Climate warming accelerates temporal scaling of grassland soil microbial biodiversity

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Climate warming accelerates temporal scaling of grassland soil microbial biodiversity

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Determining the temporal scaling of biodiversity, typically described as species–time relationships (STRs), in the face of global climate change is a central issue in ecology because it is fundamental to biodiversity preservation and ecosystem management. However, whether and how climate change affects microbial STRs remains unclear, mainly due to the scarcity of long-term experimental data. Here, we examine the STRs and phylogenetic-time relationships (PTRs) of soil bacteria and fungi in a long-term multifactorial global change experiment with warming (+3 °C), half precipitation (−50%), double precipitation (+100%) and clipping (annual plant biomass removal). Soil bacteria and fungi all exhibited strong STRs and PTRs across the 12 experimental conditions. Strikingly, warming accelerated the bacterial and fungal STR and PTR exponents (that is, the *w* values), yielding significantly ($P < 0.001$) higher temporal scaling rates. While the STRs and PTRs were significantly shifted by altered precipitation, clipping and their combinations, warming played the predominant role. In addition, comparison with the previous literature revealed that soil bacteria and fungi had considerably higher overall temporal scaling rates ($w = 0.39$–0.64) than those of plants and animals ($w = 0.21$–0.38). Our results on warming-enhanced temporal scaling of microbial biodiversity suggest that the strategies of soil biodiversity preservation and ecosystem management may need to be adjusted in a warmer world.

One of the fundamental goals in ecology is to determine how biodiversity is generated and maintained across space and time. Understanding the spatial and temporal distribution patterns of biodiversity is central to determining the underlying mechanisms shaping biodiversity[1], the development of ecological theories[2] and biodiversity conservation[3,4]. One of the most well-documented spatial patterns in ecology is that the number of species or taxa observed increases with the area investigated, that is, the species–area relationship (SAR) or taxa–area relationship (TAR)[4–6]. The SAR has been well documented in hundreds of publications[5] and has provided a conceptual foundation for theoretical ecology and important tools for assessing species diversity[7], extinction rates[8] and species hotspots[9]. Since the last decade, spatial scaling of microbial diversity has attracted substantial attention[4,10,11]; great insights were obtained in terms of the scaling factor (*z* values) and underlying mechanisms[4,6,10,12]. Various studies demonstrated that SAR exists in microbial communities; hence, SAR appears to be a universal law in ecology[4,10,11,13,14].

Similar to SAR, STR is also believed to be a fundamental pattern in ecology[3]. More than 40 years ago, it was proposed that the number of species observed in a fixed area increases with the length of time, which could follow the same form as SAR[13,15]. This increase in species richness is theoretically explained by ecological processes such as successional changes, climatic variability, metapopulation dynamics, random sampling processes and/or their combinations[16,17]. However, despite extensive studies in SAR, STR has received much less attention[17–19], particularly in microbial ecology[11,13], owing to the scarcity of long-term data sets. As a result, it is not clear whether STR exists or if it is a universal pattern in microbial ecology. Also, phylogeny-based spatial and temporal patterns are necessary for setting conservation areas and periods that optimize the preservation of evolutionary history[2,20–22], and are more powerful for testing biodiversity theory[2,23]. However, there are only a few recent studies demonstrating the existence of phylogenetic analogues of the SAR based on phylogenetic diversity, that is, phylogenetic–area relationship (PAR) in macrocommunities[2,19]. Almost nothing is known about PTR except one recent study in plant ecology[19]. Thus, there is a major gap given that STRs and PTRs are needed for soil biodiversity preservation and ecosystem management, especially in the face of climate change.

One of the greatest scientific and political challenges of the twenty-first century is to predict biological responses to climate change[24,25]. Under climate change, the surface temperature of earth has increased by 0.76 °C in the past 150 years and is expected to increase by another 1.1–6.4 °C by the end of this century, signifying the largest anthropogenic disturbance to natural systems on record[24,26]. Consequently, global and regional temperatures and precipitation patterns are predicted to shift dramatically inducing

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extreme weather events, which will profoundly affect ecosystem functions and services[24,26]. All levels of biological organization, from individuals to whole biomes, will be affected by climate change[25,26]. In turn, the feedback responses of ecosystems affect climate and atmospheric composition[24,26]. Therefore, global climate change is expected to alter the spatial and temporal scaling of ecological communities[27]. During the last two decades, intensive studies have been performed to examine ecosystem responses to changes in climate warming, precipitation and land use patterns[24,28]. However, whether and how global climate change affects the temporal scaling (that is, STR and PTR) of biodiversity remains unclear.

Based on the metabolic theory of ecology (MTE), rising temperature should have profound effects on the temporal scaling of biodiversity. MTE predicts that the metabolism of organisms, population growth rates and species diversity increase exponentially with environmental temperature[29–31]. Therefore, it is expected that climate warming will increase the rates of ecological and evolutionary processes[30], including the rates of genetic mutation, speciation and interactions. Accordingly, temporal scaling rates (that is, the STR and PTR w values) of soil microbial communities should increase under future climate warming. Furthermore, based on MTE[29], the temporal scaling rates of microbial communities are expected to be higher than plants and animals due to their smaller body sizes and much higher metabolic rates than macroorganisms. However, higher temperatures may act as a deterministic filtering factor to select more adapted microorganisms, and further constrain the stochastic drift and dispersal of species in niche-based theory[32,33]. Therefore, in contrast to MTE, climate warming could decrease the temporal scaling rates of soil microbial communities.

To understand whether and how climate warming affects STR and/or PTR in soil microbial communities, we examined the temporal scaling of soil microbial communities in a multifactorial global change experiment in a tall grass prairie ecosystem of the US Great Plains in central Oklahoma (34° 59′ N, 97° 31′ W)[34]. Our main objectives were to answer the following: (1) whether STRs and PTRs exist in soil microbial communities and if they are universally applicable to different organismal groups (that is, bacteria and fungi); (2) whether and how key climate change factors, that is, warming, alter precipitation and clipping influence in microbial STRs and PTRs?; (3) whether soil microbial STR and PTR w values are like those for plants and animals. We hypothesize that STRs and PTRs exist in both bacterial and fungal communities, that climate warming accelerates the scaling rates of both taxonomic and phylogenetic diversity and that soil microbial temporal scaling rates are in general larger than those for plants and animals.

Results and discussion

Site characteristics and sequencing statistics. We used a long-term climate change experiment established in July 2009, with a blocked split-plot design, where warming (+3 °C), half precipitation (−50% precipitation) and double precipitation (+100% precipitation) are primary factors nested with clipping (annual removal of above-ground biomass) as a secondary factor (Supplementary Fig. 1). Previous analyses showed that above-ground plants, ecosystem processes and soil conditions were significantly changed under warming and other treatment conditions[34–36]. Temporal alterations in soil variables and plant–soil feedbacks are expected to lead to changes in the temporal scaling of soil microbial diversity[37,38]. To discern whether climate warming and other treatments affect STRs or PTRs in soil bacteria and fungi, a total of 264 soil surface samples (0–15 cm) from 2009 to 2014 were analysed with two different phylogenetic markers: (1) the V3-V4 region of 16S ribosomal RNA (rRNA) gene for bacteria and archaea; and (2) the internal transcribed spacer (ITS) between the 5.8S and 28S rRNA genes for fungi. An average of 53,000 ± 26,000 and 23,000 ± 11,000 sequence reads per sample were obtained for 16S rRNA gene and ITS, respectively (Supplementary Table 1). Rarefaction curves approached saturation at a 97% identity cut-off, indicating that this level of sequencing effort was sufficient to estimate the diversity of these soil microbial communities (Supplementary Fig. 2).

Microbial STRs and PTRs under different climate change treatments. In ecology, the relationship between species richness and time is often described by the power-law equation $S = cT^{w_s}$, or its logarithmic equation, which is analogous to the power law of SAR[3,16]. S is the number of observed species within the length of time T, c is an empirically derived constant, and w_s is the STR exponent, that is, a measure of the temporal scaling rate of species richness[17,18]. Similarly, PTR analogues of STR are described by the power-law equation $PD = cT^{w_p}$ or its logarithmic equation, where PD is phylogenetic diversity and w_p is the PTR exponent. Our results revealed that the data from soil bacteria and fungi fitted the logarithmic equation very well under both warming and control conditions based on species ($r^2 = 0.844$–0.923, $P < 0.001$) and phylogenetic ($r^2 = 0.829$–0.919, $P < 0.001$; Fig. 1) diversity, suggesting that there are strong STRs and PTRs in soil bacteria and fungi under both warming and control conditions. More interestingly, permutation tests indicated that both w_s and w_p values under warming were significantly ($P < 0.001$) higher than those under control conditions (Fig. 1a,b and Supplementary Tables 2 and 3). In addition, in general w_p values were smaller than w_s values (Fig. 1a,b), indicating that the divergence of these communities in taxonomy is faster than that in phylogeny. This is most likely due to the short experimental period (6 years), which was insufficient to allow rapid phylogenetic change, and/or due to the regional species pool, which has low phylogenetic diversity[2]. Taken together, these results suggest that experimental warming significantly promoted the temporal scaling rates of soil bacterial and fungal diversity, consistent with the MTE prediction that or ganisms have faster rates of ecological and evolutionary processes at higher environmental temperatures[29–31].

Bacterial and fungal STRs and PTRs under all other treatment conditions besides single warming were also determined (Supplementary Fig. 3). Very strong logarithmic correlations were observed for all single and combined treatment conditions between time and species richness ($r^2 = 0.739$–0.948, $P < 0.001$; Supplementary Table 2), or phylogenetic diversity ($r^2 = 0.604$–0.941, $P < 0.001$; Supplementary Table 3), indicating that STRs and PTRs exist in soil bacteria and fungi under various treatment conditions. Also, the w_s values varied slightly for bacteria (0.495 ± 0.012) and for fungi (0.656 ± 0.023) across all single and combined treatments (Supplementary Fig. 3a). Similar patterns were obtained for the w_p values of bacteria (0.403 ± 0.017) and fungi (0.502 ± 0.029; Supplementary Fig. 3b). Furthermore, most single and combined treatments significantly ($P < 0.05$) altered the STRs and PTRs of soil bacteria and fungi (Supplementary Tables 2 and 3). For instance, clipping significantly ($P < 0.050$) increased the w_p values of fungi; however, it decreased the w_p values of bacteria. Interestingly, the temporal scaling rates (w_s and w_p) of bacteria and fungi under most of treatment conditions with warming were significantly ($P < 0.010$) larger than those under the corresponding treatment conditions without warming, with two exceptions: fungi under clipping; and fungi under half precipitation and clipping (Supplementary Fig. 3). In addition, w_p values were significantly ($P < 0.001$) lower than the w_s values of the corresponding treatments (17.1–43.5%) for all other single and combined treatments (Supplementary Fig. 3). These findings support the hypothesis that STRs and PTRs exist in soil bacteria and fungi and that their exponents (w values) are significantly changed by various climate change factors.

Warming predominantly accelerates microbial STRs and PTRs. Most climate change studies have focused on single factors; however, realistic scenarios present multifactorial changes to environments,

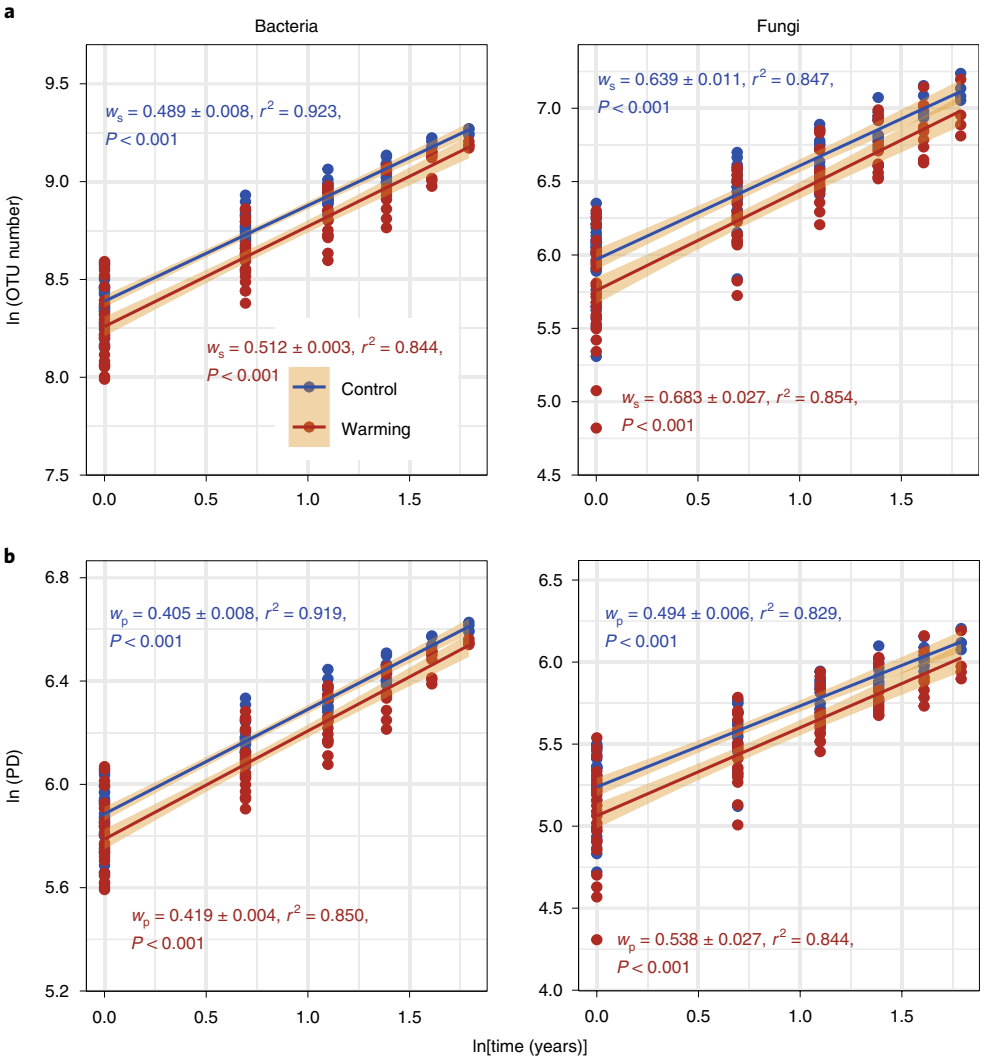

Fig. 1 | STR and PTR of bacteria and fungi under warming (red) and control (blue) treatment conditions. a,**b**, With consideration of the repeated-measures design, the logarithmic OTU number (**a**) or phylogenetic diversity (**b**) in each plot were fitted to an LMM with a fixed effect of logarithmic time, a random intercept and a slope effect among four plots. The shaded areas represent the 95% confidence intervals. The slopes of the STR (w_s) and PTR (w_p) are presented as coefficients in the fixed effect ± s.e.m. in the random effect. The r^2 values were calculated and reflect the variance explained by the whole LMM model. The P values of each STR or PTR were based on the permutation test. Further permutation tests indicated that the w_s and w_p of both bacteria and fungi were significantly different ($P < 0.001$) between warming and control treatment conditions.

such as warming with land use changes[26,39]. The influence of multiple anthropogenic disturbances has primarily been reported in research focused on plants and soil geochemistry, but fewer detailed studies on soil microbial communities[34–36,40]. It is not clear if ecosystem responses to multiple factors can be represented by single-factor studies, wherein the influence of factors is additive (no interaction). Multifactorial ecosystem responses may instead have synergistic (the observed effect is greater than the predicted effect of combined treatments assessed independently) and/or antagonistic (the observed effect is smaller than the predicted effect) behaviours[41]. To further determine how different climate change factors interact with each other to affect the temporal scaling rates of soil microbial communities, the effect size of different treatments was estimated with Cohen's d[23,24]. This effect size represents the mean difference of the temporal scaling rates between treatment and control conditions divided by the s.d. Hence, it provides a quantitative measure of the strength of the treatment. In our study, effect sizes were calculated based on the w_s or w_p values from the individual treatments or their combinations against a common control without any treatment (see Methods). Substantial variations in effect sizes were observed across different treatments for both bacteria and fungi (Table 1 and Fig. 2). Interestingly, the warming treatment had a large positive effect size in terms of both w_s and w_p for both bacteria and fungi (Table 1). In contrast, the half precipitation, double precipitation and clipping treatments, and their combinations, showed negative or relatively small positive effect sizes (Table 1). Most importantly, when the other treatments (that is, half precipitation, double precipitation and clipping) and their combinations were combined with the warming treatment, their effect sizes became larger or shifted from negative to positive for both bacteria and fungi for both STR (Fig. 2a) and PTR (Fig. 2b). For instance, the negative effect sizes of the double precipitation and clipping treatment were observed for fungal STR and PTR, whereas the warming and double precipitation and clipping treatment had positive effect sizes on fungal STR and PTR exponents (Fig. 2a,b). When comparing the effect sizes of all precipitation combined treatments on bacterial and fungal w_s/w_p, some interesting features were observed. For example, most of the precipitation combined treatments (regardless of whether half

Table 1 | Effect size of different treatments on STR w_s and PTR w_p in bacteria and fungi

Treatment	Effect on STR w_s		Effect on PTR w_p	
	Bacteria[a]	Fungi	Bacteria[a]	Fungi
Warming	1.546	0.385	1.169	1.119
Half precipitation	−0.008	0.084	−0.915	−0.938
Double precipitation	−0.531	0.282	−0.807	−0.721
Clipping	0.182	0.106	−0.298	1.170
Warming and half precipitation	1.346	0.954	1.047	2.117
Warming and double precipitation	0.776	1.174	0.248	1.193
Warming and clipping	0.960	0.319	0.409	0.497
Half precipitation and clipping	−0.056	0.100	−0.355	0.243
Double precipitation and clipping	−0.947	−1.009	−1.281	−0.849
Warming and half precipitation and clipping	1.359	0.673	0.662	0.105
Warming and double precipitation and clipping	0.252	0.619	−0.321	1.782

[a]Very small percentages (<1%) of sequences from archaea were included. Effect size is estimated with Cohen's *d*, comparing each treatment with the control treatment. $d > 0.20$, small effect; $d > 0.50$, medium effect; $d > 0.80$, large effect. A positive effect indicates a larger w_s/w_p value compared to the control treatment, with the reciprocal being true for negative effects.

precipitation or double precipitation) had larger effect sizes on fungal w_s/w_p than on bacterial w_s/w_p. This result suggested that fungi may be more sensitive to changes in soil water availability than bacteria, which is consistent with our previous study[32]. Furthermore, the effect sizes of the warming and double precipitation treatment and the warming and double precipitation and clipping treatment on bacterial w_s/w_p were much smaller than those recorded with all of the other warming combined treatments (Table 1 and Fig. 2), suggesting that higher soil water availability induced by double precipitation may partly offset the effect of warming on the temporal scaling rates of bacteria. Collectively, these results indicated that different climate change factors have differential impacts on the temporal scaling rates of soil bacteria and fungi. However, warming has predominant influences on the temporal scaling rates of both species richness and phylogenetic diversity.

Several previous studies demonstrated that the responses of microbial communities to climate change varied greatly among different microbial lineages or functional groups[28,42]. Similarly, we observed substantial variations in temporal scaling rates based on species richness and phylogenetic diversity among different bacterial and fungal lineages across the different treatments (Fig. 3 and Supplementary Tables 4 and 5). Also, like the patterns observed at the community level, we observed lower w_p values compared to w_s values for almost all phyla and all treatments (Supplementary Tables 4 and 5). In addition, overall, there were more fungal phyla (64–68%) with significantly ($P < 0.050$) increased w_s and w_p values than bacterial phyla (41–44%) across all treatments, indicating that the temporal scaling of fungal lineages could be more sensitive to climate change factors. Interestingly, most of the bacterial and fungal phyla exhibited significantly ($P < 0.001$) larger w_s and w_p values under treatments that included warming than the common control (Fig. 3a,b); more fungal phyla (79–88%) exhibited significantly ($P < 0.050$) increased w_s and w_p values than bacterial phyla (60–73%) under all combined treatments that included warming (Fig. 3a,b). These results suggest that warming could have a bigger impact on the temporal scaling of fungi than that of bacteria.

Comparison of STRs and PTRs across different groups of organisms. To obtain general insights into the temporal scaling of biodiversity across different organisms, the microbial w_s and w_p values from this study were compared with all available published data (1,201 data sets; Supplementary Fig. 4 and Supplementary Table 6). Due to differences in the unique biology of microorganisms, sampling approaches and/or analytical methods, it would be inappropriate to make exact comparisons across different studies[4,11]. Thus, only coarse-level comparisons are made. First, the temporal scaling rates (w_s values) between plants and animals were similar (0.21–0.38; Fig. 4). The species temporal scaling rates (w_s) of bacteria and fungi were between 0.39 and 0.64 (Fig. 4) and are considerably higher than those for plants and animals. This result is consistent with the MTE prediction that organisms with higher metabolic rates will have faster rates of ecological and evolutionary processes[29]. Second, phylogenetic temporal scaling rates (w_p) were considerably lower than species temporal scaling rates (w_s) for soil microorganisms (Fig. 4); this is consistent with one study on tropical tree communities[19]. However, very few to no studies have examined PTR in

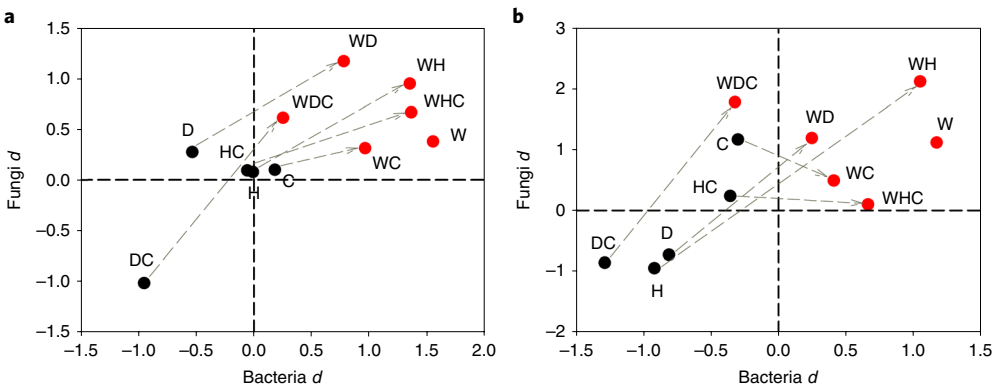

Fig. 2 | Effect size (Cohen's *d*) of all single and combined treatments. a, STR w_s values. **b**, PTR w_p values. **a**,**b**, A positive effect size indicates that the treatment has larger STR or PTR exponents than the control treatment and vice versa. The sample size was 4 for each treatment. The dotted lines indicate that the effect size is zero. The black symbols represent the treatments without warming; the red symbols represent the treatments with warming. W, warming and ambient precipitation; H, ambient temperature and half precipitation; D, ambient temperature and double precipitation; C, clipping; HC, half precipitation and clipping; CD, double precipitation and clipping; WH, warming and half precipitation; WD, warming and double precipitation; WC, warming and clipping; WHC, warming and half precipitation and clipping; WDC, warming and double precipitation and clipping.

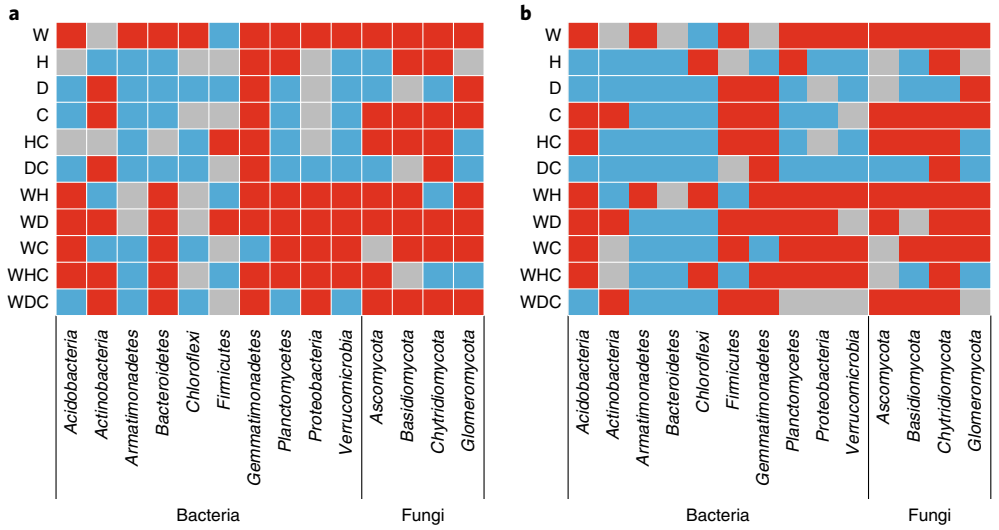

Fig. 3 | Changes in STR w_s and PTR w_p in major common phyla under different treatments. a, STR w_s values. **b**, PTR w_p values. **a**,**b**, The red-shaded cells represent the STR w_s and PTR w_p values under different treatments that were significantly ($P < 0.05$) larger than those under the common controls; the blue-shaded cells represent the STR w_s and PTR w_p values under different treatments that were significantly ($P < 0.05$) smaller than those under the common controls; the grey-shaded cells represent the STR w_s and PTR w_p values under the different treatments that were not significantly changed. The treatment labels are the same as in Fig. 2.

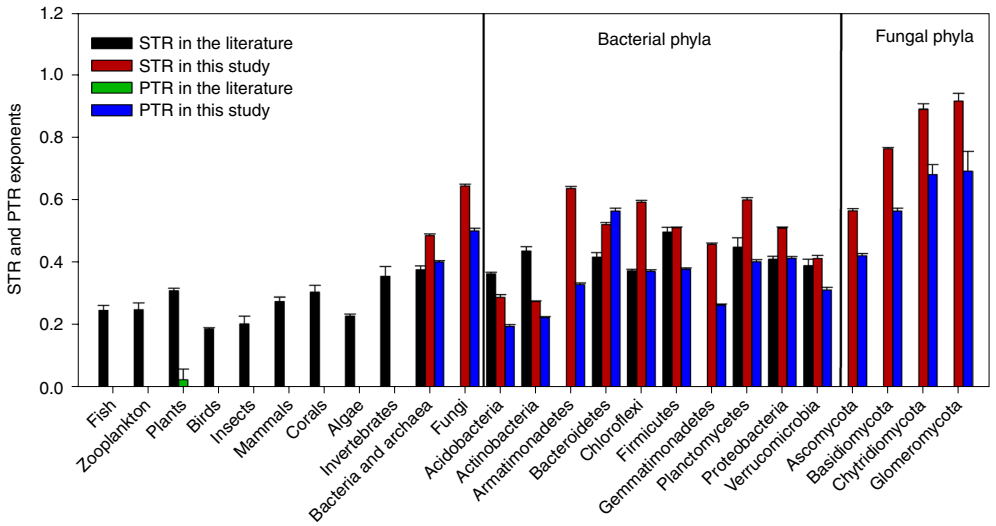

Fig. 4 | Comparison of STR and PTR exponents in micro- and macroorganisms. For macroorganisms, the STR exponents of taxonomic groups were reproduced from 984 data sets collected by White et al.[17]. The STR exponents of microbial communities were obtained from 76 data sets collected by Shade et al.[11]. Recent data (141 data sets) for micro/macroorganism communities were also included in the analyses, totalling 1,201 data sets. The information about these data sets and references is summarized in Supplementary Table 6. The STR and PTR exponents of different microbial groups from our current study were averaged across 12 global change treatments and subdivided with regard to different bacterial and fungal phyla. The error bars indicate the s.e.m.

plants, animals and microbial organisms. In addition, considerable variations in species or phylogenetic temporal scaling rates, ranging from 0.20 to 0.91, were observed among different lineages of bacteria and fungi, which could be related to differences in lifestyle strategies. For instance, *Acidobacteria*, typical oligotrophs with slow growth rates in soil[43], had considerably lower species or phylogenetic temporal scaling rates than *Bacteriodetes* or *Proteobacteria* (Fig. 4), typical soil copiotrophs with faster growth rates[43].

Conclusions

Understanding temporal scaling and its underlying mechanisms within the context of climate change is a fundamental issue in ecology and global change biology; however, very few studies have examined the relationships between species number and time in microbial communities[11,13]. First, by examining the temporal scaling of soil bacteria and fungi in a multifactorial global change experiment, this study provides explicit evidence that STRs exist for bacteria and fungi and their lineages. Hence, similar to SARs, the claim that STRs represent a universal law in ecology is reasonable and experimentally supported[17]. Importantly, our results showed that the temporal scaling rates of soil bacteria and fungi (w_s values) were considerably higher than those of plants and animals. Second, in contrast to STRs, almost nothing is known about PTRs in ecological communities, even for plants and animals[19]. This is the first study showing that soil microbes (bacteria and fungi) exhibit strong PTRs, with the overall rates (w_p values) being significantly lower than those of

STRs. Third, since temperature is a primary driver of all biological processes, it is reasonable to anticipate that climate warming has important effects on ecological patterns and processes[28,42]. As expected, our results showed that climate warming significantly accelerated both the taxonomic and phylogenetic temporal scaling rates of soil bacteria and fungi. These results are consistent with the MTE predictions that higher temperatures should increase the rates of ecological and evolutionary processes[30]. In addition, global change involves simultaneous alterations in multiple environmental factors besides warming, especially altered precipitation and land use change (that is, clipping); however, their interactive effects on ecosystems remain elusive, particularly in microbial ecology[28]. This is also the first time a study demonstrates that warming plays a predominant role in accelerating both the taxonomic and phylogenetic temporal scaling rates of soil microbial communities.

Our findings have important implications for understanding and predicting the ecological consequences of climate change and for ecosystem management. First, microbial biodiversity depends on both timescale and the size of the area sampled[4,12], suggesting that determining the appropriate timescale for biodiversity assessment is an important goal for ecosystem management[16,17]. Specifically: (1) the different temporal scaling (STRs, PTRs) rates of species suggest that different periods can be selected for the conservation of any species or an evolutionary history in a spatial context[2,17]; (2) different restoration times can be predicted for species with different STR or PTR rates in the same reservation[2,17,33]; and (3) ecosystem conservation strategies (that is, areas and timescales) should be adjusted in the future because of increased temporal scaling rates under climate warming. Second, the patterns of temporal scaling (STRs, PTRs) follow similar power law and/or logarithmic relationships with SARs and PARs, suggesting an equivalence of the underlying processes[16]. If so, space-for-time substitutions[16,44] could be a valid and efficient approach for the long-term prediction of climate change effects on biodiversity. In addition, because warming and other climate change factors stimulate both taxonomic and phylogenetic temporal scaling, biodiversity is predicted to change more quickly under future climate change scenarios. Along with faster biodiversity changes, linked ecosystem functions and services may become more vulnerable in a warmer world[42].

Methods

Site description and sampling. The long-term multifactorial global change experiment site was established in July 2009 at the Kessler Atmospheric and Ecological Field Station at the US Great Plain in McClain County, Oklahoma, USA (34° 59′ N, 97° 31′ W)[34]. The Kessler Atmospheric and Ecological Field Station is an old-field tall grass prairie abandoned from cropping 40 years ago, with light grazing until 2008. Dominant plants in this field site are C_3 forbs (*Ambrosia trifida*, *Solanum carolinense* and *Euphorbia dentata*) and C_4 grasses (*Tridens flavus*, *Sporobolus compositus* and *Sorghum halepense*)[34]. From 1948 to 1999, the monthly mean temperature in the field ranged from 3.3 °C in January to 28.1 °C in July, with an annual mean temperature of 16.3 °C. The average annual precipitation was 914 mm. In the experiment plots, the soil type was Port–Pulaski–Keokuk complex, which is loam with 51% sand, 35% silt and 13% clay[45]. The soil has a high available water holding capacity (37%), neutral pH and a deep (approximately 70 cm), moderately penetrable root zone[34]. The concentrations of soil organic matter and total nitrogen are 1.9 and 0.1%, respectively, and soil bulk density is 1.2 g cm^{-3}.

The experimental design and site description have been described in detail previously[34]. Briefly, the site has four experimental blocks, each containing six 2.5 × 3.5 m^2 plots, which were further divided into one 2.5 × 1.75 m^2 clipped subplot and one 2.5 × 1.75 m^2 unclipped subplot. The six plots within each block were under one of six randomly distributed treatments: (1) control (ambient temperature and precipitation); (2) ambient temperature and double precipitation; (3) ambient temperature and half precipitation; (4) warming and ambient precipitation; (5) warming and double precipitation; and (6) warming and half precipitation[34]. Two infrared heaters (Kalglo Electronics) were suspended approximately 1.5 m above the ground in each warmed plot to achieve a whole ecosystem warming of 3 °C. Two 'dummy' heaters were suspended in the control plot to mimic the shading effects of the heaters. Rainfall-collection-redistribution devices, which are angled catchments with the same size and shape as the plot[40], were installed to collect and redirect precipitation into double precipitation plots; rainout shelters, as described in Yahdjian and Sala[46], were used to halve precipitation. Plants in the southern subplots were clipped at a height of 10 cm above the ground and removed once every year at approximately the date of peak plant biomass in the autumn (September or October) to mimic the land use practice of mowing, while the northern subplots were not clipped[34].

From 2009 to 2014, one surface (0–15 cm) soil sample was collected annually from each subplot one day before annual clipping. Each sample was mixed from three soil cores (2.5 cm diameter × 15 cm depth) by using a soil sampler tube. Since clipping was performed after soil sampling each year, soil samples from the clipped subplots can represent soil samples from unclipped subplots in the first year (2009). Thus, we only collected 24 soil samples from all southern subplots in 2009. As for the other years, a total of 48 annual soil samples were collected from all subplots in each year. A total of 264 annual soil samples from 2009 to 2014 were collected in this study and stored in a freezer at −80 °C. To rule out as much bias as possible from sampling handling, DNA extraction, PCR amplification and sequencing, all samples were randomly reordered and further analysed in this random order.

Soil DNA extraction. Soil total DNA was extracted from 1.5 g soil using cryogenic grinding and SDS-based lysis, as described previously[47], and purified with a PowerSoil DNA Isolation Kit (MO BIO Laboratories) according to the manufacturer's protocol but without the bead-beating step. DNA quality was assessed based on spectrometry absorbance at the 230, 260 and 280 nm wavelengths (absorbance ratios: 260/280 nm, ~1.8; 260/230 nm, >1.8) detected by an NanoDrop 1000 Spectrophotometer (NanoDrop Technologies). The final DNA concentrations were quantified by PicoGreen (Invitrogen, Carlsbad, CA, USA) using a FLUOstar Optima microplate reader (BMG Labtech). Finally, all DNA samples were stored at −80°C until sequencing analysis.

Gene amplicon sequencing. The library construction and sequencing of the 16S rRNA gene and ITS between the 5.8S and 28S rRNA genes were performed as described previously[48]. The universal primer sets 515 forward (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806 reverse (5′-GGACTACHVGGGTWTCTAAT-3′) targeting the V3-V4 hypervariable regions of the bacterial and archaeal 16S rRNA gene[49], and gITS7 forward (5′-GTGARTCATCGARTCTTTG-3′) and ITS4 reverse (5′-TCCTCCGCTTATTGATATGC-3′) for the fungal ITS between the 5.8S and 28S rRNA genes[30], were used in this study.

Library preparation was carried out by using a two-step PCR to avoid additional PCR bias that could be introduced by the added components in the long primers[48]. In the two-step PCR, soil DNA was firstly diluted to 2.5 ng μl^{-1} with nuclease-free water to be used as the template in the PCR reaction. The first-step PCR was performed in a 25 μl reaction containing 2.5 μl 10× PCR buffer II (including deoxyribonucleotide triphosphates), 0.25 U DNA polymerase, 0.4 μM of both forward and reverse target-only primers and 4 μl diluted soil DNA. The reactions of 16S rRNA gene amplification were performed in triplicate and the thermal cycling conditions were as follows: initial denaturation at 94 °C for 3 min, followed by 10 cycles of 94 °C for 25 s, 53 °C for 25 s and 68 °C for 45 s, with a final extension at 68 °C for 10 min. The amplification programme described was also used for the amplification of ITS, except that 12 cycles were performed and the annealing temperature was 52 °C. The triplicate products from the first-step PCR were combined together, purified with Agencourt AMPure XP beads (Beckman Coulter) according to the manufacturer's protocol, eluted by 50 μl water and aliquoted into three new PCR reactions. The second-step PCR was carried out in triplicate in a 25 μl reaction containing 2.5 μl 10× PCR buffer II (including deoxyribonucleotide triphosphates), 0.25 U DNA polymerase, 0.4 μM of both forward and reverse phasing primers and 15 μl aliquot of the first-step purified PCR product. Amplifications were cycled 20 times following this programme. PCR products from the triplicate reactions were combined, visualized using 1% agarose gel electrophoresis and quantified using PicoGreen with a FLUOstar Optima microplate reader. The reverse primer in the second-step PCR had a barcode of 12 bases to identify different samples.

PCR products from different samples were pooled at equal molality (generally 300 samples) to be sequenced in the same MiSeq run. The pooled mixture was purified with a QIAquick Gel Extraction Kit (QIAGEN) and re-quantified with PicoGreen. Sample libraries for sequencing were prepared according to the MiSeq Reagent Kit Preparation Guide (Illumina) as described previously[48,50]. First, the combined sample library was diluted to 2 nM. Then, it was denatured by mixing 10 μl of it with 10 μl of 0.2 N fresh NaOH; it was then incubated for 5 min at room temperature. A measure of 980 μl of chilled Illumina HT1 buffer was added to the denatured DNA and mixed to make a 20 pM library. Finally, the library was further adjusted to the desired concentration (approximately 12 pM) for sequencing using chilled HT1 buffer. The library to be sequenced was mixed with a 12 pM PhiX library to achieve a 10% PhiX spike. A 500-cycle MiSeq reagent cartridge v2 (Illumina) was thawed for 1 h in a water bath, inverted 10 times to mix the thawed reagents and stored at 4 °C for a short time until needed. Sequencing was performed for 251, 12 and 251 cycles for forward, index and reverse reads, respectively.

Sequencing preprocessing. The raw reads of the 16S rRNA gene and ITS were collected by the MiSeq in FASTQ format and then submitted to our sequence analysis pipeline (http://zhoulab5.rccc.ou.edu:8080) built on the Galaxy platform for further analysis[51]. First, the spiked PhiX reads were removed using BLAST against the PhiX genome sequence in the Expect (E) value $<10^{-5}$. Second, the

reads were assigned to different sample libraries based on the barcodes. Before combining the forward and reverse reads, the primer sequences at the end of each read were trimmed and the Btrim program[52], with a quality control threshold >20 over a 5 base pair (bp) window size, was used to filter the reads. For the 16S rRNA gene and ITS, the forward and reverse reads of the same sequence with at least a 20 bp overlap and <5% mismatches were combined using FLASH[53]. Any joined sequences with an ambiguous base, or a length of <245 bp for the 16S rRNA gene or <220 bp for the ITS were discarded. Thereafter, operational taxonomic units (OTUs) were clustered using UPARSE[54] at 97% identity; singletons were removed from the remaining sequences for both the 16S rRNA gene and ITS. In UPARSE, the green reference data set[55] for the 16S data and the released UNITE/QIIME ITS reference data set (https://unite.ut.ee/repository.php) for the ITS data were used as the reference database to remove chimeras. To normalize samples to the same total read abundance, 30,000 sequences for the 16S rRNA gene and 10,000 sequences for the ITS were randomly selected (resampled) for each sample. OTU taxonomic classification of the 16S rRNA gene and ITS sequences was performed using representative sequences from each OTU through the Ribosomal Database Project Classifier with 50% confidence estimates[56]. Approximately-maximum-likelihood phylogenetic trees for the 16S rRNA gene and ITS were individually constructed based on the representative sequences for each OTU using FastTree v.2.0 (ref. [57]). Faith's phylogenetic diversity was calculated based on the phylogenetic trees and OTU tables using the R package picante[58].

STR and PTR estimation and other statistical analyses. STRs can be estimated using the power-law equation (equation (1)) or the logarithmic equation (equation (2)). PTRs, the phylogenetic analogues of STRs, can also be estimated using a similar power-law (equation (3)) or logarithmic equation (equation (4)):

$$S = cT^{w_s} \tag{1}$$

$$\ln(S) = \ln(c) + w_s \times \ln(T) \tag{2}$$

$$\mathrm{PD} = cT^{w_p} \tag{3}$$

$$\ln(\mathrm{PD}) = \ln(c) + w_p \times \ln(T) \tag{4}$$

S and PD are the numbers of species or phylogenetic diversity observed within the length of time T; c is an empirically derived taxon- and time-specific constant; w_s is the STR exponent, that is, a measure of the rate of temporal scaling of species richness[13,17,18]; and w_p is the PTR exponent, that is, a measure of the rate of temporal scaling of phylogenetic diversity. These equations are theoretically obtained by substituting time (T) for area (A) in the SAR power law $S = cA^z$[18].

In this study, OTU richness and phylogenetic diversity were calculated by using the complete-nested approach, as previously described[11,17,18]. This approach can remove systematic trends in total richness by averaging richness across periods; it is currently the dominant approach for STRs at ecological scales[11,17,18]. This approach defines the length of time T as the average of every possible window subset of consecutive sample periods of length of time T. In our annual survey data, window subset 1 is the average of all single years; window subset 2 is the average of all combinations of two consecutive years; and window subset 3 is the average of all combinations of three consecutive years, and so on. In our six-year record, there are six one-year, five two-year, four three-year and one six-year samples. Each window subset represents the mean number of species across all samples of consecutive periods of length of time T, with time defined only as an interval[18]. For this complete-nested approach, we can use the following equation (equation (5)) to calculate how the number of species sampled depends on the length of time T over which sampling occurs, $S(T)$, as suggested by Carey et al.[18]:

$$\begin{aligned} S(T) &= \frac{1}{N_T}\sum_{i=1}^{N_T} S(t_i, t_i+T) \\ &= \frac{1}{N_T}\sum_{i=1}^{N_T} (S_0 + c[0,t_i] - e[0,t_i] + n[t_i, t_i+T]) \\ &= S_0 + \frac{1}{N_T}\sum_{i=1}^{N_T} (c[0,t_i] - e[0,t_i]) + \frac{1}{N_T}\sum_{i=1}^{N_T} n[t_i, t_i+T] \end{aligned} \tag{5}$$

In this equation, $c[t_1, t_2]$ is the number of species colonization events occurring between t_1 and t_2, $e[t_1, t_2]$ is the number of species disappearing between t_1 and t_2, and $n[t_1, t_2]$ is the number of new species that enter the community between t_1 and t_2, where 'new species' is defined with regard to the species present at time t_1. N_T is the number of sample periods of length of time T used in the complete-nested approach, and t_i is the time at which the ith sample period begins.

In general, STR and PTR models can be constructed using a linear regression between logarithmic OTU richness/phylogenetic diversity and logarithmic time duration for different microbial groups and phyla (equations (2) and (4)). However, our experimental design has repeated measures at different time points in the same plot, and different plots under the same treatment do not necessarily have the same STR or PTR. Thus, we fitted the logarithmic data of each treatment using a linear mixed model (LMM) with a fixed effect of time and a random effect and exponent among plots. The significance of each LMM was calculated using a permutation test, and the P value was calculated by comparing the Akaike information criterion of the observed LMM with the permuted ones. We also tested whether the w_s values in the STRs or the w_p values in the PTRs were significantly different between any two treatments using a permutation test[59,60]. Furthermore, we calculated Cohen's d[27,28] as an estimate of multiple-treatment effect sizes on the STR w_s and PTR w_p values from different treatments by comparing them against the common control without any treatment. In Cohen's d, positive d values indicate that the response variables (w_s and w_p in this case) in the treatment have a larger value than in the control, and vice versa. Based on Cohen's suggestion[23,24], the effect sizes between 0.2 and 0.5 are small, between 0.5 and 0.8 are medium and >0.8 are large. All the analyses were performed in the R software v.3.1.1 with the packages vegan, nlme and effsize[61].

Comparison of STRs and PTRs across different groups of organisms. To obtain general insights into the temporal scaling of biodiversity across different organisms, the w_s and w_p values in this study were compared with all available published STR data (1,201 data sets) including macroorganisms[17] and microorganisms[11]. The analysis workflow of published data sets is shown as Supplementary Fig. 4. Briefly, STRs or PTRs were used as keywords to search all the available literature with regard to plants, animals and microorganisms. After duplicates were removed, data sets were selected according to the description in the literature or were directly provided by the authors. In this step, some unobtainable data sets were excluded from further analysis. All data sets were classified into different taxonomic groups. Finally, the STR and PTR w values obtained from all 1,201 published data sets were compared with those from our study. However, because species definition, generation time and diversity of microbial communities are greatly different from the communities of plants and animals[11,62,63], detailed exact comparisons would be especially difficult across different studies[11,64]. Therefore, in this study, only coarse-level comparisons were made among different types of organism.

Data accessibility. The DNA sequences of the 16S rRNA gene and ITS amplicons were deposited in the National Center for Biotechnology Information under project accession no. PRJNA331185. All other relevant data are available from the corresponding author upon request.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

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References

1. Chase, J. M. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**, 1388–1391 (2010).
2. Morlon, H. et al. Spatial patterns of phylogenetic diversity. *Ecol. Lett.* **14**, 141–149 (2011).
3. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, 1995).
4. Zhou, J., Kang, S., Schadt, C. W. & Garten, C. T. Jr. Spatial scaling of functional gene diversity across various microbial taxa. *Proc. Natl Acad. Sci. USA* **105**, 7768–7773 (2008).
5. Lawton, J. H. Are there general laws in ecology? *Oikos* **84**, 177–192 (1999).
6. Green, J. & Bohannan, B. J. Spatial scaling of microbial biodiversity. *Trends Ecol. Evol.* **21**, 501–507 (2006).
7. Storch, D., Keil, P. & Jetz, W. Universal species–area and endemics–area relationships at continental scales. *Nature* **488**, 78–81 (2012).
8. Sheik, C. S. et al. Effect of warming and drought on grassland microbial communities. *ISME J.* **5**, 1692–1700 (2011).
9. Guilhaumon, F., Gimenez, O., Gaston, K. J. & Mouillot, D. Taxonomic and regional uncertainty in species–area relationships and the identification of richness hotspots. *Proc. Natl Acad. Sci. USA* **105**, 15458–15463 (2008).
10. Horner-Devine, M. C., Lage, M., Hughes, J. B. & Bohannan, B. J. A taxa–area relationship for bacteria. *Nature* **432**, 750–753 (2004).
11. Shade, A., Caporaso, J. G., Handelsman, J., Knight, R. & Fierer, N. A meta-analysis of changes in bacterial and archaeal communities with time. *ISME J.* **7**, 1493–1506 (2013).
12. Chen, L. X. et al. Comparative metagenomic and metatranscriptomic analyses of microbial communities in acid mine drainage. *ISME J.* **9**, 1579–1592 (2015).
13. van der Gast, C. J., Ager, D. & Lilley, A. K. Temporal scaling of bacterial taxa is influenced by both stochastic and deterministic ecological factors. *Environ. Microbiol.* **10**, 1411–1418 (2008).
14. Deng, Y. et al. Spatial scaling of forest soil microbial communities across a temperature gradient. *Environ. Microbiol.* **20**, 3504–3513 (2018).

15. Preston, F. W. Time and space and the variation of species. *Ecology* **41**, 611–627 (1960).
16. Adler, P. B. & Lauenroth, W. K. The power of time: spatiotemporal scaling of species diversity. *Ecol. Lett.* **6**, 749–756 (2003).
17. White, E P. et al. A comparison of the species–time relationship across ecosystems and taxonomic groups. *Oikos* **112**, 185–195 (2006).
18. Carey, S., Ostling, A., Harte, J. & del Moral, R. Impact of curve construction and community dynamics on the species–time relationship. *Ecology* **88**, 2145–2153 (2007).
19. Swenson, N. G. et al. Species–time–area and phylogenetic–time–area relationships in tropical tree communities. *Ecol. Evol.* **3**, 1173–1183 (2013).
20. Devictor, V. et al. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* **13**, 1030–1040 (2010).
21. Winter, M. et al. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Natl Acad. Sci. USA* **106**, 21721–21725 (2009).
22. Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G. & Mirotchnick, N. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15**, 637–648 (2012).
23. Jabot, F. & Chave, J. Inferring the parameters of the neutral theory of biodiversity using phylogenetic information and implications for tropical forests. *Ecol. Lett.* **12**, 239–248 (2009).
24. *IPCC Climate Change 2013: The Physical Science Basis—Findings and Lessons Learned* (eds. Stocker, T. F. et al.) (Cambridge Univ. Press, 2013).
25. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
26. Moss, R. H. et al. The next generation of scenarios for climate change research and assessment. *Nature* **463**, 747–756 (2010).
27. Bebber, D. P., Ramotowski, M. A. T. & Gurr, S. J. Crop pests and pathogens move polewards in a warming world. *Nat. Clim. Change* **3**, 985–988 (2013).
28. Xue, K. et al. Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming. *Nat. Clim. Change* **6**, 595–600 (2016).
29. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
30. Zhou, J. et al. Temperature mediates continental-scale diversity of microbes in forest soils. *Nat. Commun.* **7**, 12083 (2016).
31. Zhao, L. et al. Soil organic carbon and total nitrogen pools in permafrost zones of the Qinghai-Tibetan Plateau. *Sci. Rep.* **8**, 3656 (2018).
32. Guo, X. et al. Climate warming leads to divergent succession of grassland microbial communities. *Nat. Clim. Change* **8**, 813–818 (2018).
33. Zhou, J. et al. Stochasticity, succession, and environmental perturbations in a fluidic ecosystem. *Proc. Natl Acad. Sci. USA* **111**, E836–E845 (2014).
34. Xu, X., Sherry, R. A., Niu, S., Li, D. & Luo, Y. Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie. *Glob. Change Biol.* **19**, 2753–2764 (2013).
35. Shi, Z. et al. Successional change in species composition alters climate sensitivity of grassland productivity. *Glob. Change Biol.* **24**, 4993–5003 (2018).
36. Xu, X. et al. Unchanged carbon balance driven by equivalent responses of production and respiration to climate change in a mixed-grass prairie. *Glob. Change Biol.* **22**, 1857–1866 (2016).
37. Bardgett, R. D., Bowman, W. D., Kaufmann, R. & Schmidt, S. K. A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.* **20**, 634–641 (2005).
38. Tscherko, D., Hammesfahr, U., Zeltner, G., Kandeler, E. & Böcker, R. Plant succession and rhizosphere microbial communities in a recently deglaciated alpine terrain. *Basic Appl. Ecol.* **6**, 367–383 (2005).
39. Shaw, M. R. et al. Grassland responses to global environmental changes suppressed by elevated CO_2. *Science* **298**, 1987–1990 (2002).
40. Zhou, X., Sherry, R. A., An, Y., Wallace, L. L. & Luo, Y. Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem. *Global Biogeochem. Cycles* **20** https://doi.org/10.1029/2005GB002526 (2006).
41. Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Mooney, H. A. & Field, C. B. Additive effects of simulated climate changes, elevated CO_2, and nitrogen deposition on grassland diversity. *Proc. Natl Acad. Sci. USA* **100**, 7650–7654 (2003).
42. Zhou, J. et al. Microbial mediation of carbon-cycle feedbacks to climate warming. *Nat. Clim. Change* **2**, 106–110 (2012).
43. Fierer, N., Bradford, M. A. & Jackson, R. B. Toward an ecological classification of soil bacteria. *Ecology* **88**, 1354–1364 (2007).
44. Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T. & Ferrier, S. Space can substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl Acad. Sci. USA* **110**, 9374–9379 (2013).
45. Li, D., Zhou, X., Wu, L., Zhou, J. & Luo, Y. Contrasting responses of heterotrophic and autotrophic respiration to experimental warming in a winter annual-dominated prairie. *Glob. Change Biol.* **19**, 3553–3564 (2013).
46. Yahdjian, L. & Sala, O. E. A rainout shelter design for intercepting different amounts of rainfall. *Oecologia* **133**, 95–101 (2002).
47. Zhou, J., Bruns, M. A. & Tiedje, J. M. DNA recovery from soils of diverse composition. *Appl. Environ. Microbiol.* **62**, 316–322 (1996).
48. Wu, L. et al. Phasing amplicon sequencing on Illumina Miseq for robust environmental microbial community analysis. *BMC Microbiol.* **15**, 125 (2015).
49. Peiffer, J. A. et al. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proc. Natl Acad. Sci. USA* **110**, 6548–6553 (2013).
50. Caporaso, J. G. et al. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *ISME J.* **6**, 1621–1624 (2012).
51. Giardine, B. et al. Galaxy: a platform for interactive large-scale genome analysis. *Genome Res.* **15**, 1451–1455 (2005).
52. Kong, Y. Btrim: a fast, lightweight adapter and quality trimming program for next-generation sequencing technologies. *Genomics* **98**, 152–153 (2011).
53. Magoč, T. & Salzberg, S. L. FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics* **27**, 2957–2963 (2011).
54. Edgar, R. C. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* **10**, 996–998 (2013).
55. DeSantis, T. Z. et al. Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Appl. Environ. Microbiol.* **72**, 5069–5072 (2006).
56. Wang, Q., Garrity, G. M., Tiedje, J. M. & Cole, J. R. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl. Environ. Microbiol.* **73**, 5261–5267 (2007).
57. Price, M. N., Dehal, P. S. & Arkin, A. P. FastTree 2—approximately maximum-likelihood trees for large alignments. *PLoS ONE* **5**, e9490 (2010).
58. Kembel, S. W. et al. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464 (2010).
59. Martiny, J. B., Eisen, J. A., Penn, K., Allison, S. D. & Horner-Devine, M. C. Drivers of bacterial β-diversity depend on spatial scale. *Proc. Natl Acad. Sci. USA* **108**, 7850–7854 (2011).
60. Deng, Y. et al. Elevated carbon dioxide accelerates the spatial turnover of soil microbial communities. *Glob. Change Biol.* **22**, 957–964 (2016).
61. R Core Team. *R: a language and environment for statistical computing* (R Foundation for Statistical Computing, 2013).
62. Stackebrandt, E. et al. Report of the ad hoc committee for the re-evaluation of the species definition in bacteriology. *Int. J. Syst. Evol. Microbiol.* **52**, 1043–1047 (2002).
63. Gevers, D. et al. Re-evaluating prokaryotic species. *Nat. Rev. Microbiol.* **3**, 733–739 (2005).
64. Fierer, N. & Lennon, J. T. The generation and maintenance of diversity in microbial communities. *Am. J. Bot.* **98**, 439–448 (2011).

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Author contributions

All authors contributed intellectual input and assistance to this study. The original concept and experimental strategy were developed by J.Z., Y.L. and J.M.T. Field management was carried out by M.Y., J.F., B.F., X.Z., A.Z., L.H., Z.L., Liyou Wu and J.D.V.N. Collection sampling, DNA preparation and MiSeq sequencing analysis were carried out by X.Z., X.G., J.F., M.Y., Y.F. and L.H. Soil chemical analysis was carried out by X.Z., X.G. and M.Y. Various statistical analyses were carried by X.G., Z.S., D.N., Linwei Wu, W.S. and Q.G. Assistance in data interpretation was provided by G.Q., X.L., Z.H. and Y.Y. All data analysis and integration were guided by J.Z. The paper was written by J.Z. and X.G. with help from J.M.T. and D.N. Because of their contributions in terms of site management, and data collection, analysis and/or integration over the last 6 years, X.G., X.Z. and L.H. were listed as co-first authors.

Competing interests

The authors declare no competing interests.

Additional information

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Software and code

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Data collection	Sequencing reads were undertaken with MiSeq platform(Illumina, SanDiego, CA, USA); Some species-time relationships of macroorganisms and bacterial communities was obtained from the published references as shown in supplementary table S6.
Data analysis	Sequencing preprocessing: Galaxy platform (http://zhoulab5.rccc.ou.edu:8080); OTU taxonomic classification: Ribosomal Database Project (RDP) Classifier; phylogenetic tree: FastTree 2.0; Faith's phylogenetic diversity: R package picante 2.5-2; Statistics: R with packages vegan 2.2-1, nlme 3.1-173, effsize 0.7.1.

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We have included a data availability statement in the manuscript. The amplicon sequencing data sets generated have been deposited in the National Center for Biotechnology Information (NCBI) under the project accession: no. PRJNA331185.

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All studies must disclose on these points even when the disclosure is negative.

Study description	Our study presented taxonomic and phylogenetic temporal scaling of soil bacteria and fungi in a long-term multifactor global change experiment with warming (+3 °C), half precipitation (-50%), double precipitation (+100%) and clipping (annual biomass removal) by determining species-time relationship (STR) and phylogenetic-time reationship (PTR).
Research sample	A total of 264 soil surface (0-15cm) samples from 2009 to 2014 were used to examine taxonomic and phylogenetic temporal scaling of soil bacteria and fungi under multifactor global change conditions. Soil bacterial and fungal community structures were determined by sequencing of 16S rRNA gene and ITS amplicons . The temporal scalings in this study were compared with all available published STR data (1201 datasets) including macroorganisms and bacterial communities.
Sampling strategy	When examining temporal scaling of microbial communities under multifactor global change conditions, it is fundamental to obtain annual samples in a long-term scale. In our study, we collected surface (0-15 cm) soil samples in 48 subplots annually (September or October) from 2009 to 2014. Each sample was mixed from three soil cores (2.5 cm diameter × 15 cm depth) by using a soil sampler tube. Since clipping was performed after soil sampling in each year, soil samples from clipped subplots can represent soil samples from unclipped subplots in the first year (2009). Thus, we only collected 24 soil samples from all southern subplots in 2009. As for the other years, a total of 48 annual soil samples were collected from all subplots in each year. A total of 264 annual soil samples from 2009 to 2014 were analyzed in this study.
Data collection	Sampling collections, DNA preparation and MiSeq sequencing analysis were carried out by Xishu Zhou, Xue Guo, Jiajie Feng, Mengting Yuan, Ying Fu, and Lauren Hale. Soil chemical analysis was carried out by Xishu Zhou, Xue Guo, and Mengting Yuan.
Timing and spatial scale	In this study, a total of 264 annual soil samples was collected annually from each subplot one day before annual clipping (September or October) from 2009 to 2014 in this long-term multifactor global change experiment site (34̊ 59′ N, 97̊ 31′W).
Data exclusions	No data were excluded from the analyses.
Reproducibility	16S rRNA gene and ITS amplicons were sequenced by MiSeq platform(Illumina, SanDiego, CA, USA) using a 500-cycle v2 MiSeq reagent cartridge (Illumina).
Randomization	In order to rule out as many biases by the following sampling handling, DNA extraction, PCR amplification and sequencing as possible, all samples were randomly reordered and further analyzed in this random order.
Blinding	Blinding was not relevant to this study. No blinding is done in temporal scaling of biodiversity more broadly.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	This study was conducted in an old-field tallgrass prairie abandoned from cropping 40 years ago with light grazing until 2008. Dominant plants in this field site are C3 forbs (Ambrosia trifida, Solanum carolinense and Euphorbia dentate) and C4 grasses (Tridens flavus, Sporobolus compositus and Sorghum halapense). Mean monthly temperature in the field ranged from 3.3 °C in January to 28.1 °C in July, with an annual mean temperature of 16.3 °C. The average annual precipitation was 914 mm. In the experiment plots, the soil is Port-Pulaski-Keokuk complex, which is loam with 51% of sand, 35% of silt and 13% of clay. The soil has a high available water holding capacity (37%), neutral pH, and a deep (ca. 70 cm), moderately penetrable root zone. The concentrations of soil organic matter and total nitrogen (N) are 1.9% and 0.1%, respectively.

Location	The long-term multifactor global change experiment site was located at the Kessler Atmospheric and Ecological Field Station (KAEFS) at the US Great Plain in McClain County, Oklahoma, USA (34˚ 59′ N, 97˚ 31′W)
Access and import/export	Project and class site use requests were completed for our study. Liability waivers were completed hard copies provided to KAEFS.
Disturbance	Infrared heaters and rainfall-collection-redistribution devices may disturb the grassland ecosystem. To minimize these disturbances, 'dummy' heaters and rainfall-collection-redistribution devices were used in this study.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging