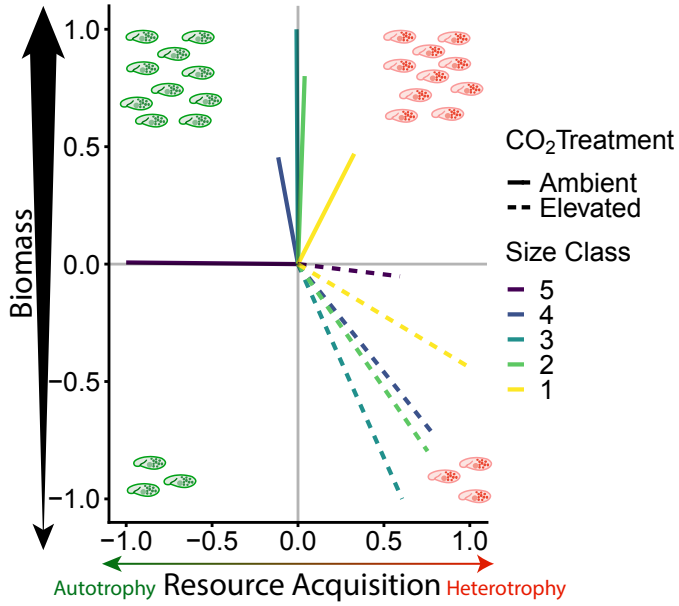

Fig. 5. Combined normalized change in biomass and resource acquisition across quadrant (I-IV) outcomes. Under elevated CO_2, the increase in respiration is offset by a loss in biomass of these organisms (IV). Given normalization of difference, slopes $\leq$ -1 indicate a net reduction in heterotrophy. Under ambient CO_2 conditions, an increase in net photosynthesis occurs for the two largest size classes (II), as both biomass and green reflectance increase. The net carbon dynamics in these plots may be offset by the normalized relative increase in biomass of the more heterotrophic smaller size classes (I).

plex than previously thought. Interactive effects of CO_2 and temperature have been reported in aquatic phytoplankton systems (60, 61, 89). However, these systems only displayed shifts in trait change magnitudes, not complete trend reversals as reported here. Our results thus emphasize the importance of addressing temperature impacts on microbial organisms in the light of simultaneous CO_2 increases. This trend reversal may be due to CO_2-induced pH changes of the peat and/or the stoichiometry of diffusion under higher temperatures and elevated CO_2. Experimental work on ocean phytoplankton showed that rising temperatures and elevated CO_2 can induce a more rapid decrease in community biomass and chlorophyll-a concentration (90), and that elevated CO_2 may lessen the demand for a higher surface-to-volume ratio as diffusion becomes easier across the cellular membrane at higher concentrations of dissolved CO_2. These changes may also be due to the increased efficiency of heterotrophic resource acquisition compared to photosynthesis (91). The shift towards heterotrophic resource acquisition (Fig. 3D) under elevated CO_2 conditions may lessen the need for energy conservation.

These reported trend reversals under elevated CO_2 may also occur indirectly, through changes in nutrient cycling and mineralization (92)—especially of N (93). Elevated CO_2 often increases the exudation of soluble organic compounds by *Sphagnum* mosses (94)—especially sugars—that contribute to the structure of microbial communities, and can increase the abundance of bacteria and heterotrophic protists (95). With higher abundances of bacteria, protists may obtain more energy through predation. (96) recently found similar interactive effects of warming and elevated CO_2 on N. Elevated temperature and ambient CO_2 conditions produced accumulation of nitrogen and a reduction in N_2 fixation, which was reversed under elevated CO_2 conditions. This in turn altered N immobilization by micro-organisms, likely leading to a change in microbial food web dynamics. Elevated CO_2 may also indirectly increase nitrogen availability through changes in *Sphagnum* exudation of C and N organic compounds (26, 97)—indirectly influencing N-releasing enzymes (98, 99)—or through symbiosis with mycorrhizal fungi (100, 101).

The trend reversal reported here (biomass, abundance, traits) was size-dependent(Fig. S10). We find strong support for a super-linear scaling relationship between body size and volume that indicates protist populations might undergo density-dependent (population) and density-independent (individual phenotypic) responses to climate change (42, 62, 88, 102, 103). Our results indicate a significant relationship between proportional changes in traits and size. Larger protists' size (Fig. S10A) and shape (Fig. S10B) change more than smaller protists per unit volume (Figs. S10A, S10B). Cellular contents follow a sub-linear size-dependency (Fig. S10C). Because smaller protist phenotypes shift much less and these smaller individuals dominate the relative abundance of the system (Figs. 2B, S3B), there may be embedded resistance to phenotypic change in these communities overall. This trend portends potential eco-evolutionary responses of protists under environmental stressors, as phenotypic traits and plasticity may drive the success and survival of individuals responding to changing metabolic demands (104, 105).

Our findings suggest important ways in which climate change may influence C cycling in peatland ecosystems by potentially altering important functional linkages within moss-associated microbial food webs (106). Given the diverse energy acquisition strategies of protists, changes in the balance of autotrophy versus heterotrophy can have cascading effects on the biological carbon cycle (107–110). Due to their predominant distributions in mid- and high-latitudes of the Northern hemisphere, peatlands are especially sensitive to climate change (111–114). The increase in the red/green ratio of 70% of size classes in our study (Figs. 6, S9) may be alarming. A decrease in the red/green ratio is as-

sociated with decreased autotrophy and therefore carbon uptake (115). However, when we normalize the β coefficents of our models, the overall increase in heterotrophy is outweighed by a decrease in biomass of heterotrophic organisms and an increase in biomass of putatively photosynthetic organisms, likely indicating a net reduction in heterotrophy (Figs. 5, S9). While tantalizing, these data-driven hypotheses need to be explicitly tested, but are suggestive of important ways in which environmental change both influences and is influenced by rapid microbial responses in functional trait composition in globally important—and highly threatened—ecosystems like peatlands.

AUTHOR CONTRIBUTIONS

CLK and JPG conceptualized the study. AC, DAP and DJW collected SPRUCE samples. SV, AY and JPG prepared the samples and extracted protist data. AAC prepared and provided amplicon sequencing data. CLK performed all analyses with support from DJW, AC, and JPG. CLK wrote the first draft and all authors contributed substantially to subsequent versions.

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COMPETING INTERESTS

The authors report no competing interests.

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